

## SEASONAL PATTERNS OF SINGING ACTIVITY VARY WITH TIME OF DAY IN THE NIGHTINGALE (*LUSCINIA MEGARHYNCHOS*)

VALENTIN AMRHEIN,<sup>1,3</sup> HANSJOERG P. KUNC,<sup>2</sup> AND MARC NAGUIB<sup>2</sup>

<sup>1</sup>Research Station Petite Camargue Alsacienne, University of Basel (Switzerland), Rue de la Pisciculture, 68300 Saint-Louis, France; and

<sup>2</sup>Department of Animal Behavior, University of Bielefeld, P.O. Box 100131, 33501 Bielefeld, Germany

**ABSTRACT.**—Seasonal patterns of singing activity of male birds have been thoroughly studied, but little is known about how those patterns vary with time of day. Here, we censused mated and unmated male Nightingales (*Luscinia megarhynchos*) at four different hours of the day throughout the breeding cycle. In unmated males, singing activity increased until the young hatched in their neighborhood, and the seasonal variation was similar at each of the four hours of the day. In mated males, however, the seasonal patterns of singing activity differed between hours of the day. In morning (about the hour of egg-laying) and during the dusk chorus, the singing activity of mated males was strongly influenced by the females' reproductive state: singing activity was low before egg-laying and during incubation, but high during the egg-laying period. In the dawn chorus, however, singing activity showed a similar seasonal pattern in mated and unmated males and was high until late stages of the breeding cycle. Our results suggest that the social context influences singing behavior to a varying degree across the season, and that this variation also depends on time of day. The hour of data collection thus is an important but often neglected factor when seasonal changes of singing activity are studied. Received 17 October 2002, accepted 15 September 2003.

**RÉSUMÉ.**—L'évolution saisonnière du chant chez les oiseaux mâles a été largement étudiée, mais peu de choses sont connues quant à sa variation au cours de la journée. Dans cette étude, nous avons recensé des mâles de *Luscinia megarhynchos* accouplés ou non, à quatre différentes heures de la journée tout au long du cycle de reproduction. Pour les mâles non accouplés, les activités de chants augmentaient jusqu'à l'éclosion des jeunes dans le voisinage, et la variation saisonnière était similaire pour les quatre différentes heures de la journée. Par contre, pour les mâles accouplés, les profils saisonniers du chant différaient entre les heures de la journée. Le matin (à l'heure de ponte) et au crépuscule, les chants des mâles accouplés étaient fortement influencés par le stade de reproduction des femelles. En effet, les chants étaient peu fréquents avant la ponte et au cours de l'incubation, mais ils étaient plus fréquents durant la période de ponte. Néanmoins, à l'aube, les chants montraient un profil saisonnier similaire pour les mâles, qu'ils soient accouplés ou non, et demeuraient très fréquents jusqu'aux dernières phases du cycle de reproduction. Nos résultats suggèrent que le contexte social influence le comportement de chant de manière plus ou moins importante au cours de la saison, et que cette variation dépend également du moment de la journée. La prise en considération de la chronologie journalière est un facteur d'importance souvent négligé dans les études portant sur l'évolution saisonnière du chant.

A PRIMARY STEP in identifying the functions of a particular bird species' song is to examine the relationship between time of day or season and amount of singing (Hutchinson et al. 1993, Catchpole and Slater 1995). Numerous studies have correlated singing activity with the periods of the females' breeding cycle (reviewed in Møller 1991 and Gil et al. 1999). In recent years, much attention has been focused on male song

when females are fertile. An elevated singing activity during that period is commonly interpreted to function in sperm competition (Møller 1991), to attract additional social mates (Hasselquist and Bensch 1991), or to stimulate or encourage the mate (Pinxten and Eens 1998, Amrhein et al. 2002). Several authors did not find a peak of song during the fertile period (Pärt 1991, Gil et al. 1999) and questioned in particular the sperm competition hypothesis. However, the results of the different studies are difficult to compare, because the time of

<sup>3</sup>E-mail: v.amrhein@unibas.ch

day that data were collected varied between studies. Some authors investigated seasonally changing singing activity at dawn (Cuthill and Macdonald 1990, Pärt 1991, Welling et al. 1995, Rodrigues 1996), but in most studies data were collected throughout the morning (Johnson and Kermott 1991, Hanski and Laurila 1993, Eens et al. 1994, Merilä and Sorjonen 1994, Krokene et al. 1996, Nemeth 1996, Gil et al. 1999, Forstmeier and Balsby 2002). Other studies covered almost all hours of daylight (Sheldon 1994, Currie et al. 1998, Amrhein et al. 2002).

