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# DAWN AND DUSK SINGING OF MALE AMERICAN ROBINS IN RELATION TO FEMALE BEHAVIOR

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ABSTRACT.—It has been assumed that females are particularly fertile during the first hour after laying when the next egg to be laid is fertilized. In many passerine birds, egg laying occurs early in the morning. Hence, it may be particularly important for males to sing at dawn to attract the mate and other females and to repel potential cuckolders. I studied song activity of mated male American Robins (*Turdus migratorius*). Egg laying occurred close to noon. However, males had a peak song activity at dawn but sang little around noon. Hence, the idea that mated males sing primarily to deter other males just before the 'fertilization window' was not supported. Male song activity tended to increase when the mate visited the nest during the day but less so when she entered the nest to roost at night. Synchronous emergence of all females at dawn resulted in synchronous termination of the dawn chorus, whereas a more asynchronous pattern of nest visits by females during the day and in the evening resulted in asynchronous and scattered periods of song. *Received 21 Nov, 1995, accepted 22 Feb. 1996.*

In the breeding season, passerine birds typically have a peak song activity at dawn and dusk (Armstrong 1973) and, in addition, egg laying often occurs early in the morning. Females may be particularly fertile during the first hour after laying, when the next egg to be laid is fertilized (Birkhead and Møller 1991). Hence, males may be singing at dawn to attract the mate and other females and to repel potential cuckolders (Mace 1986, 1987a; Cuthill and MacDonald 1990; Møller 1991). Such behavior has been reported in two hole nesting species, the Great Tit (*Parus major*; Mace 1986, 1987a, b) and the Willow Tit (*P. montanus*; Welling et al. 1995), although alternative explanations for dawn singing in these species also exist (see Slagsvold et al. 1994). I examined the possible relationship between song activity of male American Robins (*Turdus migratorius*) and female roosting behavior at dawn and dusk and female nest visiting behavior near the time of egg laying. Robins are interesting for several reasons. Egg laying does not occur at dawn but takes place in the middle of the day (Weatherhead et al. 1991, Scott 1993). Males guard their mates when fertile, suggesting that extra-pair copulations (EPCs) occur (Gowaty and Plissner 1987). I discuss how the results may help understand differences between species in daily variation of male song activity.

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## METHODS

The study was conducted during 13–28 April 1994, in a mixed deciduous-coniferous woodland in St. Edward State Park near Seattle, Washington. The territories of 12 mated males were visited 20–70 min before the males started singing at dawn. In 10 cases, observations continued until noon. Observations were also made at 10 territories from 18:30 h until dark. Male song was recorded from a distance of 20–60 m, and one or two males were observed during each visit. Song activity was expressed as the percentage of minutes in which the male was heard singing (one or more times) of the total number of minutes of observation. Males were not banded but were identified by their proximity to the nests and to the females, their movements, song posts, and roosting sites.

Female robins may spend the night on the nest during the egg-laying period (Brackbill 1985, Slagsvold unpublished data). Video was used to record female presence on the nest, except at dawn when it was too dark. At dawn, the camera was not placed near the focal nest until the female had left. A Sony Handycam (CCD-TR805E) on a tripod was placed 3–8 m from the nest and pointed towards it. Female departure from the nest at dawn was observed in seven cases using 10× binoculars. In addition, the time of first appearance at the nest at dawn was recorded for another female that did not roost in the nest. Hence, I was able to examine the possible relationship between song activity and female emergence time for eight males. Three females were in the egg-laying period, four laid the final egg on the day of observation, and one was two days after termination of laying. Relative to the time of civil twilight, time of female emergence was not related to stage of breeding or date of observation (data not shown), and so the data were pooled. Civil twilight and sunrise and sunset times were for Seattle (Federal Office Building, Pacific Standard time, adjusted by one hour to represent summer time; "Climatology of the United States," no. 40–45, Washington, D.C., 1961).

The approximate time of egg laying was recorded by inspecting nests at variable hours of the day when the female was absent, and also by analyzing at which times the female was on and off according to the videofilms. Day 1 is defined as the day when the first egg was laid. Mean clutch size was 3.2 eggs (range 3–4, N = 9). Observations of dawn and dusk singing were carried out from Day −4 to Day 5. One nest was lost before egg laying had begun, so the precise stage of breeding was unknown.

