

## MATE REPLACEMENT IS COSTLY TO MALES IN THE MULTIBROODED HOUSE SPARROW: AN EXPERIMENTAL STUDY

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**ABSTRACT.**—In species that raise several broods within a breeding season, mate replacement may be costly to males if breeding success is low for newly formed pairs. Alternatively, males could benefit from mate replacement if the new female is in better physical condition than the previous mate. Female House Sparrows (*Passer domesticus*) experimentally handicapped during their first breeding attempt were replaced more frequently than control females. Among females that changed mates, handicapped females remated less successfully than did control females. Relative to control males, males that mated with handicapped females took longer to produce a second clutch. Males that changed mates had shorter relaying intervals but raised fewer fledglings in the following breeding attempt than males that retained mates. These results suggest that mate replacement is costly to males. Courtship rate was positively correlated with male badge size, an indicator of male quality and status, but it was not correlated with any indicator of female quality or female reproductive investment. Increased levels of courtship between two breeding attempts correlated with more rapid laying by replacement females but did not affect the probability of mate replacement or the relaying interval of the original mates. These results suggest that male courtship between clutches may function as a time-saving mechanism when mate replacement occurs. Received 25 September 1995, accepted 22 February 1996.

THE RETENTION OF A MATE between successive breeding attempts may result from inherent advantages (reviewed by Rowley 1983, Newton 1989), or it may be a consequence of constraints on finding a new mate (e.g. Freed 1987). Mate retention from year to year is advantageous in birds that make only one breeding attempt per season, because breeding performance tends to increase with parental age and experience (Ollason and Dunnet 1978, Pugsek and Diem 1983, Saether 1990, Emslie et al. 1992). In contrast, the reproductive effort allocated to the first attempt may prolong the interval between clutches in species that nest more than once per season (Kluyver et al. 1977, Hegner and Wingfield 1987, Tinbergen 1987, Lindén 1988, Smith et al. 1989), potentially resulting in reduced clutch sizes in later attempts (Hegner and Wingfield 1987, Smith et al. 1989). Delays in the onset of second breeding attempts also may reduce fledgling survival, which tends to decline with fledging date (e.g. Kluyver et al. 1977, Dhondt and Olaerts 1981, Arcese and Smith 1985). Experimental evidence (e.g. supplemental feeding, clutch and brood size manipulations) suggests that several factors may influence the reproductive poten-

tial of males and females in multibrooded species (Kluyver et al. 1977, Martin 1987, Eden et al. 1989). Variation in the reproductive potential of individuals may affect mating decisions by their mates following completion of the first nesting attempt.

Males may benefit from changing mates if the replacement is in better physical condition than the first female. Females in better condition may produce a clutch sooner (Johnson and Johnston 1989) and increase subsequent reproductive success (Hegner and Wingfield 1987, Smith et al. 1989). Alternatively, males may be constrained in their ability to change mates because female aggression may prevent other females from accessing nest sites or mates (e.g. Gowaty and Wagner 1988, Arcese 1989, Slagsvold et al. 1992, Veiga 1992, Berglund et al. 1993).

Males of some multibrooded species resume courtship at the end of their first breeding attempt. Although the function of this behavior is not clear, ten Cate and Hilbers (1991) suggest that courtship between clutches acts to stimulate ovulation in the current mate, thereby advancing the start of a new clutch. Male House Sparrows (*Passer domesticus*) direct courtship toward any female that approaches their territory (Seel 1969, Veiga unpubl.data). Thus, In House Sparrows, courtship may signal a male's will-

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ingness to accept a new mate, and a male may benefit by courting in the presence of a female that could become his future social or sexual partner.

I report results of an experiment that tested whether mate replacement is advantageous to males in the multibrooded House Sparrow. Aggression among females is important in maintaining monogamy in this species (Veiga 1992). I handicapped the flying ability of breeding females to explore whether handicapped females are replaced more frequently than control females, and whether males benefit more from mate replacement than from mate retention. I also examined the function of interclutch courtship. If interclutch courtship facilitates acquisition of a superior mate, then males mated with handicapped females should spend more time courting and replace mates more frequently than males mated with control females (although courtship might be enhanced in males that view intact versus handicapped females). If courtship functions to reduce interclutch intervals, then courtship intensity should not depend on the handicapping treatment, and males that court more intensively should have shorter interclutch intervals. A third possibility, that courting males are seeking extrapair copulations, does not yield explicit predictions about frequency of mate replacement or length of the interclutch interval.

