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Male House Sparrows Behave as if a Fertilization Window Exists

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Sperm competition can occur when a female copulates with more than one male during the period when her eggs can be fertilized (Parker 1970). In monogamous species, where the male typically contributes valuable parental care, intrasexual selection should act on males to produce traits that minimize sperm competition, thus helping ensure that the investing male's own sperm fertilizes most or all of his mate's eggs (Kempenaers et al. 1995). In birds, two of the main ways a male avoids cuckoldry are mate guarding and frequent copulation (Birkhead and Møller 1992, Briskie 1992). However, both of these behaviors may be very costly for males in terms of energy expenditure and/or time (opportunity cost), so males can be expected to confine these behaviors to times when they would be most beneficial, if such times can be detected.

As laying commences, the presence of the first developing ovum in the oviduct apparently decreases the interval during which additional sperm can be introduced and have any chance of fertilizing the second ovum (Bakst and Bird 1987, Birkhead and Møller 1993, Bakst et al. 1994). This may reduce the hypothetical "fertilization window" ("insemination window" of Cheng et al. 1983) to as little as 10 to 60 min after the laying of the preceding egg, while the next ovum is in the infundibulum (Bobr et al. 1964). Thereafter, the second egg, fertilized or not, begins accumulating layers of albumen and membranes that trap sperm and act collectively as a barrier to fertilization of a third ovum (Bakst et al. 1994). Furthermore, the contractions that propel each egg through

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the oviduct oppose the movements of sperm, and the fluid of the uterine mucosa also acts as a barrier to the infundibulum where fertilization takes place (Bakst et al. 1994). As evidence of this limitation, Cheng et al. (1983) reported that female Mallards (*Anas platyrhynchos*) inseminated after the fertilization window was estimated to be closed produced only one fertile egg out of 179 that were laid.

The idea that a fertilization window exists has become increasingly controversial in recent years. Adkins-Regan (1995) showed that time of day of mating does not affect the fertilization success of the next egg in Japanese Quail (*Coturnix japonica*), and observations of copulation behavior have provided evidence both consistent with and counter to the "fertilization-window" hypothesis (Birkhead et al. 1996). For example, in diurnally mating birds such as Lesser Kestrels (*Falco naumanni*; Negro et al. 1992) and Smith's Longspurs (*Calcarius pictus*; Briskie 1992), one peak in copulation and mate-guarding activity occurs in the morning, as would be expected if a fertilization window exists (i.e. when the oviduct is free of a developing egg that could block the oviduct), but a second peak takes place in the afternoon, which would not be predicted according to the fertilization-window hypothesis. Because mate guarding is often easier to observe under field conditions than are copulations per se, Pinxten and Eens (1997) found it surprising that very few studies used mate guarding as a behavioral clue to help shed light on whether such windows are important across different species. In their observations of free-living European Starlings (*Sturnus vulgaris*) in Belgium, paired males increased their mate-guarding attentiveness during the late morning, which is an odd time for passerines to lay eggs (see Mace 1989, Sheldon 1994) but which is the time that female starlings typically lay their eggs.

The purpose of this study was to determine whether male House Sparrows (*Passer domesticus*) behave as if exploiting a fertilization window. Based on DNA fingerprinting, the frequency per nest of extrapair offspring in the population that I studied is about 16% (R. R. Whitekiller unpubl. data), so the threat of sperm competition is very real. As in the starling study mentioned above, the question was whether paired males increase their mate-guarding behavior during the putative fertilization window (i.e. just after their mates have laid an egg), when the hypothesis predicts that such acts should be the most effective, relative to a second hour-long sample taken slightly later on the same morning (when any such window would have closed). Similarly, differences in mate-guarding frequency should be greater between the two sampled hours during days in the middle of the laying period (when fertility is at stake) than for comparable samples taken on days outside of the fertile period.

Methods.—I studied House Sparrows at Norman, Oklahoma (35°20'N, 97°40'W). Numbered plywood nest boxes were mounted on posts, fences, or old buildings, with considerable variation in the distances between nearest neighbors. A sample of nearest-neighbor distances taken from this population in 1996 averaged 28.6 ± SD of 16.4 m (R. R. Whitekiller unpubl. data). For my study, boxes near dense trees were avoided to facilitate observation of mate-guarding movements by males. From mid-May to early July 1996, activities around the boxes of 16 pairs (eight during laying and eight during incubation) were observed from a car at a distance of 20 to 25 m. Ten of the 16 pairs had unique combinations of color bands.

Female House Sparrows typically entered their boxes to lay eggs between 0615 and 0645 EST. On a typical morning, I checked that day's focal nest at about 0550 to verify that a new egg had not appeared. The mean number of eggs in the nest when I arrived was 2.09 ± 0.42; one or two eggs were subsequently added to all focal nests. When the female first entered the box, she usually remained inside for 15 to 45 min, after which a new egg was laid (the precise time of laying was unknown). My first hour of observation began as soon as the female entered the box in case she laid an egg immediately upon entering. I interrupted observations briefly after 30 min to check whether an egg had been laid; if the female had not left the box, I waited until she exited. After a quick count of eggs, I resumed recording to get the second half of the first hour, which would be within the fertilization window if the female laid an egg toward the end of her time in the box. Therefore, the first hour of observation sampled a large portion of the presumed fertilization window. After this first sample, I waited 30 ± 0.5 min before starting the second 1-h observation period, which was intended to represent a baseline measure of pair behavior during the laying period but outside of the putative fertilization window. During observation periods, I recorded the times when either mate entered or exited the nest or vanished from my view.

