

Temporal patterns of territory settlement and detectability in mated and unmated Nightingales *Luscinia megarhynchos*

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In many bird species the sex ratio of adults is male-biased, which is likely to have consequences for the ecology as well as for the conservation of a species. For example, when some males remain unpaired in a population, there should be strong selection on behavioural traits that enhance pairing success. A surplus of males is also likely to have important implications for the interpretation of breeding bird survey data. In our study population of Nightingales *Luscinia megarhynchos*, about half of the males stayed unpaired, suggesting that the number of males encountered singing was greater than the number of breeding pairs. Furthermore, the detectability (the probability of encountering a male singing) of mated males was only two-thirds that of unmated males when censused in the morning or late in the breeding season. The relative detectability was more similar early in the season and during the twilight periods before sunrise and after sunset. Males that arrived earlier on the breeding grounds were more successful in attracting a mate than males arriving later. Some of the unmated males deserted their territories and prospected areas up to 4000 m distant, whereas others settled on the study site only late in the season and may actually have changed territories. We suggest that adult sex ratios and the time of the census should be taken into account when interpreting the results of breeding bird surveys.

In many bird species, there appears to be a male-biased adult sex ratio (Breitwisch 1989). Because social monogamy is the prevailing mating system in about 90% of bird species (Black 1996), a male-biased adult sex ratio often means that many males stay unpaired in a given breeding season. A surplus of males can thus cause substantial variance in male reproductive success, and selection should strongly act on any trait that can increase pairing success (Hill *et al.* 1994). For example, in migratory species, males that arrive on the breeding grounds earlier usually have a greater chance of attracting a mate (Alatalo *et al.* 1984, Potti & Montalvo 1991, Lozano *et al.* 1996, Currie *et al.* 2000). Females should benefit by choosing early arriving males, as early arrival can be costly and indicate a male's quality or the quality of its territory (Møller 1994, Kokko 1999, Forstmeier 2002, Kipper *et al.* 2006).

In several species, unmated males hold territories during at least part of the breeding season (Breitwisch 1989, Hogstad 1999, Amrhein *et al.* 2004a). These bachelors may increase their future pairing success by deserting their territories at some time during the breeding season, to prospect for better territories that they could occupy early the following year (Lawn 1994, Forstmeier 2002, Doligez *et al.* 2004).

The fact that unmated males often occupy and defend territories also has profound consequences for population monitoring and conservation, because, with a male-biased adult sex ratio, the number of singing males recorded cannot readily be equated to the number of breeding pairs (Newson *et al.* 2005). Furthermore, detectability (the probability of detection, e.g. during a bird survey) is often higher for unmated males, which may sing much more than mated males (Breitwisch & Whitesides 1987, Gibbs & Wenny 1993). Indeed, after pairing, the males of some species stop singing completely or during particular times of the day, so that surveys of singing birds may be monitoring

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bachelor males rather than the actual breeding population size (Wilson & Bart 1985, Amrhein *et al.* 2002).

Furthermore, it is well documented that time of season or time of day can substantially influence singing activity and, thus, the results of breeding bird censuses that are based on the detection of singing males (Shields 1977, Best & Petersen 1982, Kessler & Milne 1982, Verner & Ritter 1986, Calladine *et al.* 1999, Selmi & Boulinier 2003, Betts *et al.* 2005). Moreover, seasonal and daily patterns of singing activity can differ between bachelors and mated males, even if singing activities are similar in both groups when summed over several hours of the day and periods of the breeding cycle (Hayes *et al.* 1986, Amrhein *et al.* 2004b).

Here, we present results of daily censuses of singing activity in a population of Nightingales *Luscinia megarhynchos*, in which up to 49% of males may remain unmated in a given breeding season (Amrhein & Zwygart 2004, Amrhein *et al.* 2004a). Earlier work has revealed that seasonal patterns of singing activity vary with time of day and mating status (Amrhein *et al.* 2002, 2004b). Those studies assessed the biological function of changing singing patterns and therefore examined singing activity with respect to the stages of the breeding cycle of individual pairs. During a breeding bird survey, however, the individuals in a bird population usually differ in breeding status, and the exact stage of breeding cycle may not be known in most cases. In this study, we assess singing activity as continuously measured throughout the breeding season, without reference to the breeding stages of individuals. We also present more detailed information on the daily pattern of singing activity than has been previously done. Furthermore, we investigate how patterns of territory settlement and desertion relate to mating status in male Nightingales.

