



Seasonal variation in dawn song characteristics in the common nightingale

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Many male temperate zone passerines show a marked peak of singing activity before sunrise. The two main functions of this so-called dawn chorus are mate attraction and territory defence. We examined how seasonal patterns of different dawn song characteristics were related to mating status and to the breeding cycle of females in the common nightingale, *Luscinia megarhynchos*. We investigated two measures of song output: song rate and percentage performance time. We also calculated the proportion of ‘whistle songs’, a song category that is thought to be important in female choice. We predicted that if the main function of dawn singing in nightingales is to attract a social mate, then mated males should change their dawn singing behaviour after pair formation. In contrast, if dawn singing is mainly used in territory defence, we expected no difference in song traits between mated and unmated males throughout the season. We found that song rate and the proportion of whistle songs were low at the beginning of the season and did not predict future mating status. After arrival of females, all measures of dawn song performance remained largely constant throughout the breeding season, and we did not find significant differences in the seasonal variation between mated and unmated males. These findings are consistent with the hypothesis that song at dawn is important to defend a territory throughout the breeding season.

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A conspicuous singing pattern in many bird species is the marked peak of song before sunrise. Given that territorial birds must sing for some time of the day, dynamic modelling has shown that environmental factors could cause a peak of singing at dawn (McNamara et al. 1987; Hutchinson et al. 1993; Hutchinson 2002). Several functional but mutually nonexclusive hypotheses have been put forward to explain this dawn chorus (reviewed in Mace 1987b; Staicer et al. 1996). Here, we focus on the hypotheses that dawn singing plays a role in mate attraction (McNamara et al. 1987) or territory defence (Kacelnik & Krebs 1983).

In several species, dawn singing occurs long after pair formation and is linked to female fertility, for example in the great tit, *Parus major* (Mace 1987a), blue tit, *Parus*

caeruleus (Poesel et al. 2001) and willow tit, *Parus montanus* (Welling et al. 1995). In these species, the dawn chorus has been interpreted as attracting and stimulating the social female to copulate (Mace 1986), attracting extrapair females (Kempnaers et al. 1997), or being a form of mate guarding (Welling et al. 1995; for an overview of studies investigating the dawn chorus with respect to the breeding cycle see Table 1). In other species, the occurrence of dawn singing is not limited to the period of mate attraction and the fertile period of the female, for example in the collared flycatcher, *Ficedula albicollis* (Pärt 1991), common chiffchaff, *Phylloscopus collybita* (Rodrigues 1996), and wood warblers, (Parulinae; Staicer et al. 1996). Thus, dawn song has also been interpreted as a signal in territory defence (Slagsvold et al. 1994; Staicer et al. 1996; Liu 2004).

In the common nightingale, *Luscinia megarhynchos*, dawn singing starts before females arrive, and dawn singing activity remains high throughout the breeding cycle (Amrhein et al. 2004a). There is evidence that dawn singing is important for territory defence against territory-searching males (Kacelnik & Krebs 1983), because non-territorial male nightingales seem to use the dawn chorus to prospect territories (Amrhein et al. 2004b). Nightingales

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Table 1. Results from studies that implicitly investigated the dawn chorus with reference to the breeding cycle of individual females

| Species | Dawn song limited to fertile period | Peak of dawn song | Song parameter | Conclusion: primarily addressed to | Source |
|---|-------------------------------------|-----------------------|---|------------------------------------|--------------------------|
| Eurasian blackbird, <i>Turdus merula</i> | No | Fertile period | Start of dawn song Duration of dawn song | Females | Cuthill & Macdonald 1990 |
| Black-capped chickadee, <i>Poecile atricapillus</i> | (-)* | (-) | Duration of dawn song | Females | Otter & Ratcliffe 1993 |
| Blue grosbeak, <i>Passerina caerulea</i> | No† | Fertile period | Song complexity Song rate Duration of dawn song | Females | Ballentine et al. 2003 |
| Blue tit, <i>Parus caeruleus</i> | (-)‡ | (-) | Strophe length | Females | Kempnaers et al. 1997 |
| Blue tit, <i>P. caeruleus</i> | (-)§ | (-) | % Performance time | Females | Poesel et al. 2001 |
| Common chiffchaff, <i>Phylloscopus collybita</i> | No** | Fertile–postfertile | Song rate Song length | Females | Rodrigues 1996 |
| Collared flycatcher, <i>Ficedula albicollis</i> | No | Laying–incubation | Song rate Duration of dawn song | Females | Pärt 1991 |
| Great tit, <i>Parus major</i> | (-) | Fertile period | Singing activity | Males | Slagsvold et al. 1994 |
| Great tit, <i>P. major</i> | (-) | Shortly before laying | Duration of dawn song | Females | Mace 1987a |
| Common nightingale, <i>L. megarhynchos</i> | No | Incubation | Singing activity | Males | Amrhein et al. 2004a |
| Willow tit, <i>Parus montanus</i> | No†† | Fertile period | Time spent singing | Females | Welling et al. 1995 |