#### METHODS

*Study area and species.*—I conducted the study during 1992 and 1993 in a colony of House Sparrows on a 1.3-ha plot surrounded by cattle farms at Collado Villalba, central Spain. The colony consisted of 65–70 pairs that nested in boxes and a few additional pairs that used other artificial or natural nesting sites.

House Sparrows are small passerines (ca. 30 g) that usually raise several broods per season (McGillivray 1983, Singer and Yom-Tov 1988, Summers-Smith 1988). Most pairs that form at the beginning of the breeding season remain intact during subsequent breeding attempts, but mate replacements do occur (Veiga unpubl. data). Hereafter, I refer to the phenomenon of mate retention versus mate replacement as “mate tenacity.” In the population that I studied, males reduce provisioning rates (or stop feeding altogether) of their first broods before the chicks fledge. Some males then begin to court any female that approaches their territory. These behaviors also occur at the end of a second breeding attempt, and they seem to be independent of whether a male’s territory has one or more

nest boxes (Veiga unpubl. data). Hereafter, I refer to this interclutch courtship as “courtship.” Polygynous males raise more fledglings per season than do monogamous males. Most males mate with only one female at a time, however, perhaps because females aggressively exclude other females from entering their territories (Veiga 1992).

*Observational procedures.*—During February and early March, I mist-netted as many birds as possible and marked them with unique combinations of color bands. Most males (but few females) were marked before the start of my nest observations in mid-March. Females paired with marked males were captured at the nest for the handicapping experiment (see below). At the start of egg laying, nests were checked regularly to determine clutch size and hatching date. I weighed nestlings when they were 6 and 12 days old. At day 12, I measured tarsus length and outermost primary length, and marked the chicks with individual combinations of color bands.

To estimate “badge” size of breeding males, I measured the height ( $h$ ) and width ( $w$ ) of the black throat patch while holding the bird in a natural position. The area was calculated as the surface of a circular sector with radius  $h$  and chord  $w$ . Feeding rates by both parents in focal nests were measured when nestlings were 5 (stage 1) and 11 to 12 days old (stage 2). I counted the frequency of feeding trips during two 1-h periods each day (before and after noon) and measured courtship intensity of focal males during these same watches. I scored courtship rate on a discrete scale of 0 to 4 (0: total absence of courtship postures; 4: extreme courtship postures, with neck and head stretched, wings drooped and shivering, and tail raised and spread).

After chicks fledged, I checked nests at intervals of three to five days to determine when the next clutch was started. I defined “relaying interval” as the number of days between the fledging of chicks and the start of egg laying in the next clutch. The precise fledging date was unknown for most nests, but I considered chicks to have fledged when their outermost primary reached 37 mm in length (Veiga unpubl. data). I extrapolated the age at which this length was attained by calculating the daily increase of wing length on the basis of a linear growth (see Veiga 1990). Because nestlings almost always fledge before day 16, and I measured them on 12 day, the error in my estimations of fledging time is probably small.

*Experimental procedures.*—Females were trapped at night on the nest during incubation or, more frequently, when chicks were between 1 and 3 days old. Females were alternately assigned to either experimental or control groups as they were captured. I trapped 50 females in 1992 and 32 in 1993. In the experimental group, I shortened the sixth and seventh primaries of each wing and the four central rectrices by cutting each feather at its base. I clipped 1 mm from the tip of each corresponding feather in the

TABLE 1. Indicators of reproductive investment in first breeding attempts by female House Sparrows relative to experimental treatment (feathers shortened vs. "clipped") and mate tenacity (whether male retained or switched mates for second breeding attempt). Values are  $\bar{x} \pm SD$  (number of females in parentheses).

