

## Postmating sexual selection in house sparrows: can females estimate “good fathers” according to their early paternal effort?

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**Abstract.** Recently, several studies suggested that in species with biparental care, male parental effort (for instance in terms of nest building) serves as a sexual signal to females. In this study on free-living house sparrows *Passer domesticus*, we investigated how male contribution to parental care varies between breeding stages and whether early parental care of a male reflects his paternal effort in later stages. We found that nest building was performed predominantly by males. However, hatching success was not related to male participation in nest building or early nest guarding. The contribution of males to incubation and chick brooding was lower than in females. Investment in chick feeding did not differ between partners, but varied considerably between males. Only the male effort in chick feeding was related to the number of young at fledging age, suggesting that male assistance is essential to maximise reproductive success in house sparrows. Except for the positive correlation between male nest building and male incubation during egg laying, we found no relationship between early (nest building and nest guarding) and later paternal effort (late incubation, brooding and provisioning rates). Consequently, intensity of male nest building and early nest guarding do not seem to be honest indicators of later paternal effort in the house sparrow. Instead, we speculate that high early paternal effort might be a strategy of some males to manipulate the reproductive effort of their partners.

**Key words:** paternal care, nest building, sexual selection, house sparrows, breeding success

### Introduction

One important mechanism of sexual selection, female mate choice, operates through females preferring males that display certain morphological and behavioural traits (Zahavi 1975, West-Eberhard 1979, Catchpole 1980, Hamilton & Zuk 1982, Nur & Hasson 1984, Ryan et al. 1990). Females are supposed to benefit from their choice indirectly by acquiring “good genes” for their offspring (Zahavi 1975, Weatherhead & Robertson 1979, Pomiankowski 1987, Iwasa et al. 1991), or directly by a greater assistance of their mates in chick rearing or territory defence (Trivers 1972, Borgia 1979, Burley 1981, Kirkpatrick 1985, Hoesler 1989, Price et al. 1993). However, sexual selection can operate also after mate choice (see Soler et al. 1998a,b). Hereby, some males can produce more or higher quality offspring as their mates invest in reproduction differentially depending on male physical (e.g. Burley 1988, Møller 1994) or parental quality (Gibbons 1987, de Lope & Møller 1993). The latter case should especially account for the species with biparental care, for which male

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parental quality is often crucial to maximise female reproductive success (e.g. M o r e n o et al. 1999, see M ø l l e r 2000). In order to stimulate their mates to a higher reproductive effort, males should therefore try to advertise their ability and/or willingness to parental care. Females should in turn pay attention to the reliability of such advertisements. In fact, some studies showed that male song display can be an indicator about his parental quality (e.g. H o i - L e i t n e r et al. 1995, W e l l i n g et al. 1997). Other studies recently demonstrated that the number of advertised nests, nest size or male nest building activity in wrens *Troglodytes troglodytes*, black wheatears *Oenanthe leucura*, barn swallows *Hirundo rustica* and magpies *Pica pica* might represent a sexual signal involved in postmating sexual selection (E v a n s & B u r n 1996, S o l e r et al. 1996, S o l e r et al. 1998a, S o l e r et al. 2001). However, studies examining the reliability of early paternal advertisement and its potential to manipulate female reproductive decisions are lacking.

The house sparrow *Passer domesticus* is a suitable species to study postmating sexual selection with regard to paternal quality because: (i) there is no clear female preference for males with larger sexual ornament, a melanin based throat patch (K i m b a l l 1996), (ii) early reproductive decisions of females (date of egg laying, clutch size) were showed to be related to early male parental effort (V á c l a v & H o i 2002), whereas (iii) chick feeding as well as fledging success were reported to increase with size of male ornament (M ø l l e r 1988, V á c l a v & H o i 2002). In this study, we examined different male and female parental activities, including nest building, nest guarding, chick brooding and chick feeding during (i) pre-laying and laying period, (ii) incubation, (iii) chick brooding and (iv) chick feeding periods. We wanted to answer the following questions:

(i) How does the contribution of male parental care vary between breeding stages?

(ii) How important is male parental care for hatching and fledging success?

(iii) Is early paternal effort a reliable predictor of male parental effort later on during the breeding cycle?

