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# Male sperm reserves and copulation behaviour in the house sparrow, *Passer domesticus*

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SUMMARY

The aim of this study was to measure the rates of sperm utilization and production in male house sparrows, *Passer domesticus*: this is the first attempt to do this for any wild bird. The number of spermatozoa in the seminal glomera of males on days −1 to +3 (i.e. during their partner's fertile period) declined significantly throughout the course of the day. Males had about $12.13 \times 10^6$ spermatozoa in their seminal glomera at the start of the day and during 16 copulations each day used $10.31 \times 10^6$ spermatozoa, which is probably all that was available for ejaculation. Mean ejaculate size was estimated to be $0.64 \times 10^6$ spermatozoa. Seminal glomera occur only in passerines and their function is unclear, but our results suggest a new hypothesis: if spermatozoa production and spermatozoa transport to the seminal glomera are limited to a short period during the night, the seminal glomera serve as a daily spermatozoa store.

## 1. INTRODUCTION

The adaptive significance of females copulating with more than a single male during a single reproductive cycle is one of the central questions in the field of sexual selection (Hunter *et al.* 1992). The potential fitness benefits of copulating with multiple males can be either direct or indirect (genetic) (Westneat *et al.* 1990; Birkhead & Møller 1992; Kempenaers & Dhondt 1993). Fertility insurance is one of several potential direct benefits that has been proposed to account for extra-pair copulations in socially monogamous species (Walker 1980; Gibson & Jewel 1982; McKinney *et al.* 1984). However, as a general explanation for extra-pair copulations in birds, fertility insurance is considered unsatisfactory for two related reasons: the levels of both male sterility and the proportion of females seeking extra-pair copulations appear to be too low for this explanation to be plausible (Westneat *et al.* 1990; Birkhead & Møller 1992). In addition, sperm depletion is unlikely to be a source of infertility as testis size has evolved in relation to the levels of sperm production necessary under particular social and sexual circumstances, and Møller (1991) has shown that relative testes size is larger in bird species in which sperm competition is intense. However, there may be particular situations or species in which male sterility favours females that seek extra-pair copulations. For example, Wetton & Parkin (1991), in a study of house sparrows, *Passer domesticus*, found that extra-pair paternity was more likely to occur in broods in which some eggs were infertile. They suggested that females paired to males with low sperm reserves would thus benefit from extra-pair copulations in that their eggs would be more likely to be fertilized. House sparrows copulate at a relatively high rate before and during egg-laying (Birkhead *et al.* 1987; Møller 1987), and Wetton & Parkin (1991) suggested that for some males frequent copulation might result in sperm depletion.

Sperm depletion in males will occur if the rate of sperm transfer through copulation is higher than the rate of sperm production (see Birkhead 1991). Although there is now a considerable body of information about copulation frequency in birds (Birkhead & Møller 1992), relatively little is known about ejaculate size (see Møller 1988*a*; Pellatt & Birkhead 1993) or rates of sperm production in passerine birds. The aim of the present study was to test the idea that frequent copulation could result in sperm depletion. Specifically, our aims were to measure the size of the sperm reserves of male house sparrows and to estimate the likelihood of sperm depletion occurring during the pair copulation period.

## 2. METHODS

Male passerine birds store sperm for copulation in the seminal glomera, the coiled distal ends of the vas deferens (Wolfson 1954), and in most species the seminal glomera form the major component of the male's cloacal protuberance (Birkhead *et al.* 1993; see also Birkhead & Hoi 1994). In the present study we measured the total number of sperm in the seminal glomera of house sparrows collected at different times of day during the copulation period. Given that our knowledge of sperm production rates and ejaculate size in passerine birds is so limited, it is extremely difficult to test the hypothesis that frequent copulation results in sperm depletion directly. We have therefore used an indirect approach. We collected a total of 12 male house sparrows under licence