(-): No information available.

*Males were recorded during nest building and the preincubation period.

†Fertile period defined prenesting, nest building, egg laying (until the penultimate egg was laid).

‡Fertile period defined as from 5 days before the first egg was laid until the morning the penultimate egg was laid.

§Fertile period defined as from 8 days before the first egg was laid until a few days before females finished their clutches.

**Fertile period defined as from 9 days before the first egg was laid until 3 days after the first egg was laid.

††Fertile period defined as from 11 days before the first egg was laid until the penultimate egg was laid.

are best known for their nocturnal song, but singing activity, measured as the proportion of surveys on which a male was heard singing, is higher at dawn than at other times of the day (Amrhein et al. 2004b). However, neither overall diurnal singing activity (Amrhein et al. 2002) nor dawn singing activity (Amrhein et al. 2004a) before arrival of females appears to predict whether a male is able to attract a mate. As shown for other species singing at dawn (cf Table 1), it is important to assess the actual song performance once a male has started to sing, since females may base their choice of a mate on other dawn song characteristics than whether or not a male is singing (summarized in Table 1). In the present study, we therefore investigated whether male singing performance at dawn varies with mating status and over the breeding season. To do this we measured two song output parameters: song rate and percentage performance time (the latter measures how much time a bird is singing, Lambrechts 1996). In addition, we quantified the occurrence of specific categories of songs, since in species in which males have a repertoire of different song types or song categories, birds can vary not only song output but also the use of song patterns according to social context (e.g. Catchpole 1983; Kroodsma et al. 1989; Nelson & Croner 1991; Spector 1992; Wiley et al. 1994), suggesting that specific messages are conveyed by different songs.

Nightingales have large song repertoires (Hultsch & Todt 1981; Kipper et al. 2004), but songs can be grouped into two categories: the so-called whistle songs and the nonwhistle songs (Hultsch & Todt 1996; Naguib et al. 2002; Kunc et al., in press). Whistle songs contain a series of mostly unmodulated whistles (Fig. 1), and are

hypothesized to be important for attracting females (Glutz von Blotzheim 1988). In our study population, a large proportion of males remain unpaired throughout the breeding season (Amrhein et al. 2004b), providing the opportunity to compare singing between males that are successful in attracting a social mate and those that remain unsuccessful throughout the season. Both males that are able to attract a female and those that remain unpaired establish territories throughout much of the breeding season, and a comparison of the two groups of males may reveal whether structural and temporal dawn song characteristics are important in mate attraction.

We investigated song rate, percentage performance time and the use of whistle songs at dawn throughout the breeding cycle with respect to male mating status. To our knowledge, no previous study investigating temporal and structural dawn song characteristics has followed the same individuals throughout the breeding season with respect to male mating status. If the main function of dawn singing in nightingales in the early season is mate attraction, we predicted a higher song output or a higher proportion of whistle songs at dawn in males that succeeded in attracting a mate.

METHODS

Study Site and Study Species

Our study was carried out from April to June 2002 and 2003 at the Petite Camargue Alsacienne in France. Males usually arrive before females and establish their territories

