



Nocturnal and diurnal singing activity in the nightingale: correlations with mating status and breeding cycle

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This study on the nightingale, *Luscinia megarhynchos*, is the first to examine both nocturnal and diurnal singing activity of mated and unmated males throughout a species' entire breeding cycle. Nocturnal song was sung mostly by unmated males. After pair formation, males ceased nocturnal singing and resumed it if their mate deserted. These results strongly suggest that nocturnal song of unmated males functions to attract a mate. Diurnal singing activity before females settled was low and did not predict future mating status. However, unmated males showed a continuous increase in diurnal singing activity until the end of the breeding cycle, but diurnal singing activity of mated males decreased after the egg-laying period. Mated males resumed nocturnal song for, on average, 3 nights during egg laying by their mates. This second period of nocturnal song coincided with the peak of diurnal singing activity. Such a high male singing effort during egg laying might allow the female to adjust her reproductive effort to male quality, deter rival males (e.g. through honest announcement of the female's fertility) or attract females for extrapair copulations.

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Bird song has evolved under both inter- and intrasexual selection (Catchpole & Slater 1995). The males' song may attract and stimulate females and may repel rival males (Kroodsmma & Byers 1991), but the importance of these functions may differ between species and between different songs within a species. In several bird species, males change their singing behaviour after mating. Here, song is often regarded as intersexual communication. For instance, reduced singing activity after pair formation indicates that song plays a role in mate attraction (Catchpole 1973; Hanski & Laurila 1993; Gil et al. 1999a). In species in which males use several song patterns, specific patterns may be particularly important to attract females. These patterns may be produced less frequently or even be abandoned after pairing, while the output of other song patterns continues until later stages of the breeding cycle (Hasselquist & Bensch 1991; Nemeth 1996; Staicer 1996). Song sung at different times of the day may also serve different functions. For example, the

dawn chorus of male songbirds has been suggested to differ functionally from song at other times of the day (Staicer et al. 1996).

About 10 western Palaearctic species of songbirds are known to sing regular nocturnal song in addition to diurnal song (genera *Acrocephalus*, *Cettia*, *Locustella*, *Luscinia*, *Phoenicurus*; Glutz von Blotzheim 2001), providing particularly suitable species to study changes in song function with time of day. Male nightingales, *Luscinia megarhynchos*, are renowned for high nocturnal singing activity, and their nocturnal song is thought to attract nocturnally migrating females (Cramp 1988; Glutz von Blotzheim 1988). The extensive nocturnal singing is in addition to diurnal song, and there are indications that it is energetically costly (Thomas 2002). Nocturnal song might therefore be an honest signal of male quality on which females could base their mating decisions (Catchpole & Slater 1995). However, empirical evidence on the intersexual function of nocturnal song is still lacking. Until now, most studies of nocturnal song have concentrated on intrasexual communication and it has been shown that male nightingales use multiple singing strategies when interacting with rival males at night (Hultsch & Todt 1982; Naguib 1999; Todt & Naguib 2000). In the nonpasserine corn crake, *Crex crex*, the

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incidence of nocturnal song by males is reduced during pairing (Tyler & Green 1996). Some authors have suggested that nocturnal singing is confined to unpaired males in *Acrocephalus* warblers (Catchpole 1973; Kelsey 1989). However, to date, there is no quantitative evidence in passerines that nocturnal song is related to mating status.

Many songbird species, including the nightingale, sing diurnal song beyond pair formation (Catchpole & Slater 1995). After pair formation, diurnal song could function to attract additional social mates (Hasselquist & Bensch 1991) or to attract neighbouring females for extrapair copulations (Birkhead & Møller 1992; Hasselquist et al. 1996). Prolonged singing may also allow a female to reassess her mate's quality for differential reproductive allocation (Gil et al. 1999b; Sheldon 2000). Furthermore, diurnal song may repel neighbouring males (Nowicki et al. 1998; Naguib et al. 2001). Møller (1991) suggested that a male's elevated singing activity after pairing honestly announces the fertility of his mate and thereby signals his ability to defend paternity (but see Gil et al. 1999a). All these hypotheses predict a peak of singing activity in mated males when females are fertile. So far, no study has examined the singing activity of unmated males for all the corresponding periods of the breeding cycle in mated males. However, a comparison of the singing behaviour of unmated and mated males may hold clues to understanding the functions of song after settlement of females.

