*The Wilson Journal of Ornithology* 121(4):819–822, 2009

# Paired Male Song Sparrows Sing More When Their Mate is Incubating

Jennifer R. Foote[1,3,4] and Colleen A. Barber[2]

ABSTRACT.—The fertility announcement hypothesis proposes that avian males should sing at a high rate when their mate is fertile to guard their paternity. We examined if male Song Sparrows (*Melospiza melodia*) sing more during the incubation period when they are free of constraints of physical mate guarding. We assessed song rates of eight males for 1 hr-periods every 1–2 days during each breeding stage over two consecutive broods within one season. Males sang significantly more during periods when their mate was incubating than during the pre-fertile, or fertile periods, or while feeding young (second brood). Males may be singing at high rates during incubation to maintain contact with their mate and/or to advertise for extra-pair copulations. *Received 18 October 2008. Accepted 12 April 2009.*

Song has two main functions, territory defense and mate attraction (Catchpole and Slater 1995). Song rate typically decreases after pairing (Catchpole and Slater 1995), but males of many species continue to sing throughout the breeding season and some show peaks in song rate at particular breeding stages, such as when females are fertile or incubating (Møller 1991).

The fertility announcement hypothesis predicts that males should increase their song rate when their mate is fertile to protect their paternity (Møller 1991). Song Sparrows (*Melospiza melodia*) are socially monogamous passerines and extra-pair young have been documented in several populations (Hill 1999, O'Connor 2003, Major and Barber 2004); males, therefore, likely use some form of paternity guard. A recent study of song rates in Song Sparrows did not find support for the fertility announcement hypothesis (Turner and Barber 2004). Song rates were not higher during either the nest-building or egg-laying (fertile) stages compared to other stages. Thus, Song Sparrows do not appear to use high song rates as a strategy to protect their paternity, but likely use physical mate guarding instead. In several species, song rates are higher during female incubation than during the fertile period (Hanski and Laurila 1993, Nemeth 1996, Rodrigues 1996, Gil et al. 1999). Møller (1991) included Song Sparrows in his review, based on Nice's work (1943), as having a peak in song activity during female nest building which was considered part of the fertile period. Nice (1943) did not use statistical analysis, but found the typical range of songs was actually greater during incubation than during egg-laying or nest-building. Nice (1937: 126) when describing male Song Sparrow song, stated that during incubation ''his superfluous energies find expression in a considerable amount of singing''. We studied male song rates of Song Sparrows over two consecutive broods to examine if males sing more during the incubation stage on the basis of Nice's early (1937, 1943) work and our observations.

## METHODS

We studied a population of Song Sparrows from April through July 2003 at Bowlin's Miniature Horse Farm in Sackville, Nova Scotia (44° 45′ N, 63° 41′ W) which consisted of fields divided by areas of mixed forest and/or brush. Two to three people conducted three separate 1-hr observation sessions daily of eight different breeding males, each commencing 1, 2, and 3 hrs after sunrise. Song Sparrow activity (including singing, nest-building, and feeding young) appears relatively constant until mid-morning (JRF, pers. obs.), and song activity in particular remains high throughout the morning. Observation sessions of several males could be done simultaneously where territories were small and, weather permitting, each male was recorded every day. We did not record song rate during periods of rain or extreme wind that may have caused us to underestimate singing. Sunrise times for each day were obtained from the National Research Council, Herzberg Institute of Astrophysics sunrise/sunset calculator. We banded all males and females with a numbered Canadian Wildlife Service (CWS) band and a unique combination

[1] Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

[2] Department of Biology, Saint Mary's University, Halifax, NS B3H 3C3, Canada.

[3] Current address: Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.

[4] Corresponding author; e-mail: 4jf11@queensu.ca

of three color bands on their tarsi, and identified males during each song rate session.