Variable	Experimental		Control	
	Mate retention	Mate switch	Mate retention	Mate switch
Clutch size	5.00 $\pm$ 0.85 (12)	5.00 $\pm$ 0.87 (9)	5.10 $\pm$ 1.02 (20)	5.50 $\pm$ 0.71 (2)
No. young fledged	3.23 $\pm$ 1.69 (13)	2.75 $\pm$ 1.83 (8)	3.30 $\pm$ 1.34 (20)	4.00 $\pm$ 1.41 (2)
Mass at fledging (g)	24.99 $\pm$ 2.62 (13)	26.65 $\pm$ 2.02 (6)	25.25 $\pm$ 1.97 (20)	23.80 $\pm$ 2.83 (2)
Wing length at fledging (mm)	31.78 $\pm$ 4.29 (13)	31.82 $\pm$ 3.53 (6)	31.12 $\pm$ 3.89 (20)	28.40 $\pm$ 7.64 (2)
Feedings/h at day 5	6.85 $\pm$ 4.00 (13)	6.14 $\pm$ 4.14 (7)	8.55 $\pm$ 2.98 (20)	8.00 (1)
Feedings/h at day 11	11.36 $\pm$ 4.30 (11)	10.60 $\pm$ 7.92 (5)	12.47 $\pm$ 7.03 (19)	13.00 (1)

control group. All females were weighed and marked with unique combinations of color bands. Wing shortening apparently did not seriously affect female behavior or appearance. Experimental females seemed to fly as well as control females, and I did not witness conspecific "floaters" attacking them. For convenience, males initially mated with experimental or control females will be referred to as experimental or control males, respectively.

In total, 41 experimental and 41 control females were studied. A similar number of experimental and control females lost their broods (23 vs. 19, respectively). In some cases, the losses might have been a direct consequence of capture because eggs (more frequently) and nestlings often disappeared or were found dead shortly after females were handled. Experimental females that lost their brood started a new breeding attempt with their previous mate in four of nine cases. This proportion was very similar (6 of 14 cases) in control females. The difference between groups was small, and the effort made by pairs before the feeding of chicks was probably small. Consequently, I pooled relaying pairs and those that succeeded in their first breeding attempt in subsequent analyses. In total, 22 pairs in each experimental and control group could be used to estimate mate tenacity between first and second breeding cycles.

*Statistical procedures.*—Data from both years were pooled. I used one-way and two-way ANOVA to test for differences associated with the experimental treatment (shortening vs. clipping feathers) and mate tenacity (retention vs. replacement of mate) when dependent variables were approximately normally distributed. For the number of breeding attempts (either two or three), I used a three-factor log-linear analysis (Sokal and Rohlf 1981). Data on courtship rates were nonnormal and were analyzed with nonparametric procedures (Siegel 1956).

## RESULTS

*Remating by males and females.*—All focal males mated at least two breeding attempts, and 24 of them (54.5%) made a third attempt. Males paired

with experimental females remated with a new female during a second attempt more frequently than did control males (experimental males: 9 of 22; control males: 2 of 22;  $G = 6.31$ ,  $df = 1$ ,  $P = 0.012$ ). Six of the nine experimental females that were replaced after their first breeding attempt were never seen again. Two of the remaining three nested with males that had not bred previously within the colony. The third experimental female and the two replaced control females mated with experimental males whose former mates disappeared after the first breeding attempt. Based on the above information, the fate of replaced females differed significantly between experimentals and controls ( $G = 6.61$ ,  $df = 2$ ,  $P = 0.037$ ).

*Female quality and previous investment.*—Before manipulation, body size variables (i.e. mass, wing length, and tarsus length) were statistically equal between experimental and control females and between females that retained their previous mate and those that were replaced (two-way ANOVA,  $P > 0.3$  in all cases). The interaction terms were not significant (all  $P$ s  $> 0.4$ ). The variables associated with female reproductive investment (i.e. clutch size, number of young fledged, fledgling quality, and feeding rate) during the first breeding attempt did not vary with treatment or mate tenacity (two-way ANOVA, all  $P$ s  $> 0.15$ ; Table 1), and the interaction terms were not significant ( $P > 0.1$ ). Thus, reproductive investment by females during the first breeding attempt was not affected by the treatment, and female morphology and female reproductive investment did not affect mate tenacity.