## Material and Methods

### Study area and population

House sparrows were studied in a nest-box colony in the Schönbrunn Zoological Garden, Vienna in 2001. During the breeding season, 72 of 84 nest boxes were occupied. Nest-boxes were installed on the opposite walls of 7 barns. Egg laying started at the beginning of April. From then the contents of all nest-boxes were inspected at least every third day throughout the breeding season. We recorded the progress in clutch size, number of hatched and fledged young. In the analyses, we use data collected from 31 different pairs. Only the data from first breeding attempts for these pairs were used in our analyses, since the largest part of the nests are constructed prior to the first breeding attempt and afterwards the nest volume changes only slightly (see C r a m p 1994, R. V á c l a v, unpublished data). Furthermore, female investment in parental care may later be affected by male performance in the whole first breeding attempt as well as achieved breeding success. We did not succeed in collecting sufficient data of nest building behaviour for six pairs; hence the sample size for the corresponding analyses is only 25 pairs. Hatching success refers to the proportion of hatched eggs relative to clutch size. Fledgling numbers were estimated according to the number of chicks found in nest-boxes at the age of 13–15 days. Fledging success corresponds to the proportion of fledglings relative to the number of hatched chicks.

Behaviour of house sparrows was monitored from around three weeks before the first egg was laid until fledging of the last chick. The behavioural observations were carried out from 7:00 to 12:00 noon. Throughout the breeding cycle, each pair was observed on average for 4.5 hrs. The behaviour at each nesting site was recorded daily during 15 min protocols. In order to avoid an influence of daytime on behaviour, nesting sites were visited following a rotating scheme. We recorded: (i) nest guarding (time spent at or around the nest-box < 5 m), (ii) nest building (the number of arrivals with a nest material to the nest-box), (iii) time at incubation (time spent in the nest-box > 1 min), (iv) chick brooding (time spent in the nest-box after hatching > 1 min), and (v) the number of chick feeding visits. Since behavioural protocols of the studied pairs covered variable periods of the breeding cycle, we restricted our analyses to comparable time intervals of nest building, egg laying, incubation and chick feeding phases (see below). Parental care was classified as early or late, depending on whether it took place before or after clutch completion. The early parental care corresponds to the pre-laying and laying period from 5 days prior to the first egg until the last egg was laid (i.e., late nest building, and nest guarding and incubation during egg laying). This is not only the period when the presumed fertile period of females occurs in house sparrows (see M ø l l e r 1987, B i r k h e a d et al. 1994), but also the time when nest building culminates (S u m m e r s - S m i t h 1963, see C r a m p 1994). Chick feeding was restricted to the period of the first 10 days after hatching, i.e., approximately 70% of the chick feeding period (see S u m m e r - S m i t h 1963).

## Statistical analyses

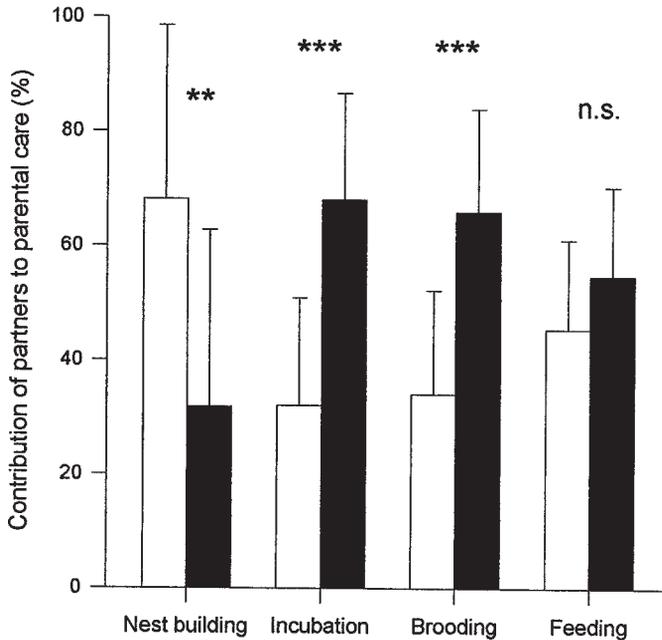
Some parametric tests were used after normalising data by a log transformation. The frequency of male chick feeding visits was related positively, though not significantly, to brood size ( $R^2 = 0.07$ ,  $\beta = 0.27$ ,  $n = 31$ ,  $p = 0.14$ ). Because the result would become significant after removing an outlier, to control for brood size, when examining the effect of male provisioning rates, we used residual values of male chick feeding. Relative to the opposite sex or absolute values of parental care activities were used in analyses. To avoid type-I errors in cases when the same variables would have to be examined more times, we used multiple regression tests. For examination of the intensity of nest guarding of identical birds during three breeding stages, we used repeated measures ANOVA. In order to minimise confounding effects of multiple parental behaviours on the parameters of reproductive success, we examined the effect of early paternal effort on hatching success and the effect of later paternal effort on the number of fledglings and fledging success.