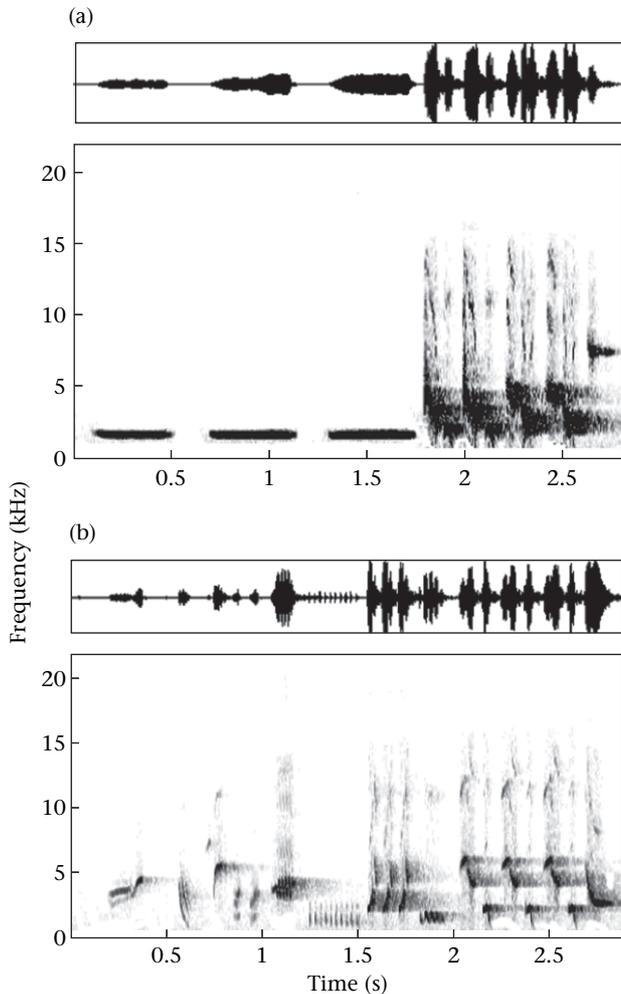


Figure 1. Oscillograms (above) and spectrograms (below) of songs of the two different categories (a) whistle songs and (b) nonwhistle songs of male nightingales.

soon after arrival (Amrhein et al. 2002, 2004a). The first males were observed on 12 April in 2002 and on 13 April in 2003. The first females were seen on 20 April in both years. Nightingales form socially monogamous seasonal pair bonds, but in our population a large number of territorial males remain unmated throughout the breeding season (Amrhein et al. 2004b). To avoid confusion with the unpaired period of all males before arrival of females, we used the term bachelors for territorial, but unmated males.

General Procedures

Since only unmated males sing regularly at night for a prolonged period (Amrhein et al. 2002, 2004a), we surveyed nocturnal singing activity of all males in our study area during every night throughout the breeding season. Based on the presence or absence of nocturnal song, and by regular mist netting throughout the breeding season, we were able to determine the mating status of males.

We recorded songs of all mated subjects in each of the following stages of the breeding cycle: (1) unpaired period:

the day a male started to advertise a territory until the day before a female settled in his territory; (2) laying period: the day the first egg was laid until the day the penultimate egg was laid (females usually lay five eggs); (3) nestling period: when nestlings were 4–6 days old; and (4) fledgling period: 1–3 days after the young left the nest. Females laid one egg per day, and egg-laying dates were determined by direct observation during the laying period or were calculated from hatching date or the age of nestlings. To allow comparisons between mated males and bachelors, we recorded bachelors on the same morning as their immediate neighbouring mated males and assigned these recordings to the same period as the recordings of the mated males.

Because it is impossible to predict for which males data can be collected over the entire season, we recorded as many males as possible at the beginning of the breeding season ($N = 48$). This allowed us to follow the same males over the entire breeding season. However, the sample size was reduced owing to depredation of females or of clutches, and one male died in a car accident. In total, we obtained recordings for all four periods of the breeding season for 22 males, of which nine were mated males and 13 were bachelors. However, for the first two periods (unpaired and laying period) we obtained a sample size of 26 males (12 mated males and 14 bachelors). Ten mated males were more than 1 year old, one mated male was a yearling (i.e. a bird that fledged in the previous year), and one mated male was of unknown age. The group of bachelors consisted of seven birds older than 1 year, two yearlings and five males of unknown age.