We counted the number of songs sung by focal males during every 1-hr observation session. We divided the breeding stages for song rate quantification into eight periods: unpaired, paired pre-fertile, fertile-first brood, incubation-first brood, feeding of young-first brood, fertile-second brood, incubation-second brood, and feeding of young-second brood. Only females incubate, but both males and females feed the young (Nice 1937, Nordlund and Barber 2005). Data for all eight stages were available for eight males for a total of 396 hrs of observation (mean ± SE: 49.5 ± 1.1 hrs/male; observation sessions in each stage [hrs/male]: unpaired = 2.4 ± 0.2; pre-fertile = 4.6 ± 0.3; fertile–first brood = 8.0 ± 0.5; incubation–first brood = 8.8 ± 0.4; feeding–first brood = 4.8 ± 0.3; fertile–second brood = 5.2 ± 0.3; incubation–second brood = 8.8 ± 0.1; and feeding young–second brood = 6.4 ± 0.3).

We located all nests to be certain of nesting stage. We defined the fertile period as 8 days prior to egg laying through laying of the penultimate egg based on data obtained from other passerines (Birkhead and Møller 1992). We were unsure whether the penultimate egg had been laid at the time of observation, and song rates from that day were omitted from the analyses. Most nests were located before laying occurred, but when they were found during egg-laying and incubation, nests were backdated based on Nice's (1937) data of one egg laid per day and a 12-day incubation period, which corresponds well with dates in our population (Turner and Barber 2004). We did not examine nest-building and egg-laying separately as females are often secretive when building nests; this behavior frequently cannot be observed, particularly for the second brood when vegetation is dense. There is also variation in when females build their nests as some build a nest during both the pre-fertile and fertile periods, some build in only the pre-fertile period, while others build only in the fertile period (JRF, pers. obs.).

Every male was observed during each of the three time periods during each breeding stage, when possible, to avoid time of day effects. Song rates of males obtained 1, 2, and 3 hrs after sunrise did not differ within stages (ANOVA: pre-fertile: $F = 0.066$; df = 2, 28; $P = 0.94$; Kruskal-Wallis: fertile: $W = 4.1$; df = 2, 101; $P = 0.13$; ANOVA: incubation: $F = 1.24$; df = 2, 132; $P = 0.29$; and Kruskal-Wallis: feeding young: $W = 3.64$; df = 2, 91; $P = 0.16$).

We calculated the median song rate per minute for each male for each breeding stage (sample sizes for some males within some stages were small and we used medians for a conservative measurement of song rates). We used a Kolmogorov-Smirnov test to test for normality of these data. All data did not deviate significantly from normality for each breeding stage. We used a repeated measures one-way ANOVA with a Bonferroni post-hoc test to compare unpaired song rate to song rates in all post-pairing breeding stages. We used a repeated measures one-way ANOVA to compare among all post-pairing breeding stages and a Tukey post-hoc test to identify where significant differences occurred. Mean ± SE are given. Results were considered significant when the $P$-value $\leq 0.05$.

## RESULTS

Males sang significantly more during 1-hr observation sessions when unpaired (3.1 ± 0.3 songs/min) than in any of the post-pairing breeding stages (ANOVA: $F = 29.14$; df = 7, 56; $P < 0.0001$) (Fig. 1). Males also sang significantly more in the first and second incubation periods than in any of the pre-fertile (post-pairing), fertile (first and second broods), or feeding young (second brood) periods (ANOVA: $F = 6.71$; df = 6, 49; $P < 0.0001$) (Fig. 1). Song rates in the period of feeding young (first brood) did not differ from those in any of the other six post-pairing stages.

## DISCUSSION

Male Song Sparrows sang at their highest rate prior to acquiring a mate, as reported by Turner and Barber (2004). This result has been observed in many other species (e.g., Hanski and Laurila 1993, Merilä and Sorjonen 1994, Nemeth 1996). Males continued to sing throughout the breeding season, but significantly less so than prior to pairing.