## Results

### Male contribution to parental care throughout the breeding cycle

Examining male parental effort over the course of the breeding cycle, we found that male share in parental care was highest during nest building (Fig. 1). In addition, this form of paternal care varied most dramatically (range: 0–100%,  $SD = 30.36$ ). Even so, male contribution to nest building was significantly higher than that of their mates (Wilcoxon matched pairs,  $Z = 2.93$ ,  $n = 25$ ,  $p = 0.003$ ; Fig. 1). In contrast to nest building, males contributed the least to incubation and chick brooding (Fig. 1). Again, between-male

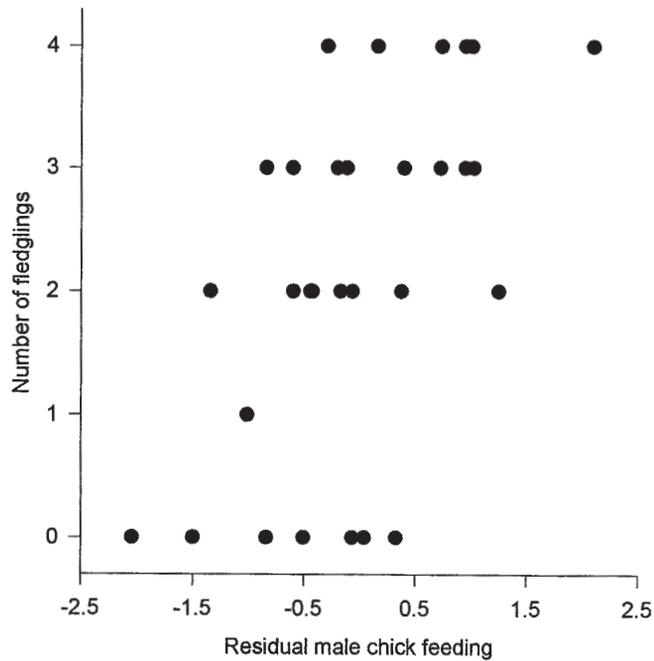
variation of the parental contribution to these activities was considerable (incubation – range: 0–62.6%, SD = 18.7, n = 31; chick brooding – range: 0–72.5%, SD = 18.0, n = 31). The average contribution to incubation and chick brooding was significantly lower in males than females (contribution to incubation: paired t-test,  $t = -5.09$ ,  $n = 31$ ,  $p < 0.001$ ; contribution to chick brooding:  $t = -4.67$ ,  $n = 31$ ,  $p < 0.001$ ; Fig. 1). In terms of chick feeding, however, male contribution was in average as high as in females (chick feeding: paired t-test,  $t = -1.64$ ,  $n = 31$ ,  $p = 0.11$ ). Male feeding contribution ranged from 14.7–93.3% (SD = 15.6, n = 31).



**Fig. 1.** Male (open bars) and female (filled bars) contributions to different categories of parental care (error bars are SD). Two asterisks (\*\*) indicate  $p < 0.01$ , three asterisks (\*\*\*)  $p < 0.001$ .