Pinxten and Eens (1998) investigated singing activity during the fertile period in European Starlings (*Sturnus vulgaris*) and found that males sang more in late morning, following egg-laying, than in early morning. They assumed that the hour after egg-laying is a time of peak fertility (but see Birkhead et al. 1996) and suggested that the elevated singing activity serves to protect paternity. We expect that in such a species a diel peak of song in the late morning is restricted to the period of the breeding cycle when females lay eggs. Furthermore, a seasonal peak of song during the fertile period should be found mainly if singing activity is censused at a time of day when egg-laying takes place. In contrast, the seasonal pattern of singing at other times of the day may be less influenced by the reproductive state of females and therefore reveal no clear peak during the fertile period. That would mean that diel patterns can influence the results of studies examining seasonal singing patterns.

However, little is known about how diel patterns in male song relate to changes in female reproductive state (Staicer et al. 1996). Day-round activity data for individual breeding pairs are difficult to obtain for all periods of the breeding cycle, because individuals do not breed perfectly synchronously and therefore almost daily data collection is required. Until now, studies that investigated day-round singing patterns in the course of seasons made population-wide surveys without reference to the breeding cycles of individual females (Catchpole 1973, Sorjonen 1977, Merilä and Sorjonen 1994, Kloubec and Capek 2000).

Here, we used a new approach by sampling male Nightingales (*Luscinia megarhynchos*) four times every day throughout the breeding cycle. We examined seasonal changes of singing activity at dawn, in the morning at a time of day

when egg-laying takes place, in the afternoon, and at dusk. Our aim was to determine if the seasonal patterns of singing activity vary with time of day. We also investigated how seasonal patterns differed between mated males and males that remained unmated. We hypothesized that at those times of the day, when the reproductive state of females most strongly influences the singing activity of their mates, seasonal changes in singing activity should most strongly differ between mated males and males that remained unmated.

## METHODS

*General methods.*—The study was conducted from April to June 2002 and 2003 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. The first males were observed on 12 April 2002 and 13 April 2003, respectively, and the first females were observed on 20 April in both years. All male and female subjects were color-banded. For the first clutches of 13 females, egg-laying dates were determined by direct observation during the laying period ( $n = 6$ ) or were calculated from hatching date ( $n = 2$ ) and the age of the nestlings ( $n = 5$ ). Clutch sizes were four ( $n = 2$ ), five ( $n = 10$ ), and six ( $n = 1$ ). For all mates of the 13 females, we have a complete data set on singing activity for the first four periods of the breeding cycle (see below). For the last two periods, the sample size was reduced to 10 and 6 mated males, respectively, because 6 broods were depredated and 1 male was found dead on a road (apparently struck by a car). Values from all periods are depicted in graphs, whereas statistical analyses include only the complete data set from the first four periods. In addition to the 13 pairs, 13 unpaired territorial males were monitored for which the term "bachelors" was used to avoid confusion with the unpaired period of all males before arrival of the females. In all bachelor territories, we monitored for the presence of a female by regularly mist-netting throughout the season. Bachelors were immediate territorial neighbors of the mated subjects ( $n = 7$ ) or were separated from a mated subject by up to three other territories ( $n = 6$ ). For bachelors, the season was subdivided according to the breeding periods of their immediate mated neighbors or, for more separated bachelor territories, according to the mean breeding dates of the 13 females. The sample size for bachelors is 13 for all periods, except the last period, in which three birds deserted their territories. Most subjects were older than one year; two mated males and two bachelors were yearlings (i.e. birds that fledged in the previous year), and one bachelor was of undetermined age.