In this study, by correlating the incidence of nocturnal song with mating status we tested the hypothesis that, in the nightingale, nocturnal song serves to attract a mate. To identify other possible functions of nocturnal and diurnal song, we correlated the singing activity of mated and unmated males with all the stages in the reproductive cycle.

METHODS

Study Site and Species

We conducted the study from 1998 to 2001 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. The area comprises a 1-km² mosaic of riverine forest, pastures, fields, reeds and artificial lakes. A dense population of about 50 singing nightingales has been monitored since 1994 (Durrer et al. 1995; Amrhein 1999). The owners of 28 territories and their mates have been regularly colour-ringed since 1997.

Nightingales form socially monogamous seasonal pair bonds. Arrival of the first males at the study site varied between years from 3 to 13 April. The first females were captured 1–3 weeks later. The typical clutch size was five ($N=21$ of 28 females). Other clutch sizes were three ($N=1$), four ($N=5$) and six ($N=1$). Females laid one egg per day, between 0800 and 1100 hours ($N=5$ females observed). Replacement clutches were initiated when the brood failed because of predation or inundation, but true second clutches did not occur. Male nightingales sing at dawn and throughout the day. Nocturnal singing usually starts before midnight and continues until dawn.

General Methods

During the breeding season (April–June), we captured males and females in mist nets in up to 19 territories per year. The birds were ringed in their territory and released within 15 min of capture. We performed mist netting for 1 h per day until we had captured both members of a pair, or until we were sure that no female was present in a male's territory. This occasionally resulted in capturing an individual more than once. However, no bird deserted its territory after capture. Furthermore, we have no indications that capturing influenced breeding success or negatively affected other bird species.

We refer to the period from the day a female settled in a male's territory until the day before the first egg was laid as the prelaying period (5–11 days, $\bar{X} \pm SD=8 \pm 2$, $N=19$). We defined laying period as the period from the day the first egg is laid to the day before the last egg is laid (usually 4 days). Prelaying and laying periods are usually regarded as the time when females are fertile (Birkhead & Møller 1992). The incubation period is 13 days, the nestling period 11 days (Glutz von Blotzheim 1988) and the fledgling period 16 days (Cramp 1988).

We use the term 'bachelors' for males that remained unpaired throughout the season to avoid confusion with the 'unpaired' period of all males before the arrival of females. To compare the singing activity of bachelors with that of mated males, we divided the season for bachelors into the same periods as for their immediate mated neighbours. For mated males, we considered singing activity only for successful first clutches. All mated males were of known identity and were included in the analyses only once. Five of 12 bachelors were ringed; for the remaining seven birds, we avoided pseudoreplication by sampling each territory only once.

Nocturnal Song

From arrival of the first males until early in June we censused nocturnal song as either present or absent between midnight and 0200 hours. This is the time that most nocturnally singing males sing, and song lasts up to several hours. Therefore, we were likely to encounter a bird singing at this time if it was engaged in nocturnal singing that night. Rounds were made nightly in 2000 and 2001. In 1998 and 1999, rounds were made less frequently towards the end of the breeding cycle (every third to fifth night). The sample consisted of 18 mated males and 12 bachelors.

Diurnal Song

To quantify diurnal singing activity throughout the season, we censused diurnal song as present or absent on one to seven rounds per day ($\bar{X} \pm SD=3 \pm 2$). Singing activity of a male is expressed as the proportion of rounds on which it was heard singing. The duration of rounds was held constant and, to avoid bias on a particular time of day, we varied the time of the rounds from day to day, covering all hours of daylight. We excluded males if data were not available for all periods of the breeding cycle.