### Relationship between paternal care, female parental effort and reproductive success

More intensive nest building and constructing bigger nests may decrease incubation or brooding bouts and increase hatching success. However, incubation and brooding time of neither parent seemed to be influenced by male nest building activity (male nest building vs. incubation time of females:  $R^2 = 0.04$ ,  $\beta = -0.21$ ,  $n = 25$ ,  $p = 0.32$ , and males:  $R^2 = 0.02$ ,  $\beta = 0.13$ ,  $n = 25$ ,  $p = 0.53$ ; male nest building vs. brooding time of females:  $R^2 = 0.08$ ,  $\beta = 0.28$ ,  $n = 25$ ,  $p = 0.18$  and males:  $R^2 = 0.001$ ,  $\beta = 0.04$ ,  $n = 25$ ,  $p = 0.87$ ). Moreover, hatching success was also not significantly related to male nest building activity ( $R^2 = 0.05$ ,  $\beta = 0.22$ ,  $n = 25$ ,  $p = 0.29$ ). To evaluate the effect of later paternal effort on reproductive success, stepwise multiple regression analyses were performed with male and female brooding time and feeding frequencies as independent variables and the number of fledglings as a dependent variable. Only residual male feeding rates (see method) entered a stepwise regression model at the significance level  $\alpha < 0.05$  ( $R^2 = 0.32$ ,  $\beta = 0.57$ ,  $n = 31$ ,  $p < 0.001$ ; Fig. 2). Likewise, variation in fledging success was also explained only by residual male feeding of chicks ( $R^2 = 0.30$ ,  $\beta = 0.55$ ,  $n = 31$ ,  $p < 0.01$ ).

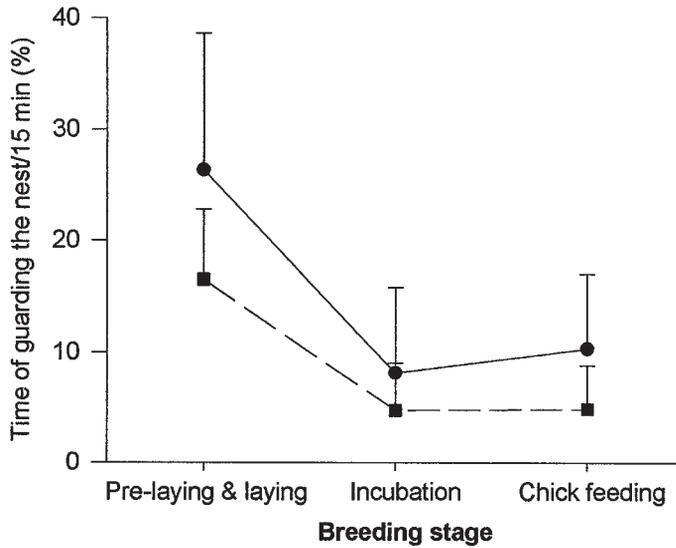


**Fig. 2.** The relationship between residual male feeding of chicks and number of fledglings. Residual values represent feeding rates after controlling for the confounding effect of brood size. Number of fledglings are estimates based on the number of chicks in the nest-box at the age of 13-15 days.

Nest guarding, especially during pre-laying and laying period, made up a considerable part of the daily time budgets of males and females (Fig. 3). A 2-way ANOVA revealed a significant effect of the sex and the stage of breeding cycle on the time parents invested in nest guarding (2-way repeated measures ANOVA: sex effect –  $F_{1,60} = 32.9$ ,  $p < 0.001$ , period effect –  $F_{2,120} = 77.3$ ,  $p < 0.001$ , interaction –  $F_{2,120} = 3.0$ ,  $p = 0.06$ ; Fig. 3). Both sexes invested in nest guarding most heavily in the onset of the breeding cycle, whereas the activity decreased towards the end of breeding cycle. A high initial nest guarding may assure a better protection of the clutch from intra- or inter-specific brood destruction. However, we found that clutch size was not correlated with the time parents guarded their nests during the period of egg laying (only female nest guarding entered a stepwise multiple regression:  $R^2 = 0.04$ ,  $\beta = 0.19$ ,  $n = 31$ ,  $p > 0.3$ ). Similarly, nest guarding during incubation period was not able to explain the number of hatchlings (only female nest guarding entered the regression model:  $R^2 = 0.10$ ,  $\beta = 0.32$ ,  $n = 31$ ,  $p = 0.08$ ), or hatching success (no sex entered the model). Finally, nest guarding during the period of chick feeding could not explain the number of young at fledging age or fledging success (no sex entered the models).

