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Food supplementation affects extrapair paternity in house sparrows (*Passer domesticus*)

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Extrapair paternity (EPP) is common among birds, but the reasons why it varies within and among species are less clear. In particular, few studies have experimentally examined how food availability influences paternity and sexual behavior. We manipulated food supply in a nest-box population of house sparrows, *Passer domesticus*, a colonial passerine with extensive biparental care. During three successive breeding attempts, we changed food availability at nest sites and examined behavior and genetic parentage. DNA fingerprinting revealed that the level of EPP within broods was five times lower in pairs nesting at sites continuously supplied with extra food. With extra food, mates spent longer time together at the nest, but this was mainly due to a change in female behavior; females but not males increased total nest attendance. Moreover, we found that individual males did not change within-pair copulation frequency across treatments, suggesting that our experiment did not influence male control over fertilizations through copulation behavior. Instead, our study shows that ecological factors can have a strong influence on the time budgets of males and females, which consequently affects the occurrence of EPP. *Key words:* extrapair paternity, food supplementation, female behavior, house sparrows, *Passer domesticus*. *[Behav Ecol 14:730–735 (2003)]*

There is a considerable variation in the frequency of extrapair paternity (EPP) within as well as among bird species, but the reasons for this variation remain largely unclear (reviewed by Petrie and Kempenaers, 1998). Socio-ecological factors such as breeding synchrony (Stutchbury and Morton, 1995; Weatherhead and Yezerinac, 1998; for review see Møller and Ninni, 1998) and breeding density (Gowaty and Bridges, 1991; Hill et al., 1994; for review see Westneat and Sherman, 1997) may influence opportunities for extrapair copulations (EPCs). The effects of these factors are, however, controversial, and opportunities for EPCs can also be influenced by other ecological factors (e.g., Westneat and Sherman, 1997). One such factor may be food availability, but except for studies by Hoi-Leitner et al. (1999) and Westneat (1994), no experimental studies have examined the role of food availability on EPP. Although Hoi-Leitner et al. (1999) reported an increase of EPP with higher food availability in serins, *Serinus serinus*, food supplementation led to a decrease of EPP in red-winged blackbirds, *Agelaius phoeniceus* (Westneat, 1994).

In this study, we experimentally investigated the influence of food availability on EPP in house sparrows, *Passer domesticus*, a colonially breeding passerine with biparental care (Cramp, 1994). The socially monogamous house sparrow is an ideal species for studying the influence of ecology on EPP for the following reasons. First, it breeds under highly variable ecological conditions (e.g., nesting habitats and climate; see Cramp, 1994). Second, the proportion of extrapair offspring varies between geographic populations, ranging from 1 up to 20% of the young (Cordero et al., 1999; Griffith et al., 1999; Veiga and Boto, 2000; Wetton et al., 1987; Wetton and Parkin, 1991; Whitekiller et al., 2000). Third, as in several other colonial species, male house sparrows are faced with a trade-off: either to guard their mates or guard their nests (Birkhead et al., 1987). Nest-site competition in colonial house sparrows is intense throughout the whole breeding season, with a high risk of losing nest sites, clutches, or nestlings when they are not guarded (Møller, 1987b; Summer-Smith, 1963; Veiga, 1992). In contrast, mate guarding seems to increase with colony size, possibly reflecting increased sperm competition when nesting in colonies (Tost, 1994). Moreover, in house sparrows frequent within-pair copulations may be used as an alternative paternity guard (Møller, 1987a).

We had two contrasting predictions when studying the effect of food availability on EPP in house sparrows. With extra food, both sexes may stay longer at the nest, resulting in males being more efficient in assuring their paternity through mate guarding (see Birkhead and Møller, 1992). Alternatively, the level of EPP may be lower at sites without extra food because females breeding under such conditions are less able to pay the energetic costs of seeking EPCs (see Slagsvold and Lifjeld, 1997). Moreover, females in poor habitats may be more dependent on male help in rearing the offspring and also for this reason less likely to seek EPCs (Gowaty, 1996; Griffith, 2000).