METHODS

General

The study was conducted from 4 April to 1 June 2004 at the Petite Camargue Alsacienne in France, 10 km north of Basel, Switzerland. This area is situated within the Upper Rhine Valley where, in an area of about 18 km² around the Petite Camargue Alsacienne, we estimated in 2003 a population size of up to 240 singing males, half of which were unpaired (Amrhein & Zwygart 2004). In 2004, there were 37 male Nightingale territories in our 1-km²

study site. Territory boundaries were delineated by recording the song posts of males on a detailed map (1 : 2000) on one diurnal and one nocturnal round of inspection per day throughout the field season (see below). In 20 territories, the identity and mating status of males were ascertained by capturing and ringing the male and, if present, its mate. Mist-netting sessions were distributed throughout the field season and were undertaken in the mornings until both members of a pair were captured or until we were sure that no female was present in a male's territory. Mist-nets were usually opened before sunrise and stayed open for about 2 h; birds were ringed in their territory and released within 15 min of capture. Yearling Nightingales (i.e. birds that fledged in the previous year) were identified by the light tips and colour differences in their greater secondary coverts and by the sharp tips of the primary coverts (Jenni & Winkler 1994).

Singing activity and settlement data

Throughout the field season, in the daytime, we made one round of inspection per day at varying hours of the day (see below). This followed a fixed route of 5600 m, and the direction of the rounds was changed from day to day. The duration of each round was 1.5 h. During each round, a male was recorded as having sung only if it sang during the period of 30 s that started after we arrived at its territory. The number of rounds on which a territory was inspected was the same for all territories. Singing activity of a territorial male is given in Figures 2 and 3 below as the proportion of rounds on which it was heard singing at least one song (Amrhein *et al.* 2002, 2004a, 2004b). This measure of singing activity corresponded to the measure of detectability that was used by Wilson and Bart (1985) and Gibbs and Wenny (1993).

We expected the males to have their daily peak of singing activity shortly before sunrise (Amrhein *et al.* 2004a, 2004b), and, to survey territory settlement, we therefore made daily rounds before sunrise until about two-thirds of the number of Nightingales we had counted in the past years had arrived. On 27 April, when 23 males had settled, we started to collect singing activity data and to vary the hours of the daily rounds. The first singing activity round was made before sunrise, but on the succeeding days we shifted the hours of data collection by 2 h per day, so that we had covered all hours of twilight and daylight (04:00–22:00 h) over a period of 9 days. After that period, the cycle started again with a

dawn round, and this was repeated four times in total. During the day, between 06:00 and 20:00 h, the rounds started on the hour, but at dawn and dusk the starting times of the rounds were adjusted so that the dawn round ended at sunrise and the dusk round started at sunset.

Additionally, we made a nocturnal round each night between 00:00 and 02:00 h, starting on 14 April. This round was mainly made to determine the mating status of our subjects, because it is usually only unmated males that sing regularly at night for a prolonged period (Amrhein *et al.* 2002, 2004b). In the two earlier studies, we found that 13 of 15 mated males (Amrhein *et al.* 2002) and seven of 13 mated males (Amrhein *et al.* 2004b) resumed nocturnal song during the egg-laying period for about three or four nights on average, and a few mated males also continued to sing during the first nights of incubation, which potentially could confound the evaluation of mating status by means of nocturnal rounds. However, in the present study, we made nocturnal rounds every night during the entire field season, so that we could clearly distinguish between mated males resuming nocturnal song for a short time period early in the season and bachelors that sing during an average of 40 consecutive nights until late in the breeding season (Amrhein *et al.* 2002, 2004b).

The settlement date for males was defined as the day when a male was heard singing for the first time, at night or during the day. The settlement date for females was defined as the day a male stopped nocturnal song, as males usually stop singing at night upon pairing (Amrhein *et al.* 2002, 2004b); for three females, however, we could not deduce the arrival date because their mates were never heard singing during the nocturnal rounds early in the breeding season ($n = 2$) or continued nocturnal song for some days after a female was seen in the territory ($n = 1$).