Males increased their song rate significantly once the female began incubation. Higher song rates during incubation have also been reported for Common Chaffinch (*Fringilla coelebs*) (Hanski and Laurila 1993), Common Reed Bunting (*Emberiza schoeniclus*) (Nemeth 1996), Common Chiffchaff (*Phylloscopus collybita*) (Rodrigues 1996), and Willow Warbler (*P. trochilus*) (Gil et al. 1999). Male Song Sparrows may sing at

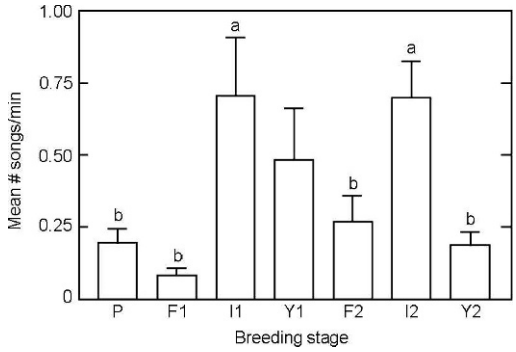


FIG. 1. Song rate/min ($\bar{x} \pm$ SE) during each breeding stage (P = pre-fertile, but paired; F = fertile; I = incubation; Y = feeding young; 1 = first brood; 2 = second brood) for 1-hr observation periods. Different letters indicate significant differences among stages, the same letter indicates no significant difference among stages, and no letter means there were no significant differences between that stage and any other stage ($n$ = 8 males).

a high rate during incubation to stimulate the female to continue incubating or to maintain the pair bond. Another possible function for incubation song is as an all-clear signal where a male lets his mate know that he is close by and that no predators are near (Johnson and Kermott 1991). Song Sparrow nests are often well concealed on the ground by surrounding vegetation (Rising 1996), and the male and female cannot maintain visual contact during incubation. Several studies support the all-clear function of incubation song. Female House Wrens (*Troglodytes aedon*) often leave the nest soon after their mate sings nearby and, when males are temporarily removed, females spend more time on the nest (Ziolkowski et al. 1997). Female Common Reed Buntings are more likely to exit the nest when males are singing, and females stay off their nest longer when their mate is singing (Wingelmaier et al. 2007).

Alternatively, males may be singing during incubation to attract extra-pair mates and to obtain paternity in their next brood. An incubating female in multi-brooded species can assess the condition of her mate as well as that of surrounding males and use this information in her choice of genetic mate for the subsequent brood. Song Sparrows often attempt a third brood and may remain paired in subsequent breeding seasons (CAB, unpubl. data), and high song rates during the second incubation period could be important. Paired males which fail to sing at higher rates during incubation could risk losing either their paternity to a neighbor or their mate to an unpaired male (Nemeth 1996). Older male Common Reed Buntings spend more time singing and also sire more extra-pair young than younger males (Bouwman et al. 2005).

Males sang infrequently during their mate's fertile period suggesting they are likely to be physically guarding their mate; our field observations confirm that males maintain close contact with the female during the fertile period (JRF, pers. obs.). However, observations of pair behavior are necessary to confirm this conclusion. Data on mate guarding are difficult to obtain for Song Sparrows as they spend much of their time together on the ground in dense vegetation (JRF, pers. obs.).

We found no support for Møller's (1991) fertility announcement hypothesis, which is similar to findings of Turner and Barber (2004). We detected significant differences in song rate among certain breeding stages whereas Turner and Barber (2004) did not. However, our study differs from that of Turner and Barber (2004) in that we: (1) defined the breeding stages differently, (2) included the pre-fertile period, and (3) observed for a longer period of time during each session. The different results between the two studies could also be due to annual variation in singing behavior in the population due to differences in climatic factors or breeding synchrony.

The prevalence of incubation song among avian species needs further investigation to understand its function. Studies of species in which males sing at the highest rates during incubation would be useful to learn if they are multi-brooded ground nesters. It would also be valuable to know if these males have more paternity in their subsequent brood and in the broods of other females than males which sing at lower rates during this time.