## RESULTS

In the morning, females left the nest/roost between 05:35–05:57 h ($\bar{x}$ = 05:50 ± 8 min [SD], N = 8), which was 9–19 min ($\bar{x}$ = 13 ± 3, N = 8) after civil twilight and 16–25 min ($\bar{x}$ = 21 ± 3, N = 8) before sunrise. After emergence, females were seen feeding on the ground. Those that had finished egg laying, or that laid the final egg later that morning, entered the nest to incubate earlier after sunrise ($\bar{x}$ = 3 ± 5 min, N = 3) than those that were still in the laying period ($\bar{x}$ = 142 ± 114, N = 4; $z = -2.31$, $P = 0.021$, *U*-test). The females spent 10–60 min ($\bar{x}$ = 31 ± 20, N = 6) on the nest on their first visit, followed by a period off of 10–105 min ($\bar{x}$ = 34 ± 34, N = 7) before a new period on. Hence, the synchronous behavior of the females at dawn, as measured by their emergence times, soon disappeared.

In the evening, females entered the nest to roost between 19:30–20:20

h ($\bar{x}$ = 20:01 ± 17 min, N = 8), which ranged from 33 before to 13 min after sunset ($\bar{x}$ = 4 ± 17, N = 8) and 20–67 min before civil twilight ($\bar{x}$ = 37 ± 17, N = 8). Variation among females was significantly greater for evening roosting times than for dawn emergence times, when considered relative to the times of sunset and sunrise, respectively ($F$ = 32.9, df = 7,7, $P < 0.001$, Variance ratio test). Before entering the nest to roost at night, the females spent 10–38 min off ($\bar{x}$ = 18 ± 10, N = 7). Before this last period off, they had spent 10–48 min ($\bar{x}$ = 26 ± 15, N = 7) on the nest.

Assuming that laying occurred halfway between two nest inspections (Weatherhead et al. 1991), and using the median value for each female in case of observations of more than one egg laid (1–3 eggs per female), the median time of laying was 11:50 h (range 10:43–15:13, N = 9; $\bar{x}$ = 12:32 ± 88 min, if using mean of mean values). Including only cases when the interval between two nest inspections was less than 5 h, the median was 11:25 h (range 10:43–12:39, N = 6; $\bar{x}$ = 11:30 ± 42 min, if using mean of mean values). Using a similar method, an average laying time of 11:32 EDT was found in eastern Ontario, Canada (Weatherhead et al. 1991).

One copulation was observed. It occurred on the ground 8 m from the nest at 06:05 h on 18 April, 10 min after the female left the nest. Between 09:04 and 12:00 h on the same day, the female laid the third egg of a clutch of four. At another nest, a male tried to copulate with a female when she was sitting on the nest rim (at 08:23 h; recorded on video), but she moved away. Between 11:12 and 12:05 h on the same day, she laid the second egg of a clutch of three.

A peak in song activity occurred at dawn, with little singing thereafter (Fig. 1). One male did not sing at all at dawn before the female left the nest. Excluding this male, males started singing from 42 min before to 7 min after civil twilight ($\bar{x}$ = 12 ± 17 min before civil twilight, N = 11), or 5–56 min ($\bar{x}$ = 24 ± 21, N = 8) before the mate left the nest. Relative to the time of civil twilight, onset of dawn singing was not related to stage of breeding (Spearman, $r_s = -0.16$, $P = 0.62$, N = 11; stage of breeding measured as the number of days elapsing until the day of the final egg laid; data ranging from five days before this date to two days after). Because some males did not start singing until soon before female emergence, song activity did not peak until just before the female left the nest (Fig. 2). Song activity was low after female emergence (Fig. 2). Comparing a 10 min period before and after female emergence, song activity dropped for seven of eight males (no difference in one case; $z = -2.39$, $P = 0.017$, N = 7, Wilcoxon matched pairs test). When males started singing, the approximate mean distance between the nest and the