*Periods of the breeding cycle.*—The periods of the breeding cycle were defined as follows: the unpaired period was from the day a male started to advertise

a territory until the day before a female settled in his territory (4–14 days,  $\bar{x} \pm SD = 8 \pm 3$ ,  $n = 13$ ). The pre-laying period was from the day a female settled until the day before the first egg was laid (5–13 days,  $\bar{x} \pm SD = 8 \pm 3$ ,  $n = 13$ ). The laying period was from the day the first egg was laid to the day the last egg was laid (five days in most cases). The incubation period was from the day after the last egg was laid until the day before the young hatched (12 days as determined by the observation of  $n = 6$  broods). The nestling period was from the day the young hatched to the day before they left the nest (10, 11, or 12 days; each  $n = 2$ ). The fledgling period was from the day the young left the nest until we finished our field work (4–12 days,  $\bar{x} \pm SD = 9 \pm 3$ ,  $n = 6$ ), and young are fed for 14 to 20 days after leaving the nest (Cramp 1988).

**Singing activity.**—Four rounds were made on the study site each day from 15 April to 9 June 2002 (56 days) and from 15 April to 7 June 2003 (54 days). Singing activity of a male is expressed as the proportion of rounds per period or per day on which it was heard singing. This measure of singing activity has been shown to be a sensitive tool in an earlier study (Amrhein et al. 2002). During each round, we passed by a male's territory for 30 s. This duration was sufficient to determine whether the bird was singing, because during a song bout, males sing continuously with pauses of about 3 to 5 s between songs. The direction of the rounds was changed from day to day, and the duration of each round was 1 h. The dawn round started 1.25 h before sunrise. The dusk round started at sunset. The morning round started at 0900 hours

(CEST); this time was chosen because egg-laying is between 0800 and 1100 hours in Nightingales (Amrhein et al. 2002). The afternoon round started at 1400 hours, to include a time with relatively low singing activity. To survey nocturnal singing behavior, an additional round was made starting at midnight (this round was not included in the analyses of singing activity).

**Statistics.**—All sample sizes refer to the number of individuals; none of the subjects sampled in 2002 were also sampled in 2003. The proportional data were normalized by applying an Anscombe transformation (Zar 1996). The general linear model (GLM) repeated measures procedures (SPSS V.11) were used, with time of day and periods of the breeding cycle as within-subjects factors (four levels each) and mating status as between-subjects factor.

## RESULTS

Mated males sang most during the laying period and sang least during the period of feeding nestlings, whereas the singing activity of bachelors continuously increased until the end of the incubation period (Fig. 1). After arrival of a female, singing activity in mated males decreased until shortly before egg-laying, then increased at the day the first egg was laid and remained high until the first days of incubation (Fig. 2).

For the following statistical analyses, we consider only the complete data set from the first