*Breeding success.*—Experimental treatment and mate tenacity did not affect the number of breeding attempts started by males (Table 2). No three-factor interaction was revealed by the log-linear analysis ( $G = 0.0002$ ,  $df = 1$ ,  $P = 1.0$ ).

TABLE 2. Indicators of reproductive success by male House Sparrows relative to experimental treatment (mate's feathers shortened vs. "clipped") and mate tenacity (whether male retained or switched mates for second breeding attempt). Values are  $\bar{x} \pm SD$  (number of males in parentheses).

Variable	Experimental		Control	
	Mate retention	Mate switch	Mate retention	Mate switch
Breeding attempts	2.61 $\pm$ 0.51 (13)	2.67 $\pm$ 0.50 (9)	2.45 $\pm$ 0.51 (20)	2.50 $\pm$ 0.71 (2)
No. young fledged (second attempt)	2.31 $\pm$ 1.44 (13)	0.78 $\pm$ 0.83 (9)	2.15 $\pm$ 1.69 (20)	3.50 $\pm$ 0.71 (2)
No. young fledged (entire season)	7.31 $\pm$ 3.66 (13)	5.11 $\pm$ 2.52 (9)	6.40 $\pm$ 2.60 (20)	8.50 $\pm$ 2.12 (2)
Mass at fledging (g) (second attempt)	24.14 $\pm$ 2.54 (9)	26.10 $\pm$ 0.82 (4)	23.74 $\pm$ 3.59 (14)	24.60 $\pm$ 2.26 (2)
Mass at fledging (g) (entire season)	24.00 $\pm$ 2.14 (13)	24.37 $\pm$ 1.28 (7)	24.86 $\pm$ 2.12 (20)	24.25 $\pm$ 0.07 (2)
Wing length at fledging (mm) (second attempt)	29.54 $\pm$ 3.56 (8)	29.52 $\pm$ 6.55 (4)	30.23 $\pm$ 4.72 (14)	31.05 $\pm$ 1.41 (2)
Wing length at fledging (mm) (entire season)	30.78 $\pm$ 3.73 (13)	31.47 $\pm$ 2.36 (7)	31.09 $\pm$ 2.96 (20)	30.50 $\pm$ 2.83 (2)
Relaying interval (days)	13.58 $\pm$ 6.03 (12)	6.86 $\pm$ 2.67 (7)	9.68 $\pm$ 3.76 (19)	6.00 $\pm$ 0.00 (2)

Models of bifactorial interaction of the effects of treatment and mate tenacity on the number of breeding attempts by focal males also were not significant (treatment:  $G = 1.06$ ,  $df = 2$ ,  $P = 0.59$ ; tenacity:  $G = 0.08$ ,  $df = 1$ ,  $P = 0.96$ ).

The mean relaying interval was 1.8 days longer for females mated with experimental males than for females mated with control males ( $\bar{x} = 11.1 \pm SD$  of 5.99 days,  $n = 19$  vs.  $\bar{x} = 9.3 \pm 3.73$  days,  $n = 21$ ; two-way ANOVA,  $P = 0.03$ ). Males that changed mates after the first breeding attempt had a considerably shorter relaying interval than males that retained their mates ( $\bar{x} = 6.8 \pm 2.34$  days,  $n = 9$  vs.  $\bar{x} = 11.2 \pm 5.06$  days,  $n = 31$ ; two-way ANOVA,  $P = 0.002$ ; Table 2).