To control for possible time-of-day effects in the aforementioned fertilization-period samples, a second set of samples was taken during the incubation period, involving pairs not used previously. These samples differed from the above protocol in only one respect: to minimize the risk of desertion that might accompany disturbance (Seel 1968) during incubation, and because the female spends a great deal more time on the eggs once laying is complete, the nest box was not opened initially to check the eggs. Instead, I stood beneath the nest briefly before returning to the car, thus causing disturbance comparable to checking a nest but not enough to cause desertion.

When a male was outside of the nest box and within 10 m of the female, he was considered to be guarding her (see Burke et al. 1989, Kempenaers et al. 1995). The total time the male spent guarding was

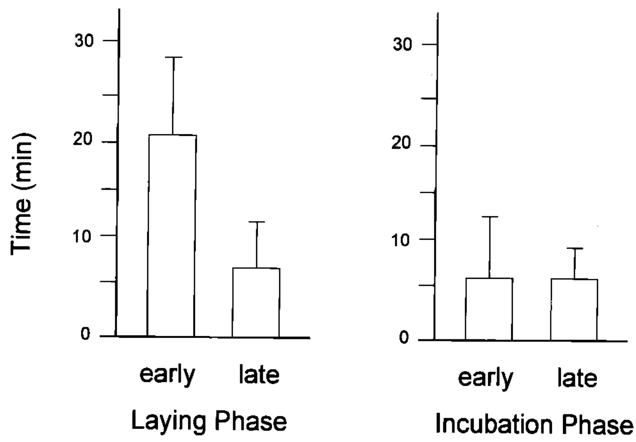

FIG. 1. Incidence of mate guarding by male House Sparrows in early and late morning observation periods during laying and incubation. Values are $\bar{x} \pm$ SD.

summed for each 1-h observation period. Paired-*t* tests were used to compare mate attendance times in the first versus the second observation periods. The difference in mate attendance between the first and second samples was calculated for both the laying and the incubation periods. Because these data were not normally distributed, I used a Mann-Whitney test to compare differences by period (i.e. laying vs. incubation). All tests were two-tailed.

Results and discussion.—No temporal effect on mate guarding occurred during the incubation period (paired $t = 0.45$, df = 7, $P = 0.67$; Fig. 1), so males did not simply reduce the amount of time spent at the nest or with the female as the morning passed. In contrast, the same comparison during the laying period showed that males spent much more time attending the female during the first sample period than during the second sample period for the morning (paired $t = 5.03$, df = 7, $P = 0.002$; Fig. 1). The differences in mate guarding between first versus second observation periods were much higher during laying (14.38 ± 8.09 min) than during incubation (0.95 ± 6.06 min; Mann-Whitney $U = 4.0$, $P = 0.003$).

As predicted, male House Sparrows spent more time close to their mates during the laying period than during the subsequent incubation period, and on laying days they tended to be near the female more during the putative fertilization window than later in the morning, a pattern wholly absent during the corresponding hours of the incubation period. Taken together, these results are consistent with the view that paired males behave as though a very brief opportunity for the successful introduction of ejaculate exists, and that paired males adjust their behavior to this circumstance in ways that minimize the risks of sperm competition from potential extrapair copulations.

One difficulty with the fertilization-window hypothesis is that its duration can only be approximated. To be conservative, I used the highest estimate of the window's duration (60 min), but other estimates range as low as 10 min (e.g. Wetton and Parkin 1991). In some species of open-cup nesters, the start of the window (which coincides with the laying of the previous egg) may be detected accurately, and in theory males could use this as a cue to determine when the window is open. Alternatively, males may have to rely on a simple behavioral rule, such as copulating in the morning. If so, that might help explain the morning peaks in copulation observed in many birds that also lay in the morning (e.g. Tree Swallows [*Tachycineta bicolor*], Lifjeld and Robertson 1993; Zebra Finches [*Taeniopygia guttata*], Birkhead et al. 1989; and Smith's Longspurs, Briskie 1992).

Behavioral patterns consistent with exploitation of a fertilization window have been noted in other birds. For example, female Mallards are more "attractive" to males and experience more attempts at forced copulation just after each laying event than at any other time (Cheng et al. 1983). This has been proposed to occur because unlike the female's mate, an extrapair male probably is not copulating repeatedly, so it would benefit him to choose the best moment to attempt an extrapair copulation (i.e. during the putative fertilization window). Another example may be the Aquatic Warbler (*Acrocephalus paludicola*), which has very intense sperm competition (multiple paternity in at least 50% of broods; Schulze-Hagen et al. 1995). During the female's prelaying fertile period, most copulations occur late in the day, but once laying begins, copulations occur most frequently in the morning and usually directly after a laying event (within the presumed fertilization window). Finally, although Common Chaffinches (*Fringilla coelebs*) reduce copulation after the start of laying and show no increase in copulations during the presumed fertilization window, males seem to guard their mates more intensely during this period (Sheldon 1994, Sheldon and Burke 1994), much like the sparrows in the present study.

In contrast, males of some other species do not guard or copulate more during the putative fertilization window. For example, male Western Bluebirds (*Sialia mexicana*) do not increase their copulation rate during the presumed fertilization window (Dickinson and Leonard 1996). Instead, mate guard and copulation increase during a general fertile period (defined as 10 days before clutch initiation through the completion of laying). This option may be the best available for species in which males cannot detect when eggs are laid by their mates.

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