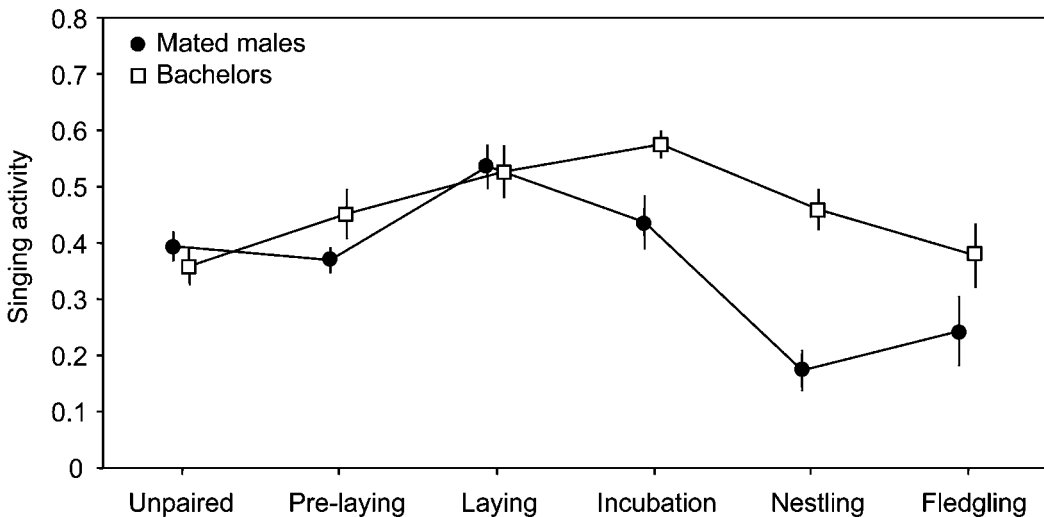


Fig. 1. Mean ( $\pm$  SE) singing activity of male Nightingales over six periods of the breeding cycle, based on four rounds conducted on the study site each day. Singing activity of a male is expressed as the proportion of rounds per period on which it was heard singing. For bachelors ( $n = 13$ ; fledgling period:  $n = 10$ ), the season was subdivided according to the breeding periods of the mated males ( $n = 13$ ; nestling period:  $n = 10$ ; fledgling period:  $n = 6$ ).

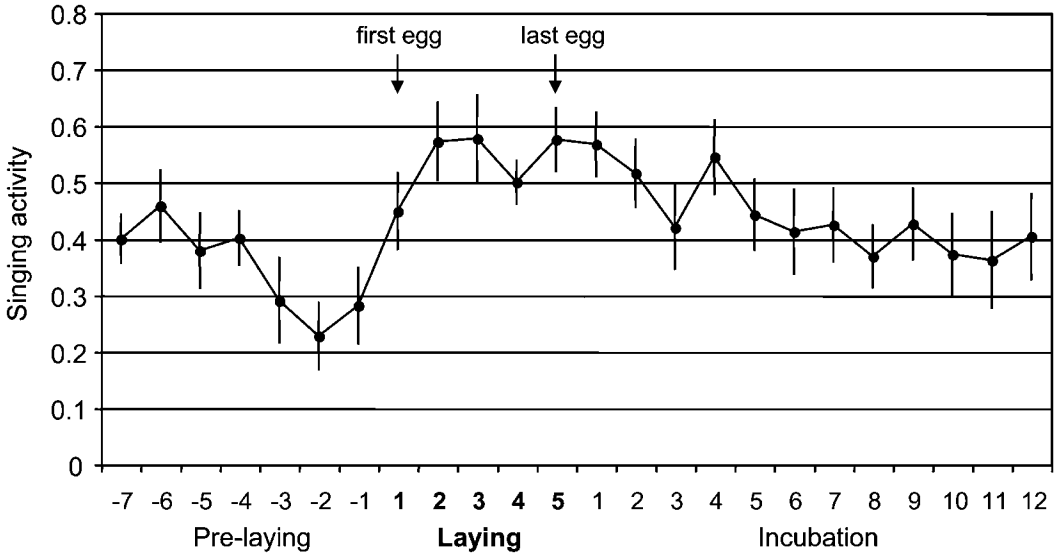


Fig. 2. Mean ( $\pm$  SE) singing activity per day in mated male Nightingales over three periods of the breeding cycle. Singing activity of a male is expressed as the proportion of four rounds per day on which it was heard singing. The last females settled in a male's territory on day -5, so the sample size is  $n = 13$  for every day except for day -6 ( $n = 11$ ) and day -7 ( $n = 9$ ).

four periods of the breeding cycle (unpaired period until incubation period). The overall diurnal song output differed between periods of the breeding cycle (Fig. 3;  $F = 11.29$ ,  $df = 3$  and  $72$ ,  $P < 0.001$ ), but not between mated males and bachelors ( $F = 1.76$ ,  $df = 1$  and  $24$ ,  $P = 0.19$ ). The overall song output differed also between hours of the day ( $F = 125.55$ ,  $df = 3$  and  $72$ ,  $P < 0.001$ ), with the highest singing activity at dawn and the lowest singing activity in the afternoon (in both mated males and bachelors; Fig. 3). To examine the interaction between seasonal and diurnal changes of singing activity, we made two separate analyses. In mated males, the interaction between periods of the breeding cycle and time of day was significant ( $F = 3.75$ ,  $df = 9$  and  $108$ ,  $P < 0.001$ ), which suggests that the seasonal patterns of singing activity vary with time of day (Fig. 3A). In bachelors, the same interaction was not significant ( $F = 1.61$ ,  $df = 9$  and  $108$ ,  $P = 0.12$ ), reflecting the finding that the seasonal patterns of singing activity were similar at different hours of the day (Fig. 3B).