Neither treatment nor mate tenacity affected the number of fledglings raised by males in their second breeding attempt (two-way ANOVA,  $P = 0.49$  and  $P = 0.15$ , respectively; Table 2). The interaction between these factors was significant, however ( $P = 0.027$ ), indicating that the effect of mate tenacity on fledging success depended on treatment. One-way ANOVAs for experimental and control groups showed that experimental males that remated with a new female raised many fewer fledglings in a second attempt than did those that retained their mates ( $P = 0.01$ ; Table 2). The opposite trend occurred in control males, but the sample size was small ( $n = 2$ ). Among experimental males, the total number of fledglings raised per season did not differ between those that changed mates and those that retained their mates (one-way ANOVA,

$P = 0.13$ ; Table 2). New pairs tended to raise fewer fledglings than did old pairs during the second breeding attempt ( $\bar{x} = 1.27 \pm 1.35$ ,  $n = 11$  vs.  $\bar{x} = 2.21 \pm 1.58$ ,  $n = 33$ ;  $t = 1.77$ ,  $P = 0.085$ ) but about the same number during the third attempt ( $\bar{x} = 3.0 \pm 0.63$ ,  $n = 6$  vs.  $\bar{x} = 2.47 \pm 1.33$ ,  $n = 17$ ;  $t = 0.94$ ,  $P = 0.36$ ). Six new females made two breeding attempts and produced more fledglings in the second attempt than in the first (first:  $\bar{x} = 1.17 \pm 1.17$ ; second:  $\bar{x} = 3.0 \pm 0.63$ ; paired  $t$ -test,  $P = 0.048$ ). Experimental treatment and mate tenacity did not influence the mass or primary length of fledglings in the second breeding attempt or averaged over the whole season (two-way ANOVA, all  $P_s > 0.2$ ), and the interaction between the two factors was not significant (all  $P_s > 0.5$ ).

*Feeding frequency and male courtship.*—Feeding frequency by males during the first attempt was not affected by treatment or mate tenacity (two-way ANOVA, all  $P_s > 0.25$ ; Table 3), and the interaction among factors was not significant (all  $P_s > 0.5$ ). Within sexes, feeding rates were correlated between stages 1 and 2 (males:  $r_s = 0.30$ ,  $P = 0.046$ ,  $n = 45$ ; females:  $r_s = 0.33$ ,  $P = 0.03$ ,  $n = 45$ ; Tables 1 and 3).

Males exhibited no courtship in 26 of 47 cases (i.e. courtship rate score = 0). Courtship rates were not related to experimental treatment or to mate tenacity (Kruskal-Wallis test; treatment:  $H = 1.28$ ,  $n_1 = 26$ ,  $n_2 = 20$ ,  $P = 0.26$ ; mate tenacity:  $H = 0.09$ ,  $n_1 = 30$ ,  $n_2 = 6$ ,  $P = 0.76$ ; Table 3). In experimental pairs, mate tenacity was not associated with courtship rate ( $H = 0.36$ ,  $n_1 = 11$ ,

TABLE 3. Feeding rates during first breeding attempt and courtship scores (0 to 4) of male House Sparrows relative to experimental treatment (mate's feathers shortened vs. "clipped") and mate tenacity (whether male retained or switched mates for second breeding attempt). Values are  $\bar{x} \pm SD$  (number of males in parentheses).

Variable	Experimental		Control	
	Mate retention	Mate switch	Mate retention	Mate switch
Feedings/h at day 5	8.69 $\pm$ 3.54 (13)	6.57 $\pm$ 5.63 (7)	7.25 $\pm$ 3.38 (20)	7.00 (1)
Feedings/h at day 11	5.54 $\pm$ 4.80 (11)	6.20 $\pm$ 6.02 (5)	6.63 $\pm$ 7.45 (19)	12.00 (1)
Courtship score (first attempt)	0.91 $\pm$ 1.22 (11)	1.60 $\pm$ 1.82 (5)	1.16 $\pm$ 1.54 (19)	0.00 (1)
Courtship score (second attempt)	0.50 $\pm$ 1.41 (8)	0.75 $\pm$ 0.96 (4)	0.55 $\pm$ 1.13 (9)	1.00 (1)

$n_2 = 5, P = 0.55$ ). The small number of cases in which males replaced mates precluded a similar comparison in control pairs. Courtship rate and feeding frequency by males were inversely related in nestling stage 2 ( $r_s = -0.45, P = 0.003, n = 45$ ) but not in nestling stage 1 ( $r_s = 0.02, P = 0.91$ ).