Recording Methods and Song Analysis

Since males make a distinct break between nocturnal song and dawn song (H. Kunc, personal observation), we could unequivocally assess the onset of dawn song in males that sang throughout the previous night. Recordings were made between twilight and sunrise, but to distinguish clearly between dawn and diurnal song, we did not record song after sunrise. For each male, we recorded the dawn song in each period of the breeding cycle for about 12 min. We used a Sennheiser ME66/K6 directional microphone and either a Sony TC-D5M or a Sony WM-D6C tape recorder. We digitized recordings on a PC with Cool Edit 2000 (Syntrillium Cooperation, Phoenix, AZ, U.S.A.; sample frequency: 44.1 kHz; resolution: 16 bit) and analysed dawn song characteristics with the software package Avisoft SASLab Pro 3.5 (R. Specht, Berlin, Germany) on a PC (time resolution: 5.8 ms; FFT: 256).

For each male, we analysed 10 min of continuous dawn song from each stage of the breeding cycle. In the analysis, we distinguished between the two song categories whistle songs and nonwhistle songs (Fig. 1). Whistle songs contain a series of mostly unmodulated whistles at the beginning of a song and can be identified clearly on the basis of their syntactical and phonological structure (Hultsch & Todt 1996). We measured (1) song rate (number of songs/min), and (2) the percentage of whistle songs. For each song category we measured separately: (3) song

length (s) and (4) pause length (the interval between the end of one song and the beginning of the next song, s). We then calculated (5) percentage performance time of a song unit (song plus the following pause), computed as song length divided by the sum of song length and pause length, multiplied by 100 (Lambrechts & Dhondt 1988). To increase song rate, birds can either shorten single songs or reduce pauses between songs. The most common pattern is that birds reduce pauses between songs to increase song rate (Catchpole & Slater 1995), which is also the case in the nightingale (Kunc et al., in press). As proposed by Lambrechts & Dhondt (1988), percentage performance time gives a more representative measure of the time spent singing than song length or song rate alone. We calculated both an overall percentage performance time and percentage performance times for whistle songs and nonwhistle songs. As percentage performance time is derived from song length and pause length, it was correlated with these two measurements; we therefore included only percentage performance time in further analyses.

Statistical Analysis

We applied repeated measures ANOVA using SPSS 11.0 (SPSS Inc., Chicago, IL, U.S.A.). Our within-subjects factor was the particular song parameter at the four defined breeding stages (unpaired, laying, nestling and fledgling period), and the between-subjects factor was mating status (mated male or bachelor). In 2002, we had investigated male territory-prospecting behaviour and had translocated 13 unmated males to our study site which for some days remained nonterritorial and silently prospected the area at dawn (Amrhein et al. 2004b). No recordings were made in or near territories in which translocated males were present, nor were translocated males used as subjects in the present study. To examine whether this artificial augmentation of the naturally occurring number of nonterritorial males influenced the dawn singing behaviour of our subjects, we included year of study as a factor in the repeated measures analyses; since we did not find differences in singing behaviour between the 2 years of the study ($P > 0.2$ for all measured song parameters), we excluded year as a factor in all subsequent analyses. Values plotted in figures are calculated from the subsample of males that was recorded in all four periods of the breeding cycle. Results are given as mean \pm SE; all reported tests are two tailed.

Ethical Note

During both breeding seasons, we captured males and females in mist nets in up to 28 territories per year. The birds were colour ringed in their territory and released within 15 min of capture. We carried out 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 procedure rarely resulted in capturing an individual more than once. No bird deserted its territory after capture, and we have no indications that capturing influenced breeding success or negatively affected other bird species. Ringing was done with permission of Henri

Jenn and the Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris.

RESULTS

For mated males, song rate at dawn was highest during egg laying, whereas bachelors sang at the highest rate during the fledgling period (Fig. 2a). However, these differences in song rate between the periods of the breeding cycle were not significant (repeated measures ANOVA: $F_{3,60} = 1.7$, $P = 0.2$) nor did we find that mated males and bachelors differed significantly in song rate ($F_{1,20} = 2.8$, $P = 0.1$). The interaction between the periods of the breeding cycle and mating status was not significant ($F_{3,60} = 1.84$, $P = 0.15$), suggesting that the seasonal variation in song rate was similar in mated males and bachelors. Using our larger data set of the first two periods of the breeding cycle and limiting our analysis to these periods revealed a significant increase in song rate from the unpaired to the laying period ($F_{1,24} = 5.9$, $P = 0.02$). Again, we found no difference in song rate between mated males and bachelors ($F_{1,24} = 0.4$, $P = 0.5$).