To examine further how the seasonal patterns varied according to mating status, we made a separate analysis for each time of day.

*Dawn.*—At dawn, differences in singing

activity between periods of the breeding cycle were significant ( $F = 4.61$ ,  $df = 3$  and  $72$ ,  $P = 0.005$ ), and bachelors sang more than mated males (Fig. 3;  $F = 7.09$ ,  $df = 1$  and  $24$ ,  $P = 0.014$ ). However, the interaction between mating status and periods of the breeding cycle was not significant ( $F = 1.85$ ,  $df = 3$  and  $72$ ,  $P = 0.15$ ), reflecting the finding that the patterns of seasonally changing singing activity were similar in mated males and bachelors. In both mated and unmated males, elevated singing activity at dawn was maintained until the end of the nestling period (Fig. 3).

*Morning.*—At 0900 hours, singing activity differed between periods of the breeding cycle ( $F = 7.61$ ,  $df = 3$  and  $72$ ,  $P < 0.001$ ), but not between mated males and bachelors ( $F = 2.93$ ,  $df = 1$  and  $24$ ,  $P = 0.10$ ). However, the interaction between mating status and breeding cycle was significant ( $F = 9.93$ ,  $df = 3$  and  $72$ ,  $P < 0.001$ ), which suggests that at this time of the day there are different patterns of seasonally changing singing activity in mated males and bachelors. In mated males, this pattern was characterized by low singing activity in the pre-laying and incubation periods, and by a peak of singing activity when the females were laying eggs (Fig. 3A).