In some cases, a bachelor deserted its territory before the end of the field season, which was clearly indicated by an early cessation of nocturnal and diurnal song (bachelors usually sing at night and during the day until late in the season; Amrhein *et al.* 2002, 2004b). The day of territory desertion was defined as the day after we heard the bachelor singing for the last time. Furthermore, two of the initially territorial bachelors were caught in other occupied territories at the study site, and those two prospecting males were equipped with a radio-transmitter that was glued to their back feathers, to see where they would range or settle in other territories. Radiotelemetry methods are given in Amrhein *et al.* (2004a).

Statistics

All sample sizes refer to the number of individuals. All tests are two-tailed; descriptive statistics in the text are given as mean \pm sd. Data analysis was undertaken using R 2.2.0 (R Development Core Team 2005). To account for the repeated sampling of the same individuals and, thus, the non-independence of data points, we used a mixed-effects model with individual subject fitted as a random factor (Crawley 2002). Our response variable 'singing activity' was binary (a bird either did sing or did not sing), and to account for the binomial error distribution we fitted a generalized linear mixed model, using the `glmmPQL` function in R. Mating status was included as a fixed factor, time of season was included as an ordered fixed factor, and time of day was included as a covariate. To test for a possible curvilinear pattern in the diurnally changing singing activity, we additionally fitted the quadratic term (time of day)² to the model; from the maximal model, we then removed non-significant interaction terms (Crawley 2002, Engqvist 2005). In the figures, we give the mean values of singing activity with bootstrapped 95% confidence intervals (10 000 iterations; Crawley 2002).

RESULTS

Territory settlement

Of the 37 Nightingale territories that were occupied at our study site, 17 (= 46%) were occupied by males that remained unmated until the end of the season. For the following analyses, we excluded three territories of mated males that were further from our rounds and could not be reliably surveyed on a daily basis, so that the overall sample size is $n = 34$ territories, half of which were occupied by unmated males.

The first three males settled in a territory on 5 April (Fig. 1). After a period of 9 days without further male arrivals, the bulk of males then settled between 15 April and 3 May. The females settled between 21 April and 3 May ($n = 14$, mean \pm sd = 26 April \pm 4 days), and first-egg dates were between 30 April and 9 May ($n = 5$ females observed).

The pairing success of males was correlated with settlement date. The 17 males that mated had settled earlier (18 April \pm 7 days) than the 13 males that arrived before the last female settled but did not attract a mate (23 April \pm 7 days, Wilcoxon rank sum