In contrast to song rate, the proportion of whistle songs differed significantly between the four stages of the

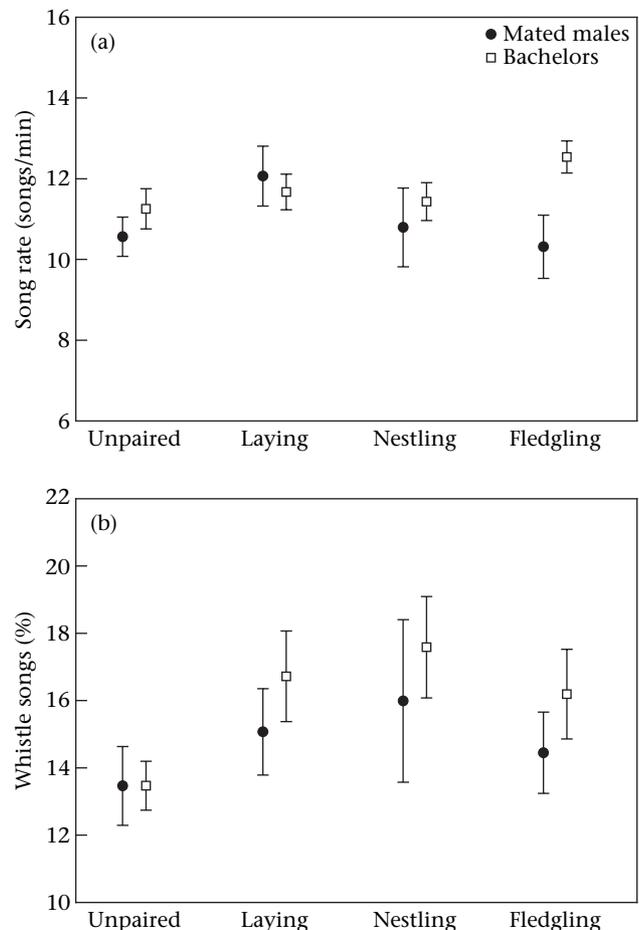


Figure 2. Changes in (a) song rate at dawn ($\bar{X} \pm$ SE) and (b) the percentage of whistle songs at dawn ($\bar{X} \pm$ SE) over the breeding cycle of male nightingales for mated males ($N = 9$) and bachelors ($N = 13$).

breeding cycle (ANOVA: $F_{3,60} = 3.2$, $P = 0.03$; Fig. 2b), but did not differ significantly between mated males and bachelors ($F_{1,20} = 0.7$, $P = 0.4$). The interaction between periods of the breeding cycle and mating status was not significant ($F_{3,60} = 0.28$, $P = 0.8$), indicating that the variation in the proportion of whistle songs did not differ significantly between mated males and bachelors. We obtained similar results by analysing the first two periods of the breeding cycle, using the larger data set (seasonal variation: $F_{1,24} = 8.9$, $P = 0.006$; male mating status: $F_{1,24} = 0.15$, $P = 0.7$; interaction between periods of the breeding cycle and male mating status: $F_{1,24} = 0.02$, $P = 0.88$).

Mated males reduced their percentage performance time towards the end of the breeding season, whereas bachelors continued to sing with a high percentage performance time throughout the season (Fig. 3). The seasonal variation in percentage performance time was not significant (ANOVA: $F_{3,60} = 0.5$, $P = 0.67$), but mated males sang with a lower percentage performance time than bachelors ($F_{1,20} = 11.1$, $P = 0.003$). However, the interaction between the periods of the breeding cycle and mating status was not significant ($F_{3,60} = 1.44$, $P = 0.24$). Analysing percentage performance time for the first two periods with the larger data set, we did not find a difference between the unpaired and laying period ($F_{1,24} = 1.1$, $P = 0.3$) and no effect of male mating status ($F_{1,24} = 1.0$, $P = 0.3$).