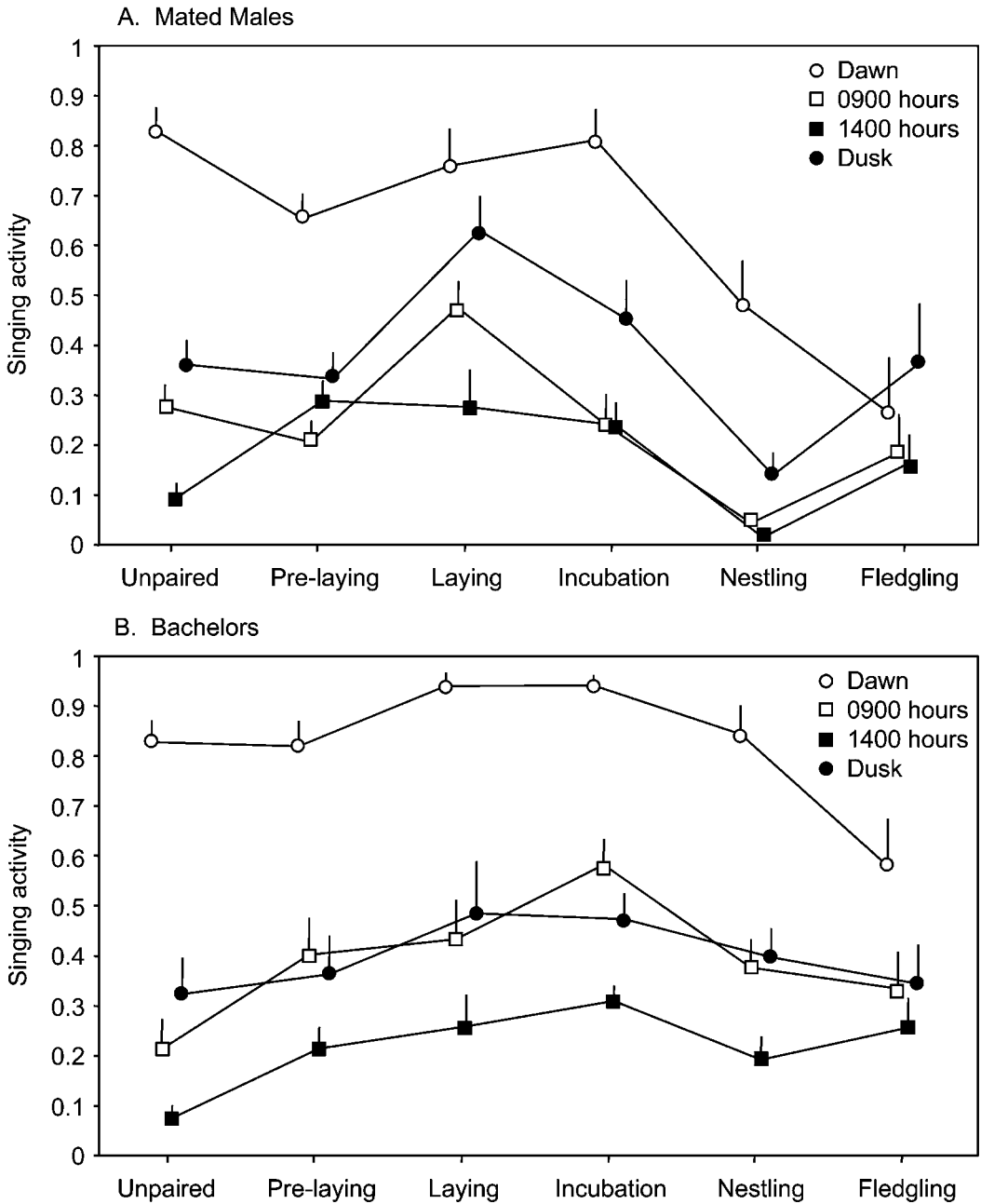


Fig. 3. Mean (+ SE) singing activity of mated male Nightingales (A) and of bachelors (B) at four different hours of the day. For the definition of singing activity and sample sizes, see Figure 1.

*Afternoon.*—At 1400 hours, singing activity differed between periods of the breeding cycle ( $F = 7.5$ ,  $df = 3$  and  $72$ ,  $P < 0.001$ ), but not between mated males and bachelors ( $F = 0.02$ ,  $df = 1$  and  $24$ ,  $P = 0.89$ ). Also, the seasonal changes in

singing activity were not found to differ between mated males and bachelors (interaction:  $F = 1.01$ ,  $df = 3$  and  $72$ ,  $P = 0.39$ ).

*Dusk.*—At dusk, singing activity differed between periods of the breeding cycle ( $F = 6.09$ ,

df = 3 and 72,  $P < 0.001$ ), but not between mated males and bachelors ( $F = 0.19$ , df = 1 and 24,  $P = 0.66$ ). Similar to the pattern at 0900 hours, there was a peak of singing activity in mated males during the egg-laying period (Fig. 3A). However, the interaction between mating status and breeding cycle was not significant at dusk ( $F = 0.78$ , df = 3 and 72,  $P = 0.51$ ).

*Nocturnal song.*—Mated males sang nocturnal song before pairing and partly during the egg-laying and incubation period; bachelors sang nocturnal song throughout the season. Of 13 mated males, 1 male was never heard singing at night. Twelve mated males sang nocturnal song during a total of 5 to 27 nights ( $\bar{x} \pm SD = 11 \pm 7$ ). Of those 12 males, 11 males sang before pairing during 2 to 14 nights ( $\bar{x} \pm SD = 8 \pm 3$ ). All males stopped nocturnal song upon pairing, but one mated male stopped singing for only two nights and then continued to sing until the fourth day of the incubation period. Additionally, six mated males resumed nocturnal song during the egg-laying period for two to six nights ( $\bar{x} \pm SD = 4 \pm 1$ ), starting in the night before the first egg was laid, or one or two nights later (each  $n = 2$ ). Of those six males, four males continued to sing during the incubation period for two to seven nights ( $\bar{x} \pm SD = 4 \pm 2$ ). One mated male resumed nocturnal song during the nestling period after its mate had left the territory following depredation of the brood. All 13 bachelors sang nocturnal song throughout the season for a period of 31 to 48 days ( $\bar{x} \pm SD = 40 \pm 5$ ).