## ACKNOWLEDGMENTS

Funding was provided by the Natural Sciences and Engineering Research Council of Canada through a graduate research scholarship to JRF and a Discovery grant to CAB, and by Saint Mary's University through grants to CAB from the Faculty of Graduate Studies and Research. We thank Alice and Gerald Bowlin for allowing us the opportunity to study Song Sparrows on their miniature horse farm. K. A. Murphy, Maha Markabi, and J. S. Benjamin assisted with field work.

## LITERAUTRE CITED

BIRKHEAD, T. R. AND A. P. MØLLER. 1992. Sperm competition in birds: evolutionary causes and consequences. Academic Press, London, United Kingdom.

BOUWMAN, K. M., R. E. VAN DIJK, J. J. WIJMENGA, AND J. KOMDEUR. 2005. Older male Reed Buntings are more successful at gaining extrapair fertilizations. Animal Behaviour 73:15–27.

CATCHPOLE, C. K. AND P. J. B. SLATER. 1995. Bird song: biological themes and variations. Cambridge University Press, Cambridge, United Kingdom.

GIL, D., J. A. GRAVES, AND P. J. B. SLATER. 1999. Seasonal patterns of singing in the Willow Warbler: evidence against the fertility announcement hypothesis. Animal Behaviour 58:995–1000.

HANSKI, I. K. AND A. LAURILA. 1993. Variation in song rate during the breeding cycle of the Chaffinch, *Fringilla coelebs*. Ethology 93:161–169.

HILL, C. E. 1999. Song and extra-pair mate choice in Song Sparrows. Dissertation. University of Washington, Seattle, USA.

JOHNSON, L. S. AND L. H. KERMOTT. 1991. The functions of song in male House Wrens (*Troglodytes aedon*). Behaviour 166:190–209.

MAJOR, D. L. AND C. A. BARBER. 2004. The frequency of extra-pair paternity in first and second broods of an eastern Song Sparrow population. Journal of Field Ornithology 75:152–156.

MERILÄ, J. AND J. SORJONEN. 1994. Seasonal and diurnal patterns of singing and song-flight in Bluethroats (*Luscinia svecica*). Auk 111:556–562.

MØLLER, A. P. 1991. Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. American Naturalist 138:994–1014.

NEMETH, E. 1996. Differential singing styles in mated and unmated Reed Buntings *Emberiza schoeniclus*. Ibis 138:172–176.

NICE, M. M. 1937. Studies in the life history of the Song Sparrow. I. A population study of the Song Sparrow. Transactions of the Linnaean Society of New York 4:1–247.

NICE, M. M. 1943. Studies in the life history of the Song Sparrow. II. The behavior of the Song Sparrow and other passerines. Transactions of the Linnaean Society of New York 6:1–329.

NORDLUND, C. A. AND C. A. BARBER. 2005. Parental provisioning in *Melospiza melodia* (Song Sparrows). Northeastern Naturalist 12:425–432.

O'CONNOR, K. D. 2003. Extra-pair mating and effective population size in the Song Sparrow (*Melospiza melodia*). Dissertation. University of British Columbia, Vancouver, Canada.

RISING, J. D. 1996. A guide to the identification and natural history of the sparrows of the United States and Canada. Academic Press, San Diego, California, USA.

RODRIGUES, M. 1996. Song activity in the Chiffchaff: territorial defence or mate guarding? Animal Behaviour 51:709–716.

TURNER, W. C. AND C. A. BARBER. 2004. Male Song Sparrows (*Melospiza melodia*) do not advertise their female's fertility. Journal of Avian Biology 35:483–486.

WINGELMAIER, K., H. WINKLER, AND E. NEMETH. 2007. Reed Bunting (*Emberiza schoeniclus*) males sing an 'all-clear' signal to their incubating females. Behaviour 144:195–206.

ZIOLKOWSKI, D. J. J., L. S. JOHNSON, K. M. HANNAM, AND W. A. SEARCY. 1997. Coordination of female nest attentiveness with male song output in the cavity-nesting House Wren *Troglodytes aedon*. Journal of Avian Biology 28:9–14.