Separate analyses of percentage performance time of whistle songs and percentage performance time of non-whistle songs showed similar results as for the overall percentage performance time (Fig. 4a, b). Percentage performance times of whistle songs and nonwhistle songs did not vary significantly over the breeding season (ANOVA: whistle songs: $F_{3,60} = 1.7$, $P = 0.2$; nonwhistle songs: $F_{3,60} = 0.5$, $P = 0.7$), but in both song categories, mated males sang with a significantly lower percentage performance time than bachelors (whistle songs: $F_{1,20} = 9.7$, $P = 0.005$; nonwhistle songs: $F_{1,20} = 10.7$, $P = 0.004$). This difference was particularly conspicuous

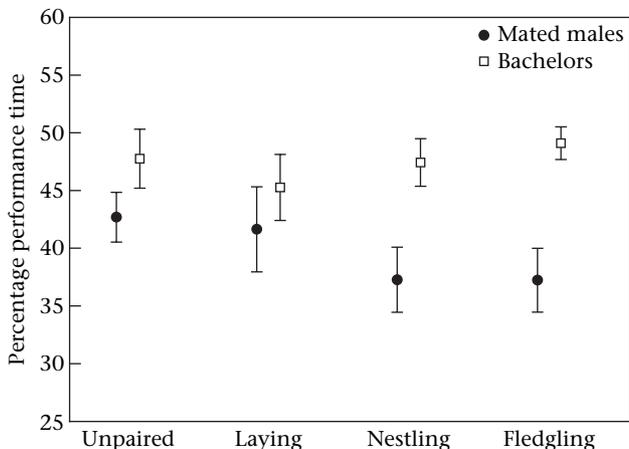


Figure 3. Variation in percentage performance time at dawn ($\bar{X} \pm SE$) over the breeding cycle of male nightingales for mated males ($N = 9$) and bachelors ($N = 13$).

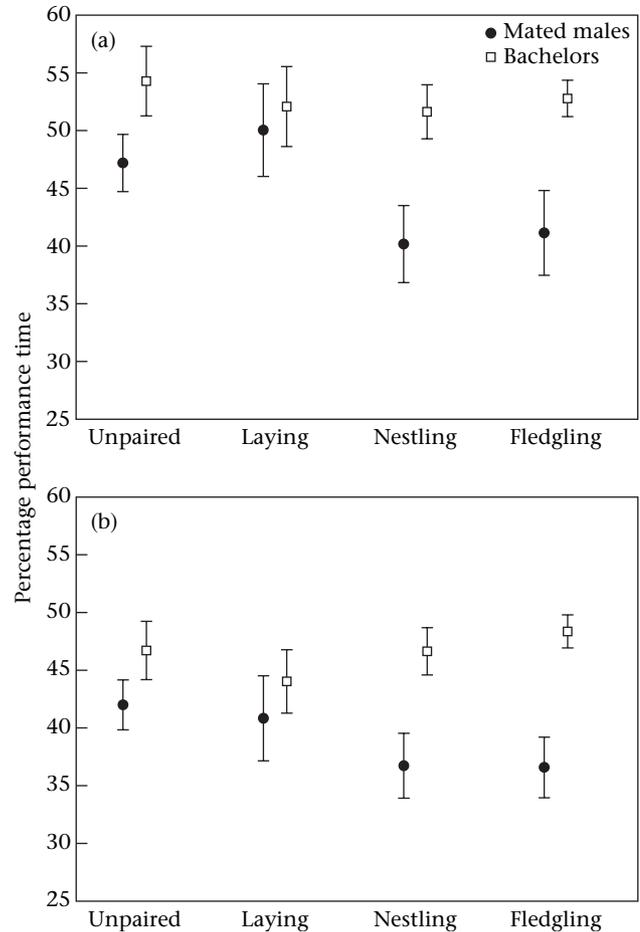


Figure 4. Course of percentage performance time of (a) whistle songs and (b) nonwhistle songs at dawn ($\bar{X} \pm SE$) over the breeding cycle of male nightingales for mated males ($N = 9$) and bachelors ($N = 13$).

in the last two stages of the breeding cycle (Fig. 4a, b). However, the interactions between periods of the breeding cycle and mating status in percentage performance time of whistle songs ($F_{3,60} = 0.9$, $P = 0.1$) and percentage performance time of nonwhistle songs ($F_{3,60} = 1.6$, $P = 0.2$) were not significant.

DISCUSSION

Analysis of dawn song in the nightingale did not reveal significant differences in song rate or in the proportion of whistle songs between mated males and bachelors, but song rate and the proportion of whistle songs increased from the unpaired to the laying period. However, the analysis of song rate of the subsample of males that was recorded throughout the breeding season did not show a significant variation.