#### DISCUSSION

Male Nightingales sang most at dawn and sang least in the afternoon, whereas they sang at an intermediate level in the morning and at dusk. In unmated males, that pattern was consistent throughout the breeding season. In mated males, however, the diel patterns of singing activity varied between periods of the breeding cycle.

The difference in singing patterns between mated and unmated males suggests that singing activity in mated males was influenced by the reproductive state of the females. That influence on singing activity was strong in the morning and at dusk. In contrast, the singing activity of mated males at dawn and in the afternoon appeared to be less influenced by the reproductive state of females. Although mated males sang less at dawn than bachelors, they still

maintained high singing activity at dawn until the end of the nestling period. Those results are in line with studies on the Collared Flycatcher (*Ficedula albicollis*; Pärt 1991), on the Chiffchaff (*Phylloscopus collybita*; Rodrigues 1996), and on wood-warblers (Staicer et al. 1996). In those species, singing activity at dawn remained high until late stages of the breeding cycle or was not affected by mating status. Such findings support the idea that singing during the dawn chorus is important to defend the territory against rival males or to adjust social relationships among territorial neighbors (Staicer et al. 1996). If dawn singing would mainly serve to attract a mate, it should be confined to unmated males; if dawn singing would mainly serve to guard or stimulate a fertile mate, it should peak during the pre-laying or laying period in mated males.

In the morning, about the hour of egg-laying, mated males showed low singing activity in the pre-laying and incubation periods but showed high singing activity when the females actually were laying eggs. At that time of day, the seasonal pattern was significantly different in bachelors, which continuously increased their singing activity until the end of the incubation period. Also at dusk, the singing activity of mated males was elevated during the laying period in comparison to the pre-laying and incubation periods. It appears that in mated males the patterns in the morning and at dusk are largely responsible for the overall peak of singing activity during the laying period and during the first days of incubation. For the same time period, half of the mated males also resumed nocturnal singing that they had stopped after pairing, which confirms our previous findings (Amrhein et al. 2002). The elevated singing activity during the laying period could serve to encourage the female to increase the investment in the brood according to male quality (Sheldon 2000, Amrhein et al. 2002). Furthermore, high singing activity during egg-laying may serve to protect paternity, either through repelling rival males or through stimulating the female to solicit copulations (Pinxten and Eens 1998). However, as Birkhead et al. (1996) have pointed out, copulations around the hour of egg-laying are not very likely to result in fertilization, making it rarely worthwhile for pair members to copulate or for males to guard the female in the morning during the laying period. Alternatively, mated males may sing more during egg-laying because

in the pre-laying and incubation periods they are engaged in other activities that conflict with singing. If in Nightingales, as in many other bird species, pair members stop copulating once egg-laying has started (Birkhead and Møller 1993), the male may be less closely associated to the female during egg-laying then before and thus have more time to sing. It should be possible to address these functional issues by investigating how males sing depending on the proximity to the female. In the present study, the day-by-day analysis showed that singing activity of mated males was particularly low during the three days before the first egg was laid. If we assume that this time period is when females reach peak fertility, our results may add to the evidence that singing activity is not important as a paternity guard (Sheldon 1994, Gil et al. 1999).

Our study shows that seasonal patterns of singing activity can differ between hours of the day. In mated male Nightingales, we found high singing activity at dawn until late stages of the breeding cycle; but in the morning and at dusk, the singing activity was elevated only when females were laying eggs. To address the functions of those singing patterns, subsequent studies are needed that investigate to whom song is directed at which time of season and day. Nevertheless, it appears that the social context influences singing behavior to a varying degree across the season, and that this variation also depends on time of day. The hour of data collection thus is an important factor when seasonal changes of singing activity are studied.

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