Males that had larger badges courted at higher rates ( $r_s = 0.43, P = 0.048, n = 22$ ; Fig. 1), but courtship rate was not correlated with other morphological variables in males or their mates (all  $P_s > 0.4$ ). There was no correlation between courtship rate and relaying interval in control males ( $r_s = 0.20, P = 0.40, n = 19$ ; Fig. 2A) or in experimental males that retained their mates ( $r_s = -0.48, P = 0.13, n = 11$ ; Fig. 2B). Among experimental males that replaced their mates, however, relaying intervals declined with increasing courtship rates ( $r_s = -0.97, P = 0.05, n = 5$ ; Fig. 2C).

DISCUSSION

Males may benefit from breeding successively with the same female. Breeding success may

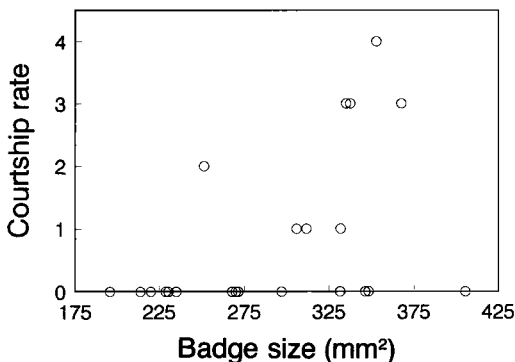


Fig. 1. Relationship between badge size and courtship rate in male House Sparrows.

be improved by mate retention because it may facilitate coordination of the breeding cycles of both partners (Friedman 1977) or increase the breeding performance of the pair in some other

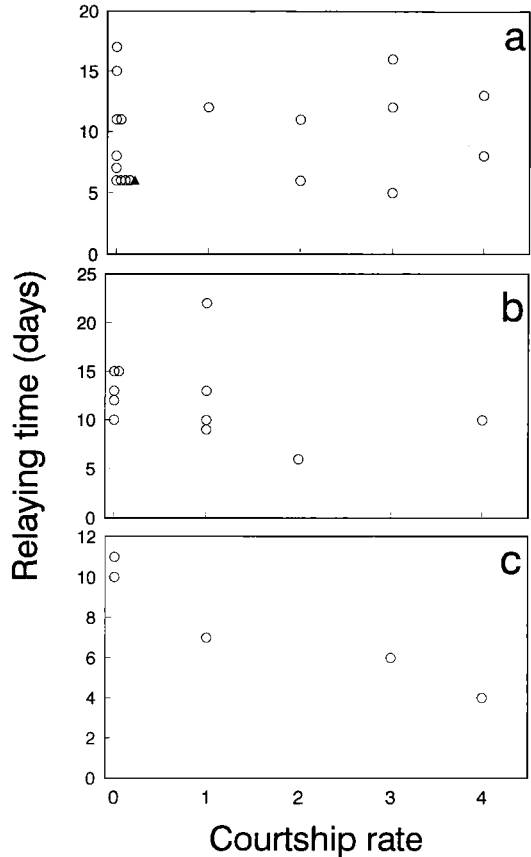


Fig. 2. Relationship between courtship rate and relaying interval (time between fledging of first brood and start of second clutch) in (A) control males (circles: males that retained mate; triangle: male that replaced mate); (B) experimental males that retained mate; and (C) experimental males that replaced mate.

way (Emslie et al. 1992). However, the ability to retain a mate may be limited in several ways. The mate may suffer a significant loss of condition after concluding a breeding attempt and desert or be unable to contend with challengers. To date, however, no empirical evidence suggests that asymmetry in resource-holding potential may favor the intruder. Female House Sparrows that were experimentally handicapped during their first breeding attempt remated with the same male less frequently than did control females. Most experimental females whose mating bond was broken after the first attempt did not breed again within the study colony. These handicapped females may have refrained from starting a new breeding attempt because of increased reproductive effort from the treatment effects. However, females can produce clutches during four months of the year, suggesting that physiological condition is unlikely to constrain new breeding attempts. Even in species whose breeding seasons are shorter than those of House Sparrows, females forced to increase their reproductive effort in the first breeding attempt still can lay a second clutch (e.g. Smith et al. 1989, Slagsvold and Lifjeld 1990; but see Lindén 1988).