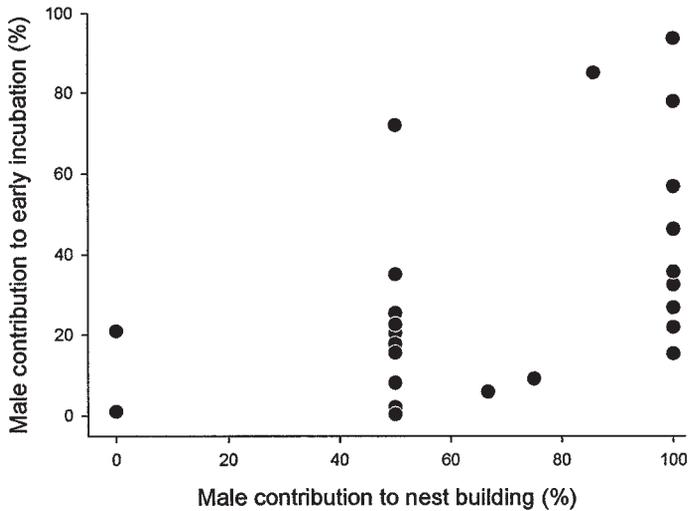
Does early male parental contribution reflect his investment in later breeding stages?

We were unable to detect that the contribution to early male parental activities would have explained the contribution of male parental care in later stages of the breeding cycle (regressions between male contribution to nest building vs. (i) incubation:  $R^2 = 0.02$ ,  $\beta = 0.15$ ,



**Fig. 3.** Time males (solid line) and females (broken line) spent at nest guarding throughout the three periods of the breeding cycle (error bars are SD).

$n = 25$ ,  $p = 0.46$ , (ii) chick feeding:  $R^2 = 0.03$ ,  $\beta = 0.17$ ,  $n = 25$ ,  $p = 0.40$ , and (iii) chick brooding:  $R^2 = 0.001$ ,  $\beta = -0.03$ ,  $n = 25$ ,  $p = 0.88$ ). The early nest guarding likewise proved to be a weak predictor of later paternal effort (early nest guarding vs. (i) incubation:  $R^2 = 0.002$ ,  $\beta = -0.04$ ,  $n = 31$ ,  $p = 0.83$ , (ii) chick feeding:  $R^2 = 0.04$ ,  $\beta = -0.21$ ,  $n = 31$ ,  $p = 0.26$ , and (iii) chick brooding:  $R^2 = 0.02$ ,  $\beta = 0.12$ ,  $n = 31$ ,  $p = 0.50$ ). However, after dividing incubation into early (incubation of incomplete clutches) and late (incubation after clutch



**Fig. 4.** The relationship between male contribution to nest building and early incubation. Male contribution to nest building and incubation refers to the relative activity of males to that of their partners. The early incubation represents the period of time from onset to termination of egg-laying.

completions), we found that the male contribution to nest building, but not to early nest guarding, significantly explained the variation of his contribution to early incubation (nest building and early incubation:  $R^2 = 0.21$ ,  $\beta = 0.46$ ,  $n = 25$ ,  $p = 0.022$ ; Fig. 4; early nest guarding vs. early incubation:  $R^2 = 0.001$ ,  $n = 25$ ,  $p = 0.87$ ).