The increase in song rate from the unpaired to the laying period is in line with previous studies that found a peak of dawn song after the male attracted a mate (Table 1). However, in comparison to other studies, the difference we found in song rate between the two periods was small. In previous studies, song rates were at least

twice as high in one period as in the other (Hanski & Laurila 1993; Gil et al. 1999). In our study, the average dawn song rate was about 10 songs/min in the unpaired period and 11 songs/min in the laying period. Therefore, we hesitate to conclude that these small but statistically significant differences in song rate are of major biological relevance. Furthermore, we found no significant differences in song rate between mated males and bachelors, suggesting that the settlement of females and their reproductive state did not influence song rate at dawn.

The maintenance of high song rates at dawn in mated males beyond pair formation contrasts with the general finding that, after dawn, diurnal song rates decrease once a male is mated (all studies mentioned in Table 2 in Gil et al. 1999, except that of Welling et al. 1995 in which data collection was restricted to dawn song). Thus, it appears that singing at dawn is functionally different from singing at other times of the day.

Several authors have proposed that a main function of dawn singing is to attract a social mate, to stimulate the female, or to attract extrapair females, although the occurrence of dawn singing in many of the species studied is not limited to the period of mate attraction or the fertile period of females (Table 1). In the nightingale, whistle songs are hypothesized to play a role in mate attraction (Glutz von Blotzheim 1988), so we predicted a difference in the proportion of whistle songs between mated males and bachelors if dawn song were important for mate attraction. However, all males sang fewer whistle songs at the beginning of the season than after the settlement of females, and we found no significant difference in the proportion of whistle songs between mated males and bachelors throughout the breeding season. There are at least two possibilities to explain this finding. First, whistle songs in general may not be important in mate attraction. Second, whistle songs may be important in mate attraction not at dawn but at other times of the day or night. In the nightingale, nocturnal song is thought to function in mate attraction (Amrhein et al. 2002), and the proportion of whistle songs may differ between mated males and bachelors at night. Our results are in line with several other studies that also found that the use of specific song patterns at dawn is not influenced by male mating status (Kroodsma et al. 1989; Spector 1991; Staicer 1996).

Percentage performance time did not differ significantly between the stages of the breeding cycle but was higher in bachelors than in mated males. This could be explained by mated males providing parental care (Glutz von Blotzheim 1988) and thus having different constraints on allocating time and energy to singing.

Percentage performance time (Lambrechts & Dhondt 1988; Poesel et al. 2001) and song length (Lambrechts & Dhondt 1986; Rodrigues 1996; Kempnaers et al. 1997) have been interpreted as indicating male quality. It is therefore surprising that bachelors sang with a higher percentage performance time even in the period of mate attraction before settlement of females. This pattern was found for both the whistle songs and nonwhistle songs. Furthermore, males that were able to attract a mate neither sang at a higher rate nor sang more whistle songs before the settlement of females than males that remained

unpaired. Thus, the females did not appear to base their choice of social mate on song rate, the proportion of whistle songs or percentage performance time at dawn. It is, however, possible that the increase in song rate and the proportion of whistle songs after the settlement of females is related to the attraction of extrapair females. For example, in the superb fairy-wren, *Malurus cyaneus* (Double & Cockburn 2000), females visit other territories to search for extrapair males during the dawn chorus. In the nightingale, however, females were not found to make extraterritorial excursions during their fertile period at dawn (Amrhein 2004).

Alternatively, dawn singing may serve territory defence. Kacelnik & Krebs (1983) argued that dawn singing of territorial males could function as a keep-out signal to nonterritorial males. Unmated male nightingales often leave their territories after being territorial for a certain time, and nonterritorial males prospect occupied territories almost exclusively at dawn (Amrhein et al. 2004b). It therefore seems important for both mated males and bachelors to announce territory occupancy at dawn throughout the breeding season.

In conclusion, song rate and the proportion of whistle songs at dawn were low at the beginning of the season and did not predict future mating status. After arrival of females, all measures of dawn song performance remained largely constant throughout the breeding season, and we did not find significant differences in the seasonal variation between mated and unmated males. Thus, our findings suggest that dawn singing in nightingales does not function primarily to attract a social mate. Our results are consistent with the hypothesis that dawn singing functions to defend the territory, but we cannot rule out that dawn singing could also function to attract females for extrapair copulations at least during part of the breeding season.

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