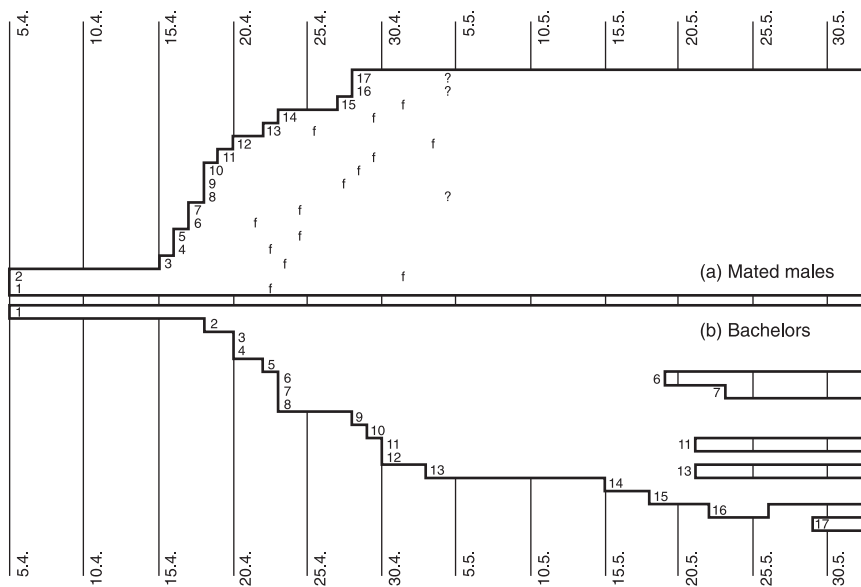


Figure 1. Settlement patterns of (a) mated male Nightingales ($n = 17$) and (b) bachelors ($n = 17$). The dates of territory settlement and desertion are given in a daily sequence from left to right, so that the areas enclosed by the thick lines represent the number of males residing in territories at the study site. The mated males and bachelors are numbered in the order of their settlement date. For example, bachelor no. 7 was heard singing in its territory for the first time on 23 April and was heard there for the last time on 22 May. For $n = 14$ females, an 'f' indicates the settlement date in a territory of a mated male; a question mark signifies that female settlement date was unknown.

test, $W = 51.5$, $P = 0.01$; Fig. 1). These 13 bachelors settled at about the same time as the 14 females (Wilcoxon rank sum test, $W = 66.5$, $P = 0.24$). Four additional bachelors settled in a territory later during the breeding season ($21 \text{ May} \pm 6 \text{ days}$), i.e. 12–26 days after the last female arrived.

Among the 13 early arriving bachelors, four males deserted their territories on $21 \text{ May} \pm 2 \text{ days}$, after being present for 18–30 days (Fig. 1). Two of those floating males were radiotagged, and their position was checked on a number of occasions. One was re-located 3 days after deserting its territory, around 4000 m from its original territory, and on the fourth day it was found to prospect several territories in the neighbourhood of its original territory. The second radiotagged bachelor was located each day between the fifth and eighth days after territory desertion, each time in the same area 1500 m from its original territory.

For 17 males that were captured, their approximate age was determined. The six first-year birds arrived later ($25 \text{ April} \pm 11 \text{ days}$) than the 11 males that were older than 1 year ($18 \text{ April} \pm 6 \text{ days}$); however, this difference was not statistically significant (Wilcoxon rank sum test, $W = 19.5$, $P = 0.19$).

Singing activity

For the analysis of diurnal singing activity, we excluded four late arriving bachelors (see above), so that the sample size was $n = 30$ males (17 mated males and 13 bachelors).

Visits to occupied territories were made on 1015 occasions during the day, and singing was recorded on 494 occasions, i.e. in 49% of cases. Across the entire breeding season and all hours of daylight, the average probability of encountering a male Nightingale singing during an observation period of 30 s was thus around 0.5 (Fig. 2). From the maximal generalized linear mixed model, we removed the non-significant three-way interaction (mating status: time of day: time of season; $P = 0.50$) and a non-significant two-way interaction (time of day: time of season; $P = 0.41$).

The final model suggested large differences in singing activity among the nine daily time periods (time-of-day squared: $F_{1,976} = 29.87$, $P < 0.0001$; Fig. 3), with the highest singing activity in the morning and particularly during the 1.5 h before sunrise. The significance of the quadratic term further indicated a non-linear relationship between singing activity and time of day: After the morning peak, singing activity

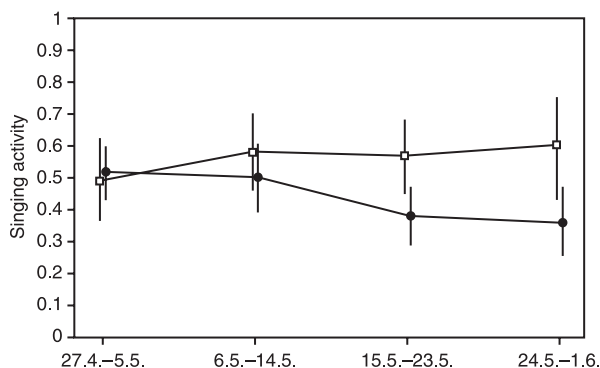


Figure 2. Mean (and bootstrapped 95% confidence interval) singing activity of male Nightingales during four time periods in the breeding season, based on nine rounds of 1.5 h duration conducted on the study site per period (one round each day). Singing activity of a male is expressed as the proportion of rounds per period on which it was heard singing. Filled circles are $n = 17$ mated males, and open squares are $n = 13$ bachelors (for the last period: $n = 9$ bachelors).

decreased until noon and slightly increased again in the evening.