METHODS

Study site and population

We studied house sparrows at the Schönbrunn Zoo in Vienna from March to July 1999. At this site, house sparrows often nest close to available food sources (i.e., food offered to the captive animals). We placed 80 nest-boxes on opposite, external walls of five barns (four barns being approximately 100 m apart and about 300 m away from the fifth). Five or 10 nest boxes were hung approximately 80–100 cm apart on each wall. Because birds nesting on the opposite walls of a barn had no visual contact with each other, we thus created 10 separate nesting sites. Over the course of three successive breeding attempts, 45, 42 and 42 pairs, respectively, produced eggs. It is likely that the short distances between nest-boxes and the

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aggressive behavior of resident nest-box owners prevented other birds from settling in the remaining nest-boxes as the breeding season progressed. Finally, only 24, 33 and 39 pairs, respectively, produced nestlings. We did not detect any nest site changes among resident birds as a response to the experimental treatment. Adult birds were trapped, color-ringed, measured, and bled during incubation and chick feeding throughout the breeding season. The whole procedure did not take longer than 5 min. We repeatedly confirmed the identity of individuals nesting in the nest-boxes.

Experimental design

In the beginning of March, approximately 3 weeks before laying of the first egg, we distributed food at each nesting site (wall). The food consisted of millets *Panicum miliaceum*, offered on the sides of each nest-box. At each site, we additionally installed two feeders filled with a commercially sold mixture of seeds for captive birds. We also spread the seeds on top and below of all nest-boxes. Thus, breeding birds within each nesting site did not have to compete for the supplemented food.

At each barn, we randomly selected one site (wall) from where the food supplementation was to be removed. We then completely removed the extra food when the first pair started egg-laying at each of these sites. At the remaining sites, we continued supplying birds with extra food. We thereby created two experimental groups: one with uninterrupted food supplementation lasting until clutch completion of the last pair at the nesting site (i.e., until the end of the presumed fertile period), and a second group with the extra food being removed when the first pair at the site started egg-laying. To avoid any influence of food supplementation on EPP in the latter group, we excluded the first laying pair at each nesting site from our analyses. Moreover, to avoid effects of asynchrony, we excluded all pairs that did not start egg-laying within 1 week after the first breeding pair at each site. We altered food availability throughout the breeding season, so that all nesting sites experienced treatments with and without extra food. This allowed us also to use pairwise comparisons when testing the influence of food supply on EPP.

Behavioral observations

We monitored behavior throughout the whole breeding season. Copulation activity in house sparrows peaks around 2–3 days before start of laying and remains high until the last egg is laid (Møller, 1987b; Tost, 1994; Václav, unpublished data). Because temporal patterns of copulations are supposed to reflect intensity of sperm competition (Birkhead and Møller, 1992), we only analyzed behavior from 2–3 days before the start of egg laying until the penultimate egg was laid. In our daily 15-min protocols, we monitored the time when birds were alone or together with their mates at the nest site (within 1 m), as well as copulation frequency. At all nesting sites, birds were observed from 0700 to 1000 h because copulation frequency is highest then (Tost, 1994; Václav, unpublished data), and fertilization is likely to take place at that time. Daily observations followed a rotating scheme. Because we wanted to examine the effects of the treatments on individual birds, we restricted the analyses of behavior to 13 pairs that nested in both treatments.

DNA fingerprinting

We collected blood samples (about 50–100 µl per individual) by puncturing the brachial vein. The blood was suspended in Queen's lysis buffer (Seutin et al., 1991) and stored at 4°C until analysis. During three breeding attempts, we obtained blood samples from 24 families (8, 9, and 7) with extra food and from 22 families (6, 7, and 9) without extra food. In total, we analyzed 46 families produced by 23 pairs. Of these, six families (three pairs) only included males and chicks (we were not able to trap the females).