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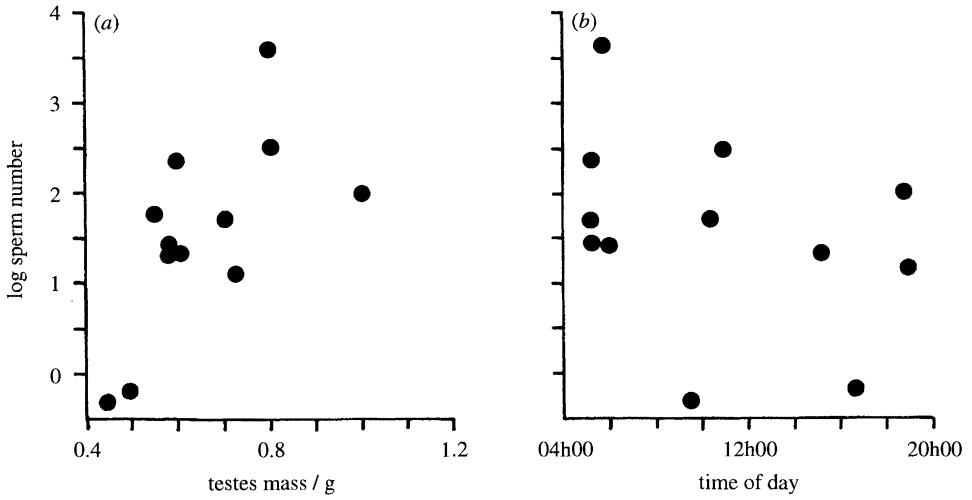


Figure 1. (*a*) Relation between testes mass and log number of spermatozoa in the seminal glomera. (*b*) Relation between time of day and log number of spermatozoa in the seminal glomera. A multiple regression showed that both testes mass ($p = 0.002$) and time of day ($p = 0.005$) independently affect the numbers of spermatozoa in the seminal glomera (see text).

from a colony near Madrid, Spain, between days −1 and +3 (where day 0 is the day on which the first egg of their clutch was laid), around the middle of their pair copulation period (see Møller 1987). The colony comprised 75 breeding pairs in an area of 1.3 ha† in 1993. Birds were trapped by using mist nets and nest traps between first light and dusk in the evening; they were killed by using chloroform, and were frozen and later thawed and fixed in 5% formalin before being dissected. Immediately after death the body mass, tarsus length and black throat 'badge' size were measured. Badge size was calculated from the height (*h*) and width (*w*) of the black bib while the bird was held in a natural position, and the area was calculated as the surface of a circular sector with radius *h* and chord *w*. Testes dimensions (maximum length and width to the nearest 0.01 mm) and mass (to the nearest 0.0001 g using a Mettler AE 160 electronic balance) were measured. The vas deferens and seminal glomera were removed, and the number of spermatozoa in the seminal glomera counted by using an Improved Neubauer chamber, as described elsewhere (Birkhead *et al.* 1991).

## 3. RESULTS

The number of spermatozoa in the seminal glomera declined the later in the day the birds were collected (figure 1). A multiple regression showed that both testes mass ($\beta = 5.65$, $p = 0.002$) and time of day ($\beta = -0.142$, $p = 0.005$) independently had significant effects on the number of spermatozoa in the seminal glomera (regression equation: log sperm = −0.713 + 5.65 testes mass − 0.142 time). Together these two variables explained 73% of the variance in spermatozoa numbers in the seminal glomera, i.e. after controlling for testes mass the number of spermatozoa showed a significant decline through the day. Controlling for testes mass is important because the amount of testicular tissue determines the rate at which spermatozoa are produced (Møller 1989). In the zebra finch, *Taeniopygia guttata*, for example, testes mass is significantly and positively correlated with the number of spermatozoa in the seminal glomera among rested males (i.e. males with maximum spermatozoa numbers) (Birkhead *et al.* 1993). In the present study the mean mass of both testes combined was 0.671 g ± 0.164 s.d. (coefficient of variation 24.4%), or 2.40% ± 0.06 s.d. (coefficient of variation 25.5%) of body mass. The coefficient of variation of testes mass as a proportion of (tarsus length)$^3$ was 30.17%; there is thus considerable variation in testes size.