## Discussion

Our results revealed variation in paternal care between individuals as well as between breeding periods. We show that male parental share was highest during nest building, decreased during incubation and increased again during chick feeding period. Only chick provisioning turned out to be comparable between partners, whereas nest building was more intense for males, and incubation and brooding for females. Provided that male parental care in house sparrows is essential to maximise reproductive success, females may benefit from correctly assessing male parental ability. Because we found variation of parental effort among male house sparrows, females should invest in reproduction according to some male cues that honestly indicate his condition and perhaps also his future parental effort. Although house sparrows are distinctly sexually dimorphic in their plumage, female assessment of male condition based on epidermal sexual characters such as plumage may not be accurate. This is because plumage does not inform about the current male condition, but about the condition during his previous moult (Owens & Short 1995). That is why the size of sexual ornaments of collared flycatchers *Ficedula albicollis* or house sparrows was suggested as informing females mate's about a male previous rather than future reproductive effort (Gustafsson et al. 1995, Griffith 2000). Hence, in order to estimate male condition and his paternal ability, females may pay attention to specific male activities happening prior to pairing and/or copulations. In our study, the fact that male contribution to nest building was highest of all parental activities suggests that this behaviour could be in the house sparrow a candidate for sexual signal. Male nest building was indeed demonstrated to be involved in sexual signalling in several bird species (Garsón 1980, Møller 1982, Borgiá 1985, Evans & Burn 1996, Soler et al. 1998b), but also in invertebrates (e.g. Backwell et al. 1995). For instance, the number of advertised nest cups, nest volume or intensity of nest building were shown experimentally to affect mating success in wrens (Evans & Burn 1996), laying date and clutch size in barn swallows (Soler et al. 1998a) and magpies (Soler et al. 2001). Similarly, Václav & Hoi (2002), who studied the same house sparrow population, found that females started to breed earlier and laid larger clutches when mated with those males investing in early paternal care more heavily than other males. Larger nests in penduline tits *Remiz pendulinus* provide a better insulation and increase hatching success (Grubbaer & Hoi 1996). In collared flycatchers, the time of incubation bouts shortens with increasing nest size, whereas hatching success is not compromised (Moreno et al. 1991). However, we were unable to find any significant relationships between the intensity of male nest building and hatching success or time at incubation. Because we did not measure any physical parameters of the nest, we cannot rule out the possibility that intensity of nest building during the observed period did not reflect, for example, a nest size. However, R. Václav (unpublished results) found for a Viennese population of house sparrows a positive correlation between the intensity of early parental care and nest weight. Overall, our results suggest that instead of constructing a well insulated nest to protect the clutch and chicks from cold, exaggerated male nest building in the house sparrow may

represent a sexual display. Nest guarding may also increase reproductive success, because it lowers the likelihood of egg or brood destruction (Summers-Smith 1963, Veiga 1990, for house sparrows). Nevertheless, nest guarding that was maintained in our house sparrows high until clutch completion did not explain the variation in clutch size.

Male assistance in parental care was lowest in terms of incubation and brooding. This has likely to do with the fact that, as in many other passerines, male house sparrows have lower capacity to incubate than females (Selander & Yang 1966). Yet, we detected that the intensity of male incubation of incomplete and complete clutches was not consistently correlated with the intensity of nest building. The loss of the relationship between male nest building and the incubation of complete clutches might be explained by a reduction of the circulating testosterone of aggressive males as the fertile period of their partners finished. This is a typical image for males in many species with biparental care (Wingfield & Moore 1987, Wingfield et al. 1990). However, such a result could also be a consequence of less aggressive males withdrawing to further advertise their parental ability after clutch completion. The highest egg losses that were found in the nests of males investing heaviest in the early forms of parental care (Václav & Hoi 2002) could in reality be the consequence of such a reduction of paternal care. Importantly, we found that the intensity of male nest building was not only unrelated to late incubation, but also to male feeding visits. This finding is important because we have shown that male parental assistance is critical during the period of chick feeding. Namely, as in several other studies (e.g. Bart & Tornes 1989, Markman et al. 1996, Dickinson & Weathers 1999), we found that solely male provisioning was able to explain the variation in fledgling numbers and fledging success. Similarly as for nest building, early nest guarding was related neither to male incubation, nor to chick feeding. Moreover, intensity of nest guarding itself was not consistent throughout the breeding cycle, declining with time of the breeding cycle.

No matter how intensively they are displayed, male nest building and early nest guarding do not always seem to reliably indicate later paternal effort, say during chick feeding. Some other behaviours, such as courtship feeding in common terns *Sterna hirundo*, might serve as more reliable signals of paternal quality (Nisbet 1973). Nevertheless, as Václav & Hoi (2002) reported, female house sparrows do allocate their reproductive effort in relation to the intensity of early parental activity of their partners. Hence, males are potentially able to manipulate (stimulate) females to start breeding earlier and lay bigger clutches by displaying a high initial paternal effort or, alternatively, just by providing them a complete nest earlier than other males. The latter option is however less likely, because females were often found to lay eggs into almost empty nest-boxes (pers. obs.). As a result of elevated investment in early parental activities, males can benefit through stimulating females to lay larger clutches and potentially produce more offspring. However, as such males are occupied with parental care and leave their partners unguarded just when they are fertile, the likelihood that they will be cuckolded may likewise increase (Václav et al. 2002).

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