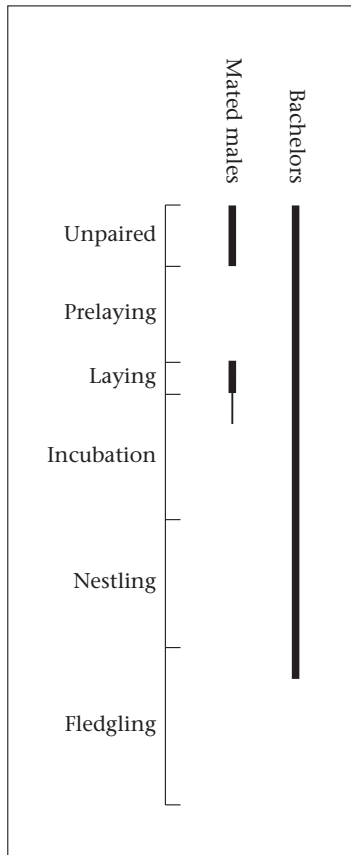


Figure 1. Schematic presentation of nocturnal singing activity in male nightingales over six periods of the breeding cycle. Nocturnal song was censused as present versus absent between midnight and 0200 hours. The indicated periods of song and of breeding activity correspond to mean values for 18 mated males and 12 bachelors. The thin line indicates that only a few mated males continued singing after the laying period.

The final sample included nine mated males and 10 bachelors.

Statistics

All sample sizes refer to the number of individuals; all tests are two tailed. Descriptive statistics in the text are given as ranges and mean \pm SD. Proportional data were normalized using an Anscombe transformation (Zar 1996). We used GLM repeated measures procedures with SPSS V.10 for Macintosh.

RESULTS

Nocturnal Song Before Pairing

Of 18 males that attracted a female, 16 were engaged in nocturnal singing before pairing for 1–18 nights (6.0 ± 5.7 ; Fig. 1). As counted from the last night on which a male sang, we captured a female in his territory the next morning (day 0) to 2 days later (0.7 ± 0.8 days, $N=12$; in four cases, we did not mist-net during the prelaying period). We never observed or captured a

female before the male stopped singing at night. Thus, all 12 males stopped singing at night after a female had settled in their territory.

Two males stopped nocturnal singing after a female arrived in their territory, but resumed when the females disappeared. One of the females returned after 2 days, and the male again ceased nocturnal singing. Another male resumed nocturnal singing during the nestling period after its mate had died. A fourth male resumed nocturnal song after its mate had disappeared following predation of the brood, but ceased nocturnal singing again after a new female had settled in his territory.

Nocturnal Song After Pairing

For 15 mated males, we were able to examine whether they resumed nocturnal singing in later stages of the breeding cycle. Of these males, 13 resumed nocturnal singing once the females started egg laying.

Nine of these mated males were sampled every night during the laying period (4 days). They sang for 1–4 nights (2.8 ± 1.4 ; Fig. 1). Of 12 males for which we have information on the onset of nocturnal song, five resumed singing the night before the first egg was laid, four resumed singing before the second, two before the third, and one before the fourth egg was laid. After egg laying, three of 10 regularly censused males continued singing during the first nights of incubation for 2, 3 and 6 nights (Fig. 1).

For 11 males, we could examine whether nocturnal song during the laying period was closer to egg laying of their mate than to egg laying of neighbouring females. In the neighbouring territories, egg laying started from 7 days earlier to 7 days later than in the focal territories. The 11 focal males resumed nocturnal song significantly closer to the day when their mate laid the first egg (0.8 ± 0.6 days) than to the day when neighbouring females laid their first egg (3.9 ± 2.4 days; Wilcoxon signed-ranks test: $T=2$, $N=11$, $P<0.005$). Furthermore, the onset of nocturnal song was not related to the prelaying period of neighbouring females, since only five of the 11 males resumed nocturnal song before the first egg was laid in neighbouring territories.