The slope of the multiple regression suggested that, after 16 h of daylight, males would have only $1.82 \times 10^6$ spermatozoa remaining in their seminal glomera, assuming no sperm production during the day (see below). If we also assumed that the mean number of spermatozoa in the seminal glomera at first light was the mean from the five birds collected before 06h01, i.e. $12.13 \times 10^6$ spermatozoa, males use on average $10.31 \times 10^6$ spermatozoa in a day, or about 85% of the contents of the seminal glomera at the start of the day. House sparrows copulate at a high rate (Summers-Smith 1963; Møller 1987) from about day −4 until the clutch is complete (Møller 1987), with copulations occurring in bouts with a mean of 4.11 ± 0.44 s.e. copulations per bout ($n = 47$) (A. P. Møller, unpublished results). During the time the birds in the present study were collected (days −1 to +3; see above), the mean copulation rate was at its maximum at 0.224 bouts per hour (Møller 1987), or 3.9 bouts and 16 copulations per 16 h day. If we assume that all copulations result in insemination, males transferred $0.64 \times 10^6$ spermatozoa during each copulation ($10.31 \times 10^6/16$). In the zebra finch only 67% of copulations result in ejaculation (Birkhead *et al.* 1988; see also Birkhead 1991); if house sparrows are similar then each ejaculate would contain $0.96 \times 10^6$ spermatozoa.

In the zebra finch, males that are experimentally depleted use 84% of the spermatozoa in the seminal glomera for copulation (A. Staples, unpublished results). If house sparrows are similar in this respect then our data suggest that on average males completely utilize their sperm supplies during the day. Moreover,

† 1 ha = $10^4$ m$^2$.

Table 1. *Sperm production rates in birds*

| measure | turkey | chicken | guineafowl | Japanese quail | house sparrow |
|---|---|---|---|---|---|
| testes mass/g | 28 | 28 | 3.78 | 3.12 | 0.67 |
| body mass/g | 8700 | 2300 | 1850 | 100 | 28 |
| relative testes mass[a] | 0.322 | 1.22 | 0.204 | 3.12 | 2.39 |
| DSP absolute ($\times 10^6$)[b] | 520 | 2000 | 70 | 308 | 31 |
| DSP (g testis mass)$^{-1}$[b] | 18.6 | 71.4 | 18.5 | 98.7 | 46.3 |
| DSP (g body mass)$^{-1}$[b] | 0.06 | 0.87 | 0.04 | 3.08 | 1.11 |
| references[c] | (1) | (2) | (3) | (4) | (5) |

[1] Relative testes mass = (testes mass/body mass) × 100.
[b] DSP = daily sperm production.
[c] References: (1) Cecil & Bakst (1988); (2) de Reviers & Williams (1981); (3) Brillard & de Reviers (1981); (4) Clulow & Jones (1982); (5) this study.

if we assume that the difference between the numbers present in the evening and in the early morning represents the overnight replenishment of sperm number, i.e. $10.31 \times 10^6$, this represents a sperm production rate of approximately $1.3 \times 10^6$ h$^{-1}$, or $31 \times 10^6$ d$^{-1}$, which is low compared with several domestic galliforms (table 1), the only other birds in which sperm production rates have been measured (but see below). However, in terms of sperm production per gram of testes tissue or body mass, the values for the house sparrow fall within the range of domestic galliforms (table 1).

We also considered the possibility that male sperm reserves might decline over successive days of the copulation period. By using the five males collected early in the morning (between days −1 and +3), we found only a weak negative relation between day number in the breeding cycle and log spermatozoa numbers (controlling for testes mass) in the seminal glomera ($r = -0.206$, 3 d.f., n.s.), suggesting little or no decline over successive days (although the sample size is very small).