Laboratory procedures followed those previously described in detail by Krokene et al. (1996). In brief, we loaded 3–5 µg of *Hae*III-digested DNA onto 20 × 40 cm 0.8% agarose gels in 1× TBE buffer. The gels were electrophoresed at 1.2 V/cm for about 40 h. DNA was transferred onto nylon membranes by Southern blotting and hybridized with the minisatellite probe *per* (Shin et al., 1985). The probe was radioactively labeled with ^{32}P-dCTP by random priming using the Prime-a-Gene labeling system (Promega).

All fingerprints were scored by R.V., following standard methods (e.g., Westneat, 1993). Scoring was done blindly with respect to the experiment. On average, 29.7 ± 1.15 DNA bands were scored in adults (range 15–48, $n = 45$) and 29.7 ± 0.59 bands in chicks (range 10–46, $n = 140$). When chick profiles were markedly less intensive than those of the parents ($n = 23$ chicks), we ignored light bands in the parental fingerprints (e.g., Westneat, 1993). Following other workers (e.g., Krokene et al., 1996), we used novel fragments (i.e., chick bands not present in either of the putative parents) and band-sharing when determining parentage. Assuming that all 80 chicks without any novel bands were offspring of their putative parents and that one novel band in 9 chicks was due to mutation or other random causes, the probability of finding three novel bands by random causes alone was 0.001 ($[9/89]^3$). Thus, we would expect to find only 0.13 chicks with 3 novel bands in our sample of 123 chicks. We therefore concluded that chicks with more than two novel bands represented cases of extrapair parentage. We calculated the band-sharing coefficient (D), the proportion of bands shared between two individuals, as described by Wetton et al. (1987). As the expected lower limit of band-sharing between chicks and their genetic parents, we used the lowest D value (0.41) among chicks with no novel bands (e.g., Krokene et al., 1996). Other workers have used statistically determined thresholds for band-sharing between genetic parents and their young (e.g., Westneat, 1993). Following this method, we found that the lower, one-tailed 95% limit of the band-sharing distribution was 0.43 (parents and chicks with zero novel bands; mean = 0.57, SD = 0.08, $n = 80$). Moreover, the upper 95% limit for band-sharing between supposedly unrelated adults (pair members) was 0.38 (mean = 0.23, SD = 0.09, $n = 21$), suggesting that there was no overlap between these two distributions. Using the value 0.43 instead of 0.41 for the lowest expected band-sharing between genetic parents and young did not change our results, the number of extra-pair chicks, nor the difference in EPP between experimental treatments (see below).

Statistical analyses

Even if there was no significant difference in brood size between treatments (with extra food: 4.1 ± 0.56, $n = 18$, without extra food: 4.2 ± 0.56, $n = 16$, Mann-Whitney: $U = 132$, $p = .68$), we controlled for this variable by analyzing the proportion of extrapair young in each brood. To avoid pseudoreplication, we randomly selected one brood for each breeding pair when testing the seasonal pattern of EPP. Moreover, we used mean values for pairs that were exposed to the same treatment more than once. We used parametric statistics when the assumptions for these methods were met. Means ± SEs are given unless otherwise stated.

RESULTS

Genetic parentage

In 65% of chicks (80/123), the fingerprints showed no novel fragments; they completely matched those of the putative parents (Figure 1). Mean band-sharing with the putative mother and father was 0.57 ± 0.01 (range: 0.41–0.78) and 0.56 ± 0.01 (range: 0.43–0.79), respectively. We conclude that all these chicks were genetic offspring of their social parents.