Nocturnal Song of Bachelors

To monitor the mating status of males that continued singing at night throughout the breeding season, we regularly performed mist netting in four of these territories. Here, females were never captured nor observed. We considered these males, as well as eight additional males which were never seen with a female, as having remained unpaired. These 12 bachelors were engaged in nocturnal singing over 28–53 nights (38 ± 9 ; Fig. 1). On average, they stopped singing at night 4 days after the mean fledging date (Fig. 1).

Diurnal Song of Mated Males and Bachelors

Males sang diurnal song throughout the breeding season (Fig. 2). The overall diurnal song output differed

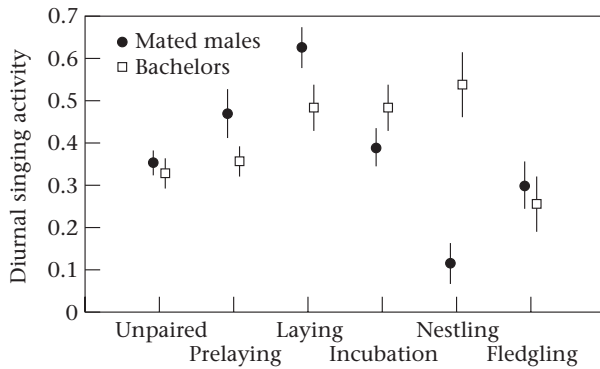


Figure 2. Mean \pm SE diurnal singing activity of male nightingales over six periods of the breeding cycle, based on 3 ± 2 ($\bar{X} \pm SD$) rounds per day conducted on the study site throughout the breeding season. Singing activity of a male is expressed as the proportion of rounds on which it was heard singing. The time periods for bachelors ($N=10$) were determined by the breeding periods of their closest mated neighbours ($N=9$ mated males).

between periods of the breeding cycle (GLM repeated measures: $F_{5,85}=7.72$, $P<0.001$), but not between mated males and bachelors ($F_{1,17}=1.13$, $P=0.30$). However, the interaction between mating status and periods of the breeding cycle was significant ($F_{5,85}=9.16$, $P<0.001$), suggesting that seasonal changes in diurnal singing activity differ between bachelors and mated males.

Before arrival of the females, all males started with diurnal singing activity at an intermediate level, and singing activity did not predict later mating status (t test between mated males and bachelors for the unpaired period: $t_{17} = -0.66$, $P=0.52$; Fig. 2). However, during the laying period, mated males sang more than bachelors, although this was marginally nonsignificant ($t_{17} = -2.096$, $P=0.051$).

For bachelors, a separate repeated measures GLM revealed differences in diurnal singing activity between periods of the breeding cycle ($F_{5,45}=4.39$, $P=0.003$). The singing activity of bachelors increased until the nestling period (from the unpaired period until the nestling period, the linear term of the repeated measures GLM was significant: $F_{1,9}=7.83$, $P=0.021$).

In mated males, too, diurnal singing activity differed between periods ($F_{5,40}=12.99$, $P<0.001$). Mated males had their highest song output during the laying period. They sang least during the period of feeding nestlings. In mated males, diurnal singing activity in the laying period differed significantly from that of the unpaired, nestling and fledgling periods (Bonferroni-adjusted post hoc multiple comparisons: all $P<0.02$).

DISCUSSION

Our study provides the first quantitative evidence in songbirds that nocturnal song is related to mating status. Male nightingales ceased nocturnal singing with pair formation and resumed it if their mate deserted. Furthermore, males that remained unmated continued to sing at night until the end of the breeding season. These results strongly suggest that a main function of nocturnal song is

mate attraction. We also found that diurnal singing activity before the settlement of females was comparatively low and did not predict future mating status. This observation may indicate that singing during the day is less important for mate attraction in the nightingale.

Low background noise at night makes nocturnal song particularly suitable for long-distance advertisement to migrating females (Wiley & Richards 1982). Since sound transmission is better at night than in the day, nocturnal song might preferably be used by females to assess differences in male singing traits. If nocturnal song is costly (Thomas 2002), the advertisement through nocturnal singing may be an honest signal reflecting male quality.