The interaction between mating status and time of day ($F_{1,976} = 9.46$, $P = 0.002$) indicated that the daily patterns of singing activity and, thus, detectability, differed between mated and unmated males. Bachelors sang more than mated males in the morning hours, but in the afternoon both groups showed similar singing activity (Fig. 3). The detectability of a mated male during the two census periods between 08:00 and 12:00 h was about two-thirds that of a bachelor (Fig. 3).

The interaction between mating status and time of season ($F_{3,976} = 3.49$, $P = 0.015$) indicated that the seasonal patterns of singing activity differed between mated males and bachelors. Whereas mated males seemed to sing less as the season progressed, the singing activity of bachelors remained constant or increased slightly until late in the season (Fig. 2). The detectability of a mated male during the last 9 days of the field season was about two-thirds that of a bachelor (Fig. 2).

DISCUSSION

In our study population of Nightingales, about half the males remained unmated throughout the breeding season. Although all males were territorial for at least part of the breeding season, the temporal patterns of territory settlement differed between mated and unmated males.

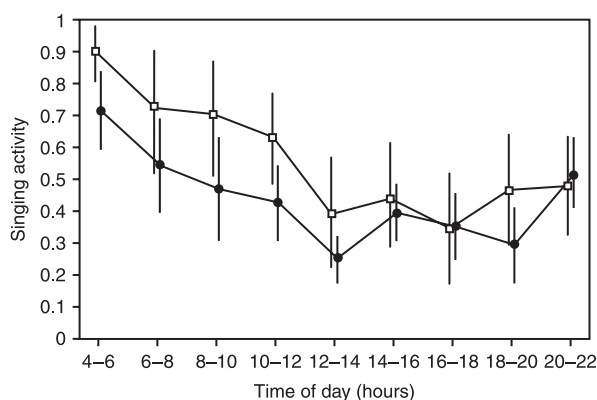


Figure 3. Mean (and bootstrapped 95% confidence interval) singing activity of male Nightingales at nine times of the day, based on four rounds of 1.5 h duration conducted per time of the day (rounds were conducted in four different time periods of the season). Filled circles are $n = 17$ mated males, and open squares are $n = 13$ bachelors.

The males that subsequently attracted a mate settled earlier than those that stayed unpaired. For this correlation, males that arrived after the last female settled were excluded, so the results indicate that many males remained unpaired despite arriving no later than the females. Rather, females may have actively chosen males that arrived early. A correlation between male arrival date and mating success has also been found in other species. Studies on the facultatively polygynous Pied Flycatcher *Ficedula hypoleuca* found that earlier arriving males attracted more females or paired earlier than later arriving males (Alatalo *et al.* 1984, Dale & Slagsvold 1990, Potti & Montalvo 1991). Four studies on songbirds in which the overall proportions of males that stayed unpaired ranged from 20% to 30% found that, as with the Nightingale, socially monogamous females seem to pair preferentially with early arriving males (Landmann & Kollinsky 1995, Aebischer *et al.* 1996, Lozano *et al.* 1996, Currie *et al.* 2000). There are several mutually non-exclusive hypotheses about the benefits of such a female preference. Early arriving males may be of better quality than later arriving males. For example, early arriving males may be older, larger or in better condition than late arriving males, and an early arrival date may indicate that a male is able to cope with costs such as low food abundance and poor weather conditions early in the breeding season (Francis & Cooke 1986, Møller 1994, Lozano *et al.* 1996, Potti 1998, Kokko 1999, Smith & Moore 2005). Kipper *et al.* (2006) found that, within the

same age class, earlier arriving male Nightingales tended to have larger song repertoires and to have longer wings and be heavier; thus, the higher pairing success of early arriving male Nightingales may correlate with their quality. Alternatively, females may choose territory characteristics rather than male quality, which also could favour early arriving males, because they often occupy the best territories (Alatalo *et al.* 1984, Aebischer *et al.* 1996, Currie *et al.* 2000, Forstmeier 2002, Smith & Moore 2005). Whatever the cause, in a polygynous mating system or a population with male-biased adult sex ratio, current evidence suggests strong selection on the arrival date of male songbirds.