The fingerprints of the remaining 43 chicks showed 1–16 novel fragments (Figure 1a,b). With three exceptions, all chicks were the genetic offspring of their putative mother. The remaining three chicks had low band-sharing with their social mother (Figure 1a). According to the band-sharing values for the chicks with 5 and 13 novel bands (mother–chick: $D = 0.30$ and 0.19, respectively, father–chick: $D = 0.38$ and 0.26, respectively), they were unrelated to both putative parents. In the third case (10 novel bands), high band-sharing with the social father ($D = 0.62$) but not with the mother ($D = 0.27$) suggests that this chick was sired by the putative father but had another genetic mother. Thus, the first two chicks were likely a result of intraspecific brood parasitism, whereas the third chick represents a case of quasi-parasitism. Using 0.43 as the cut-off point (see Methods), two chicks fell just below this threshold (0.41 and 0.42, respectively), but their fingerprints showed no novel bands. We therefore conservatively assumed that they were genetic offspring of their tending mother. These chicks were from the food treatment (two broods with no extrapair young), and excluding them from the analyses did not change the results presented below.

Three chicks shared relatively few bands with their putative father ($D = 0.35$, 0.38, and 0.38), but their fingerprints showed only two novel bands (Figure 1b), so we conservatively assumed that they were sired by their social father. Two of these chicks were from the non-food treatment (two broods, one with and one without extrapair young). The third chick was from the food treatment (no extrapair young in the brood). Thus, excluding these chicks from the analyses did not change the results presented below. For all other chicks with 0–2 novel bands, band-sharing with the putative father was above the critical value for parentage exclusion (i.e., 0.41 or 0.43).

Mean band-sharing between putative fathers and offspring with more than two novel bands was low (0.29 ± 0.02, range: 0.03–0.62, $n = 27$) and comparable to that between pair mates (i.e., supposedly unrelated individuals; 0.23 ± 0.02, range: 0.03–0.35, $n = 21$). With two exceptions, all 27 chicks fulfilled both criteria for paternity exclusion (Figure 1b), and we conclude that they were sired by extrapair males. The two remaining chicks, with 9 and 10 novel bands had high band-sharing with their social father (Figure 1b). One of them (10 novel bands) corresponds to the case of quasi-parasitism mentioned above. The second chick (9 novel bands; father–chick $D = 0.53$, mother–chick $D = 0.47$) remains uncertain, and we refrained from determining parentage for it. This chick was from the non-food treatment, and the rest of the brood contained only within-pair young. Thus, classifying the chick as a case of EPP would support our finding that cuckoldry was more frequent in the non-food treatment (see below).

In the families where only the putative fathers were sampled (17 chicks from 6 broods), we used band-sharing when examining parentage. The lower limit for band-sharing was the same as in the cases where both social parents were sampled ($D = 0.41$). Three of 17 chicks were below the critical limit: $D = 0.19$, 0.30 and 0.39. However, because one of them had relatively high band-sharing with its putative father (even if we used 0.43 as cut-off), we conservatively concluded that only two of these chicks (from two broods) were sired by extrapair males. The third chick was from the food treatment (with only within-pair young in the brood). Nevertheless, classifying this chick as a case of EPP does not qualitatively change the results presented below (because its parents produced two additional broods: one without EPP in the food treatment and one with EPP in the non-food treatment).