The increase in diurnal singing activity after the arrival of females might have resulted from changing environmental conditions such as increased temperature and food availability (Gottlander 1987). However, such a causal relationship does not explain the observed fluctuations in singing activity of mated males. Males may sing in the day throughout the season to repel other males (Nowicki et al. 1998). Indeed, male nightingales with high diurnal song rates suffered from fewer territorial intrusions by neighbouring males than did males with lower song rate (Naguib et al. 2001). The greater increase in diurnal singing activity until the end of the laying period in mated males than in bachelors is in line with this intrasexual function of diurnal song, because mated males may be especially vulnerable to intrusions from other males seeking extrapair copulations.

Mated males resumed nocturnal singing when their mates laid eggs. This resumption of nocturnal song coincided with the peak of diurnal singing. Because diurnal song has been shown to repel rival males, and we found that nocturnal song functioned to attract females, it is possible that the high overall singing activity during egg laying serves both intrasexual and intersexual functions. It is, however, unlikely that during egg laying, nocturnal song serves to attract additional social mates. We never observed true cases of simultaneous polygyny, nor are these reported in the literature. Nevertheless, this second period of nocturnal song may serve other intersexual functions. An increase in song output of mated males during the fertile time of their mates is also known for other species, and there are several mutually nonexclusive hypotheses to explain this phenomenon.

We found that the onset of the second period of nocturnal song was linked to the mate's egg laying and not to that of neighbouring females. This suggests that the breeding behaviour of his mate is the primary factor determining a male's decision to resume nocturnal song. One functional explanation could be that a male sings during the laying period to encourage his mate to increase the investment in the brood. The simultaneous performance of nocturnal song and a high level of diurnal singing during egg laying may be costly, and hence could indicate male quality. Therefore, females may adjust their reproductive effort with regard to male singing activity during egg laying (Sheldon 2000). Females might modify the number of eggs (Kroodsma 1976) or adjust the allocation of resources into the yolk (Gil et al. 1999b).

However, female birds begin to deposit yolk 3–5 days before egg laying (King 1973). To encourage their mates efficiently, males should therefore increase their song output some days before the first egg is laid. However, mated males never started nocturnal song more than a day before the first egg was laid.

Alternatively, males could honestly announce the fertility of their own mates to rival males by singing more, to signal their good condition and thus their ability to defend paternity. This 'fertility announcement hypothesis' (Møller 1991) predicts the highest singing effort when the females are most fertile. We found that mated males had their highest diurnal singing activity and also resumed nocturnal singing during the laying period. In his hypothesis, Møller (1991) made no distinction between the prelaying and the laying period, treating both as a time of peak fertility. Similar to our results, Gil et al. (1999a) found a peak of singing activity during the laying and not during the prelaying period in the willow warbler, *Phylloscopus trochilus*. They regarded this as evidence against singing as an announcement of fertility, apparently assuming that females are not fertile during egg laying. Indeed, the receptivity of females for new sperm seems to be lower during egg laying (Brillard & Bakst 1990), and, accordingly, most species show a marked reduction or total cessation of copulation after the first egg is laid (Birkhead & Møller 1992). However, as long as it cannot be excluded that, during egg laying, copulations take place and may lead to a reasonable number of fertilizations, it remains possible that elevated singing activity during this period serves to defend paternity.

Finally, males may sing more during the laying period of their mates to attract females for extrapair copulations (Hasselquist et al. 1996). In this case, it would be interesting to investigate why males appear to resume nocturnal song at the start of their mate's egg laying and not earlier, when neighbouring females might already be fertile.

Several other field studies have found an elevated level of song during egg laying. Of the 13 studies that Gil et al. (1999a) reviewed with regard to the fertility announcement hypothesis, three did not discriminate between the laying period and the prelaying period. Of the remaining 10 studies, at least five reported an elevated level of singing activity or of some other song parameter during egg laying. Therefore, a clear distinction between the prelaying period and the laying period is important for studies that aim to identify the functions of male song during the fertile period of females. More attention should also be paid to the singing of unmated males, because this may increase our understanding of the singing behaviour of their mated conspecifics.

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