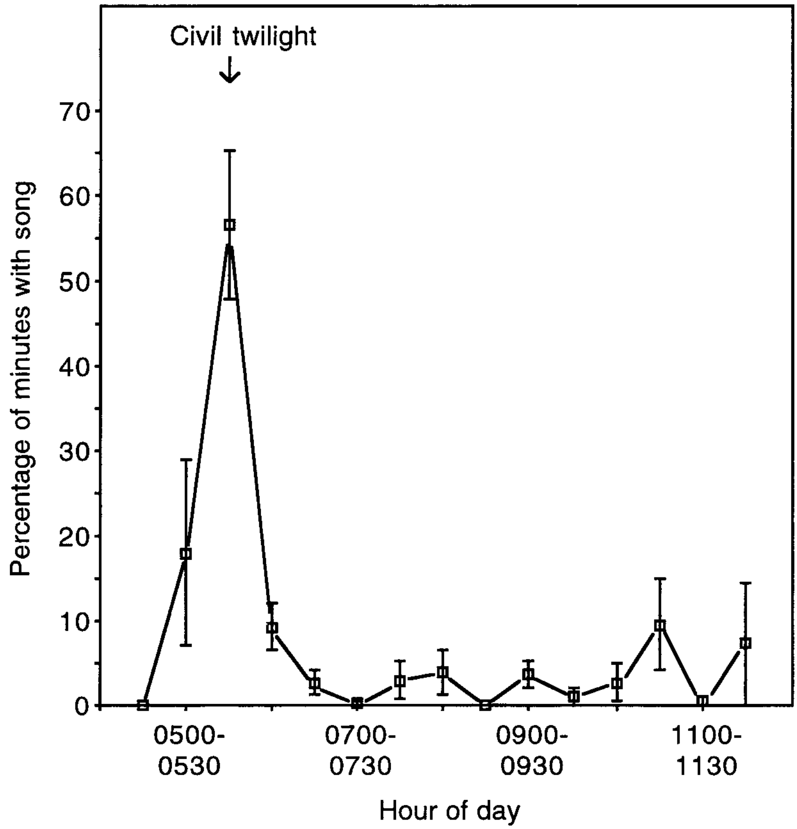

FIG. 1. Mean (±SE) song activity of ten male American Robins, calculated for consecutive 30-min periods from dawn to noon.

perch (distance along the ground) was 33 m (SD = 9, range 20–50, N = 11). Distance was not related to stage of breeding ($r_s$ = 0.03, $P$ = 0.92, N = 11). No males were seen flying to a nest before female emergence. However, later in the day (between 06:57–19:29 h), at least six males visited the nest without the females being present, and two males visited the nest to feed the mate.

Song activity was low between dawn and noon (Fig. 1) despite the fact that most eggs were laid around noon. I compared the data from all periods when the female was on the nest (1–6 periods combined for each male, $\bar{x}$ = 119 min of observation) with the data from all periods when the female was off the nest (1–7 periods combined for each male, $\bar{x}$ = 136 min of observation). Males (N = 9) were observed singing during