## 4. DISCUSSION

Although our results suggest that sperm depletion on a day-to-day basis could occur in the house sparrow, we still consider it unlikely that depletion could account for the association between the occurrence of infertile eggs and the occurrence of extra-pair paternity observed by Wetton & Parkin 91991). Like all birds examined so far, female house sparrows store spermatozoa, and even relatively small numbers of sperm can result in fertilization (Taneja & Gowe 1961; Lake & Ravie 1975), i.e. even if a female had performed only a few copulations with her partner it is likely that she would have sufficient sperm to fertilize her eggs. Moreover, if female sparrows sought extra-pair copulations as a consequence of their partner's infertility, we might expect to find fewer, rather than more, infertile eggs in nests with high levels of extra-pair paternity (Lifjeld 1994).

Our results do, however, raise some interesting questions regarding spermatozoa dynamics in the house sparrow and other passerine birds. The results of this study suggest that, on average, male house sparrows have sufficient spermatozoa for several copulations each day, but that on each day they utilize most of the spermatozoa in their seminal glomera. The seminal glomera are unique to passerines and, although they clearly serve as some kind of storage area for spermatozoa, their precise function is unknown. The storage function of the seminal glomera was clear from a comparative study which showed that the size of the seminal glomera and the cloacal protuberance they form are positively correlated with copulation rates across species (Birkhead *et al.* 1993). Wolfson (1954) suggested that the seminal glomera served as a site for the maturation of spermatozoa analogous to the external testes in certain mammals: he found that spermatozoa in the seminal glomera were maintained at a temperature about 4 °C lower than deep body temperature. The fact that deep body temperatures of passerines are higher than those of non-passerines of the same body mass (McNab 1966; Birkhead *et al.* 1993; but see Prinzinger *et al.* 1991) is consistent with the idea that male passerines would benefit from storing spermatozoa in a relatively cool location, such as the cloacal protuberance. Bedford (1979) suggested that the rate of sperm production in passerines might be low compared with that of non-passerines, and that as a consequence males would be required to store most of the spermatozoa they needed for a breeding cycle. He therefore indicated that the seminal glomera serves as a sperm store for the entire breeding cycle. However, our results suggest that this is unlikely, and indicate another function for the seminal glomera. House sparrows perform about 47 copulation bouts during each breeding cycle (A. P. Møller, cited in Birkhead *et al.* 1987). Assuming 4.11 copulations per bout (see above), and that each copulation results in the transfer of spermatozoa, a total of 193 ($47 \times 4.11$) copulations would utilize $123 \times 10^6$ spermatozoa ($193 \times 0.64 \times 10^6$), which is more than three times the maximum ($36 \times 10^6$) we recorded in the seminal glomera of a single bird. We suggest another explanation for the occurrence of the seminal glomera. Riley (1937) and Quay (1988) have shown in the house sparrow and other passerines that spermatogenesis is confined to a short period during the night, the period of least activity and lowest body temperature (see Aschoff 1981). Because spermatogenesis occurs only at this time, and because the seminal glomera appear to be replenished only at night (Quay 1987; see also Middleton 1974), males are forced to store their daily sperm requirements, i.e. the function of the seminal glomera is not to store

spermatozoa for the entire copulation period but to store it for each day of the copulation period. We checked the likelihood of this hypothesis in the following way. By using an independent estimate of ejaculate size (predicted from Møller's (1988) equation) of $0.9 \times 10^6$, the total number of spermatozoa used in 16 copulations during a day is $0.9 \times 16 \times 10^6 = 14.4 \times 10^6$, similar to that which we estimated above ($10.31 \times 10^6$ spermatozoa). We can then compare an output of $14.4 \times 10^6$ with the number that enter the seminal glomera over this same time period, assuming that the daytime replenishment rate is the same as the overnight rate (i.e. $10.31 \times 10^6/8 = 1.29\ h^{-1} \times 10^6 = 1.29 \times 16 \times 10^6 = 20.64 \times 10^6$. This latter figure suggests that, if the rate at which the seminal glomera were replenished was constant over the 24 h cycle, we should not have been able to detect a drop in spermatozoa numbers in the seminal glomera, i.e. these figures are consistent with the idea of overnight rate replenishment of the seminal glomera and little or no addition of spermatozoa during the day.