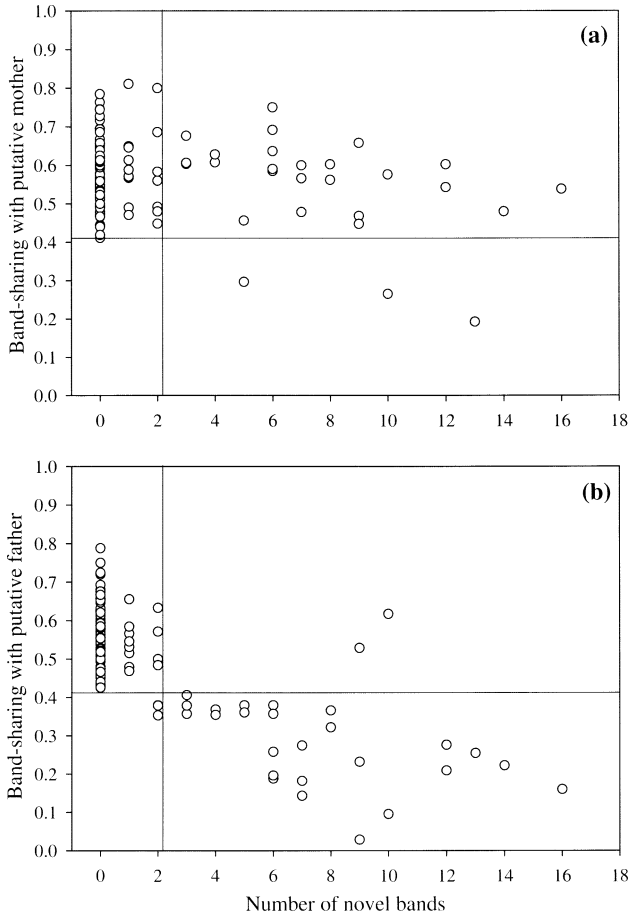

Figure 1
Relationship between the number of novel bands in offspring fingerprints and band-sharing with (a) the putative mother and (b) the putative father. Lines indicate criteria for parentage exclusion.

In summary, extrapair males sired 18% (25/136) of the chicks in 43% (20/46) of the broods. Moreover, we recorded 1 case of quasi-parasitism (1% of chicks [1/140] and 2% of nests [1/46]) and 2 cases of intraspecific brood parasitism (1% of chicks [2/140] and 4% of nests [2/46]). The latter three cases are not dealt with further in this paper.

Extrapair paternity and habitat quality

The proportion of extrapair chicks per brood did not differ significantly among successive breeding attempts (Kruskal-Wallis ANOVA: $H = 1.14$, df = 2,23, $p = .56$). We found, however, that pairs nesting at sites with additional food had significantly fewer extrapair chicks per brood than those without extra food (Figure 2). Restricting the analysis to the 11 pairs that nested in both treatments yielded the same result (without extra food: 0.33 ± 0.09; with extra food: 0.06 ± 0.04; Wilcoxon matched pairs: $T = 6.5$, $p = .032$). In addition, we examined the proportion of broods containing extrapair young by combining the 12 pairs that nested in only one of

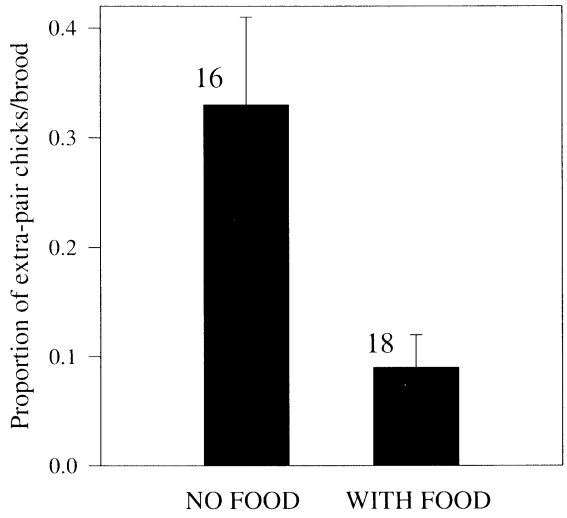

Figure 2
Proportion of extrapair offspring (mean ± SE) in relation to experimental treatment. Numbers above bars denote sample sizes. Mann-Whitney: $U = 77.5$, $p = .015$.

the treatments with a randomly selected treatment and brood for the 11 pairs that nested in both treatments. This showed that pairs without extra food tended to more often have extrapair young in their broods than those with extra food (6/9 vs. 3/14 broods; Fisher's Exact test, $p = .08$).

Behavior and habitat quality

When provided with extra food, mates stayed longer at the nest together (Figure 3a). This was probably caused by a change in female behavior: females but not males increased the total time that they stayed at the nest (Figure 3b,c). However, within-pair copulation rate did not differ between treatments (without extra food: 0.50 ± 0.20 copulations per 15 min; with extra food: 0.66 ± 0.31; paired t test: $t = 0.38$, $n = 13$, $p = .71$).