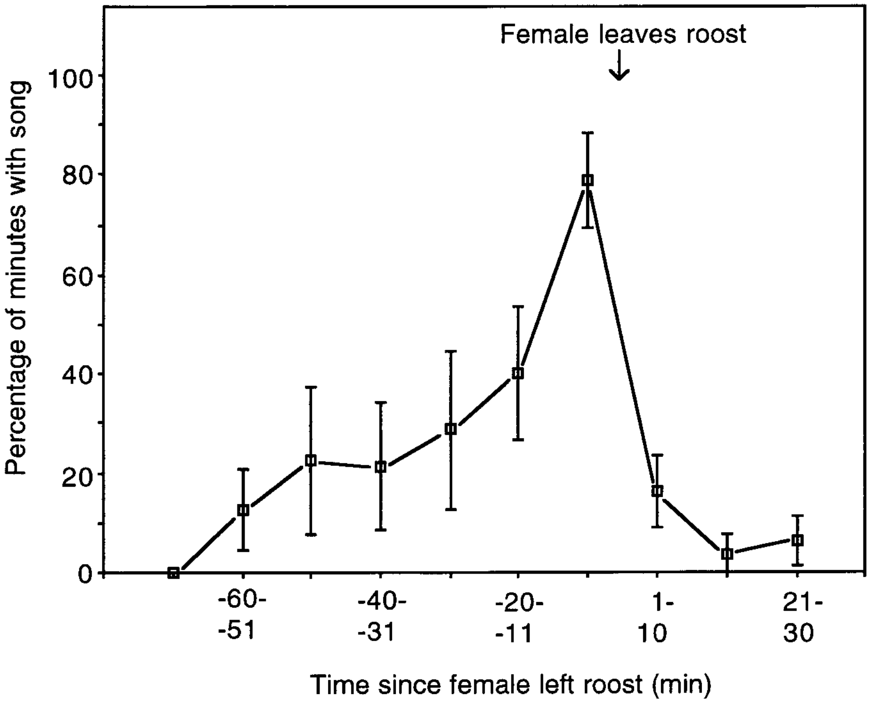

FIG. 2. Mean (+SE) song activity of eight male American Robins, calculated for consecutive 10-min periods before and after the female left her night roost at dawn.

0–17% ($\bar{x}$ = 5 ± 6) of the minutes when a mate was on the nest, and 0–4% ($\bar{x}$ = 1 ± 2) when she was off the nest. The difference was nearly significant ($z = -1.86$, N = 7, $P = 0.063$, Wilcoxon matched pairs test; two males did not sing at all).

Song activity of mated males was low in the evening (Fig. 3). After 18:30 h, three of the ten males included in Fig. 3 did not sing at all. The other seven males had only one or two periods of song during that period (separated by at least 10 min without song). The periods of singing lasted only 1–9 min ($\bar{x}$ = 4 ± 3, N = 7). When the female entered the nest to roost at night, two of seven males immediately started singing for eight and nine minutes, respectively. These were the longest song periods recorded of any mated male in the evening. The seven males that did sing after 1830 h stopped singing from 84 min before to 20 min after sunset ($\bar{x}$ = 21 ± 35 min before sunset) and 17 to 117 min before civil twilight ($\bar{x}$ = 54 ± 35).

Male (N = 7) song activity was recorded after 18:30 h and before the

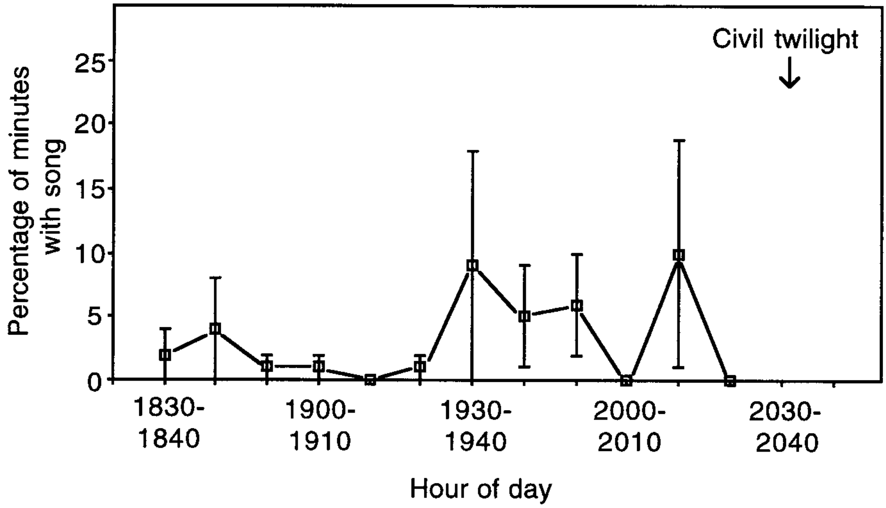

FIG. 3. Mean (+SE) song activity of ten male American Robins, calculated for consecutive 10-min periods in the evening.

final roosting time of the mate when the female was on the nest (1–3 periods combined per female, $\bar{x}$ = 36 min of observation) and when off the nest (1–3 periods combined per female, $\bar{x}$ = 51 min of observation). Song activity (percentage of minutes with male heard singing) was low in both cases (female on the nest: $\bar{x}$ = 1.1 ± 1.9; female off the nest: $\bar{x}$ = 0.6 ± 1.7; $z = -0.45$, $P = 0.65$, Wilcoxon matched pairs test).

## DISCUSSION

Two important results were found. First, mated male robins exhibited peak song activity at dawn but sang little around the time of egg laying at noon. Hence, the hypothesis that mated males sing primarily to deter other males just before the "fertilization window" (Mace 1987a) was not supported. Second, song activity appeared to be influenced by female roosting behavior. Singing rates declined when the female left the night roost.