Changes in detectability are likely to have implications for bird monitoring projects; an adult sex ratio of two males per female would mean that the number of reproductive pairs is only half as large as the number of singing males. However, bird census results are probably also confounded by the different temporal pattern of singing activity in mated and unmated males: a diurnal Nightingale census undertaken in the morning or late in the breeding season, when mated males are less easily detected than bachelors, would have a bias towards detecting unmated males. When the number of unmated males is then deduced by counting the males that also sing regularly at night (Amrhein & Zwygart 2004), the proportion of bachelors is likely to be overestimated, as mated males, which usually sing only during the day (Amrhein *et al.* 2002, 2004b), are then more easily overlooked. The detectability of male Nightingales was less biased towards bachelors during the days just around or shortly after the arrival of females, and during the hour before sunrise or after sunset. In several bird species, singing activity at dawn also seems to vary less in the course of the breeding season than singing during the daylight hours (Amrhein *et al.* 2004b, Kunc *et al.* 2005). Similar to our results, Hayes *et al.* (1986) found that unmated Kirtland's Warblers *Dendroica kirtlandii* sang at a higher rate than mated males in the morning, but that this difference became less pronounced later in the day. It is also important to note that the difference in detectability between mated and unmated birds seems to diminish the longer a territory is observed. In the Ovenbird *Seiurus aurocapillus*, the detectability of mated males was about one-third that of bachelors during a listening interval of 1 min, but when a territory was observed for 10 min, this proportion more than doubled (Gibbs & Wenny 1993).

In practice, because many observers usually walk through their study site rather slowly, the problem of different detectability of mated and unmated male Nightingales may tend to diminish. For breeding bird surveys in general, however, it seems advisable to take biased sex ratios into account (Newson *et al.* 2005). It may be common across many species for up to 50% of males to be unmated, but that proportion is likely to vary spatially and temporally and between species (Breitwisch 1989, Hill *et al.* 1994, Lozano *et al.* 1996, Currie *et al.* 2000). Studies that do not attempt to estimate sex ratio might incorrectly identify the relative importance of different populations, and will often overestimate them. Paradoxically, if a songbird population in which 50% of males are unpaired is censused at dawn or early in the breeding season, the census results might reflect the actual breeding population size less reliably than when censused at other times. For example, if at dawn all mated and unmated males are encountered singing, the estimated population size would be twice as large as the number of breeding pairs. Were the same hypothetical population to be censused at a time when only the unmated males sing, half of the males would be missed, but the census result would better reflect the number of breeding pairs present. However, when only a small proportion of males are unmated and these sing much more than mated males, this could also result in an underestimation of the effective population size. Therefore, for reliable population estimates, not only the sex ratio but also the relative detectability of the males must be taken into account.

Although unmated Nightingales are usually territorial, their settlement patterns are much more dynamic than those of mated males. Unmated males that settled very late in the season presumably had not just arrived from migration but had changed territories (cf. Lawn 1994). Including such territories in bird surveys can thus lead to further overestimation of the population size. In our study, several bachelor Nightingales left their territories late in the season, and, as in other studies of songbird species (Shutler & Weatherhead 1994, Tobler & Smith 2004), radio-telemetry showed that such floaters can range widely. Furthermore, failed breeders or young birds have been shown to prospect the area late in the season in other species (Boulinier *et al.* 1996). In the Nightingale, such prospecting could occur at the end of the breeding season because this is an optimal time to gather information on the reproductive success of conspecifics in other territories (Boulinier

et al. 1996, Doligez *et al.* 2004). However, bachelors could also stay in their territories simply as long as there is a chance to attract a late arriving female, and then desert the territory only late in the season. Regardless, floaters may temporarily occupy new territories to enhance their chances of establishing a good territory in the following year (Lawn 1994, Hogstad 1999, Forstmeier 2002), and can thus be a territorial threat to residents late in the season (Amrhein *et al.* 2004a). As predicted by Verner (1992), the dynamics of the floater segment of a bird population appear to be of interest for conservation biology as well as for our understanding of avian ecology.

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