If this hypothesis is true than it is feasible that males could deplete their sperm stores through frequent copulation: a high frequency of copulation during the morning, perhaps as the result of frequent extra-pair copulation opportunities, could leave a male with few spermatozoa for the rest of the day, until his reserves were replenished overnight. Because testes size determines the rate of sperm production (Møller 1989; Birkhead *et al.* 1993), and because testes size in house sparrows varies considerably (this study; see also Møller & Erritzøe 1988), it might appear at first sight that males with relatively small testes and hence small sperm reserves would be particularly likely to experience sperm depletion. However, Møller (1990) has shown that males with smaller badges (and presumably smaller testes; see below) copulate at a lower rate than those with larger badges. In addition, it is possible that ejaculate size may also vary in proportion to the size of spermatozoa reserves.

Møller & Erritzøe (1988) found a significant positive correlation between badge size and testes mass in a large sample of house sparrows ($r = 0.23$, $n = 149$, $p < 0.01$, $r^2 = 0.053$). We also found a similar positive relation which, although not significant ($r = 0.484$, 10 d.f.), actually explained a higher proportion of the variance ($r^2 = 0.235$) than in Møller & Erritzøe's study. We also found a similar relation between badge size and log number of sperm in the seminal glomera, after controlling for time of day ($r^2 = 0.248$, $p < 0.1$). It is possible therefore that one benefit that females may obtain from pairing and performing extra-pair copulations with males with large badges (see Møller 1988*b*, 1990) is large numbers of spermatozoa.

Ejaculate size during natural copulations in birds is poorly known (Pellatt & Birkhead 1933). Møller (1988*a*) summarized data derived from artificial insemination studies (mainly non-passerines), and found that the number of spermatozoa per 'ejaculate' was positively and significantly correlated with testes mass. The ejaculate size for testes the size of a house sparrow's (0.67 g) predicted from this relation was $0.9 \times 10^6$, close to the estimate in the present study. More recently, Pellatt & Birkhead (1993) have measured the ejaculate of zebra finches more directly, by using model females with a false cloaca. In their study, mean ejaculate size in rested male zebra finches was between $4 \times 10^6$ and $7 \times 10^6$ spermatozoa (see also Birkhead *et al.* 1993). The zebra finch (15 g) is considerably smaller than a house sparrow, and also has relatively small testes (see Møller 1991), so these ejaculates appear to be relatively large. However, it is important to point out that rested males always produce relatively large ejaculates (see Amann 1981; Cecil *et al.* 1988; Birkhead 1991), and those of regularly copulating zebra finches are considerably smaller, about $1 \times 10^6$ spermatozoa (T. R. Birkhead & F. Fletcher, unpublished results). In addition, it is important to note that ejaculates are inherently variable in size, even when collected under standardized conditions (Amann 1981; T. R. Birkhead & F. Fletcher, unpublished results). A further possibility is that zebra finches and house sparrows may differ in the way males allocate spermatozoa to ejaculates. Zebra finches show a rapid decrease in ejaculate size as spermatozoa are used up (T. R. Birkhead & F. Fletcher, unpublished results), whereas house sparrows with larger spermatozoa reserves may be able to maintain several ejaculates of similar size until their supplies are very low, as occurs in some mammals (see Bedford 1991).

Sperm competition occurs regularly in the house sparrow (Møller 1987, 1990), and Wetton & Parkin (1991) found that 13.6% of all offspring were extra-pair and that 26.1% of broods contained at least one extra-pair offspring. In birds in general, several features of male reproductive anatomy are associated with the intensity of sperm competition, and not surprisingly the house sparrow has relatively large testes (observed mass = 0.67 g; mass predicted from Møller's (1991) interspecific comparison = 0.40 g), and relatively large cloacal protuberance and seminal glomera (Birkhead *et al.* 1993). These structures are necessary to sustain the relatively high rates of pair copulation performed by house sparrows, which in turn are necessary for males as a paternity guard (Birkhead *et al.* 1987; Møller & Birkhead 1991).

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