The principal function of dawn singing in mated male robins seems to have something to do with the female's being on the nest. Why should males be singing then? Dawn song may have several functions (see review in Slagsvold et al. 1994): (1) serve as pair-bond reinforcement and stimulate hormonally-mediated aspects of breeding in females; (2) tell the mate that she can emerge from the roost and nest without risk of predation and of revealing the location to nest predators; (3) attract the mate for copulation; (4) attract a new mate in case the former mate has disappeared during the night; (5) attract other females for EPCs; (6) deter other males and so avoid that they will try to copulate with the mate; and (7) defend the nest site and the territory. The hypotheses are not mutually exclusive and may work in concert (Mace 1987b, Slagsvold et al. 1994). Further studies are needed to single out the relative importance of each.

The fact that male robins sang little close to the time of egg laying does not exclude the possibility that song is used as a mate guarding tactic. The only copulation seen occurred soon after the female left the roost at dawn, and so dawn singing may be related to this event. Although Weatherhead et al. (1991) suggested that robins lay eggs around noon because this may be a suitable time for copulation, no observations of copulations were reported. Gowaty and Plissner (1987), studying mate guarding in robins in the fertile period, observed copulations at all hours of the morning except for the hour after dawn; no observations were made after noon. However, few copulations were observed, and the authors did not report the actual frequencies. Further studies are needed to see if dawn is the regular time of within-pair copulation in robins as has been observed in some other passerine birds (Mace 1987a, Birkhead and Møller 1991, Davies 1992). In birds, females may actively seek EPCs with males of high quality (e.g., Kempenaers et al. 1992). No information exists on when and where EPCs take place in robins. However, as found in another passerine, the Great Reed Warbler (*Acrocephalus arundinaceus*; Hasselquist et al. 1995), they may prefer extra-pair mates with large song repertoires. In European Starlings (*Sturnus vulgaris*), females would only solicit copulation if the social or extra-pair mate sings (Eens and Pinxten 1990).

My results support those of others (e.g., Mace 1986, 1987a; Cuthill and MacDonald 1990; Pärt 1991; Otter and Ratcliffe 1993; Slagsvold et al. 1994; Welling et al. 1995) that male song activity is influenced by female behavior. Male robins start dawn singing about an hour or less before female emergence, as do male Great Tits, even though female Great Tits leave the roost, on average, 49 min later than female robins when measured relative to civil twilight (Slagsvold et al. 1994). In both species, males may increase song activity if the mate enters the nest during the day and at dusk. Hence, knowledge of factors that influence female roosting behavior may help explain differences in daily variation of male song activity within and between species of passerine birds. For instance, the fact that most of the males within a particular species, like the robin, stop singing more or less at a constant time in relation to light intensity at dawn, may not necessarily be related to a sensitivity of males to light per se but occur because this is the time when their mates leave their respective roosts. When the emergence at dawn of female Great Tits was experimentally delayed, males continued singing for a longer period (Mace 1986).

Female robins left the roost, on average, 13 min after civil twilight, and the variation among females was low (range 9–19 min). At that time of the day, light intensity changes very fast, apparently synchronizing emergence. A more synchronous emergence in female robins than in female Great Tits (see Mace 1987b, Slagsvold et al. 1994) may also be due to the fact that robins do not lay an egg before leaving the night roost in contrast to the tits. Later in the morning, female behavior was more asynchronous, as were egg laying times, resulting in asynchronous periods of singing by males. In some other passerines, egg laying occurs in midmorning and may be more synchronous than in robins, resulting in stronger synchronization of male song activity. In support of this idea, song activity of many passerine birds drops after a peak at dawn but reaches a new but lower peak later in the morning (Klockars 1941, Gyllin 1967, Lomholt 1971). One explanation for the initial drop is that males need to forage after dawn singing (Klockars 1941, Lomholt 1971). However, the drop may also reflect a more synchronous mate guarding by males early than late in the morning.

I conclude that to understand further daily variation in male song activity in passerine birds, more attention should be paid to the role of the females and, hence, on the factors that influence their copulation and roosting behavior. Information is needed concerning female emergence times at dawn and dusk and on the degree of synchronization of these events between females.

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