Females might have dispersed after their first breeding attempt to pair with a new male some distance from their former nest (e.g. Grant and Grant 1987), or they might have deserted after their nesting site was taken over by an intruding female. Female-female competition plays an important role in the mating strategy of several bird species, including the House Sparrow (Yasukawa and Searcy 1982, Arcese 1989, Slagsvold et al. 1992, Veiga 1992). In my study colony, and possibly where there are many female floaters, female territory owners are frequently challenged by potential settlers. Physical condition was not directly measured in this study, but experimental females that remated with their previous mate took longer to relay than control females, possibly indicating poorer condition (e.g. Johnson and Johnston 1989) and reduced competitive ability.

Although experimental females could have been replaced by females in better condition, my results suggest that these new females were inexperienced, or that new pairs lacked coordination. Relaying intervals were shorter after mate replacement, but the overall number of breeding attempts per season was not affected by treatment or mate tenacity. Males whose handicapped mates were replaced raised fewer

fledglings in subsequent attempts. Thus, replacement of even a handicapped mate was disadvantageous to males. Consequently, the hypothesis that males can increase reproductive success by mate replacement was not supported.

Males seemed to benefit from interclutch courting behavior. Those that courted at a high rate had no difficulty retaining their current mate, and the relaying interval was shorter for active courters in cases where experimental females were replaced. If replacement cannot be avoided, and the previous female is ejected by a floater, males could potentially benefit from an early start of their second breeding attempt. It is not clear, however, whether males can use behavioral cues to assess the probability of losing a mate. Investment by the female during the first breeding attempt was not affected by the experimental treatment, and it did not influence subsequent mate retention. Courtship rate did not seem to be influenced by treatment, although the procedure used to quantify courtship may have been insufficient to detect any possible operative variation in courtship behavior. It is more parsimonious to assume that the male is not able to use any cue to predict whether or not his mate will be replaced. By courting indiscriminately, males apparently incur no additional risk of losing a mate, while at the same time improving their chances of reducing relaying time if a mate replacement does occur.

In the House Sparrow, courtship typically occurs in communal displays that function in obtaining both primary mates and extrapair copulations (Møller 1987, Veiga unpubl. data). In the population that I studied, polygynous males were rare owing to female-female aggression, but they raised more fledglings per season than did monogamous males (Veiga 1992). In the present study, no cases of simultaneous polygyny were observed. However, it is possible that under other circumstances, such as with larger distances between nests, or when large numbers of floaters are present, female-female aggression would be less effective in preventing males from pairing with additional females. In the Pied Flycatcher (*Ficedula hypoleuca*), males apparently are polyterritorial to reduce the probability of aggression among females (Breihagen and Slagsvold 1988, Slagsvold et al. 1992). In the House Sparrow, males with large badges courted at a higher rate and obtained more extrapair copulations (Møller 1988, 1992). Even if the chance of obtaining additional females or

extrapair copulations is highly unpredictable, large badge size and high courtship rate will be favored if fitness costs of these traits are reasonably small. In my study, males that courted at a higher rate fed chicks less frequently, but they did so with no apparent reduction in the number or quality of their offspring.

In conclusion, my study shows that mate retention between successive breeding attempts was advantageous for male House Sparrows. The possibility that this was constrained by the ability of the female to fend off floaters deserves further study. Such effects emphasize the importance of mate selection by males at the start of the breeding season. Mate choice by males, and the possible cues they use in exercising it, have rarely been investigated (see Muma and Weatherhead 1989, Hill 1993). Future investigations should address the influence of population variables such as sex ratio, abundance of male and female floaters, and spatial limitations within breeding colonies on courtship behavior, mate tenacity, and breeding success. A comparative study within the subfamily Ploceinae, which has a well-established phylogeny (viz. Summers-Smith 1988, Sibley and Ahlquist 1990) and includes an array of species along the monogamy-polygamy continuum, would be a useful means of investigating the evolutionary relationships between mating systems and mate retention in multibrooded species.

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