DISCUSSION

Our study shows that habitat quality can have a strong influence on the time use of house sparrows and, consequently, on the occurrence of EPP. After ceasing to supply pairs of house sparrows with extra food, we found that the number of broods with extrapair chicks increased by about three times. Moreover, within broods the proportion of young sired by extrapair males was about five times lower when pairs were continuously supplied with extra food. Similarly, Westneat (1994) reported that male red-winged blackbirds supplemented with extra food sired more chicks in their broods than did control males. Our results also suggest that female house sparrows nesting close to food sources avoided EPCs or were at least indifferent to them. The strongest indication for this comes from the finding that females prolonged their bouts at the nest when allowed to breed in a food-rich habitat and, consequently, EPP declined. This is contrary to the findings of Westneat (1994), who reported that the decline of EPP was associated with a change in male behavior. Nonetheless, both studies are congruent in that changes in time allocation may have consequences for paternity. Therefore, any factor, such as food availability, that influences the time a male and female stay together near the nest would be expected to affect the level of EPP. For

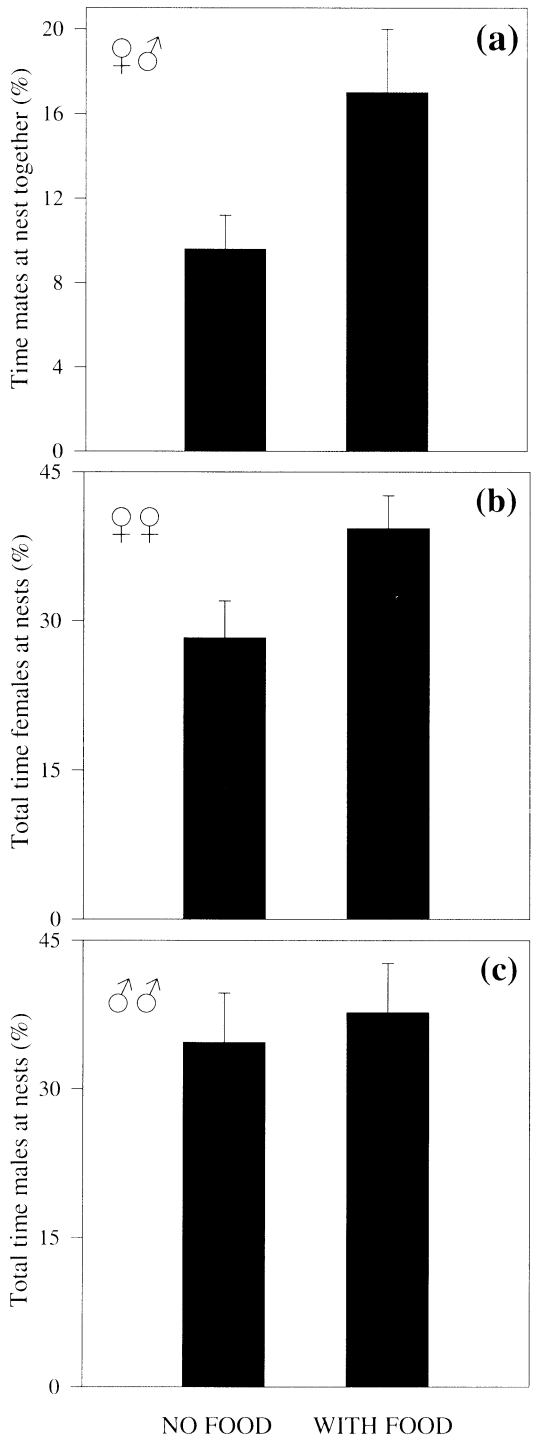

Figure 3
Time spent at the nest (%, mean ± SE): (a) time mates stayed together at the nest (paired t test: $t = 2.18$, $n = 13$, $p = .049$) and total time spent at the nest by (b) females ($t = 2.23$, $n = 13$, $p = .046$) and (c) males ($t = 0.59$, $n = 13$, $p = .57$). Total time includes time alone and with the mate. Data from pairs nesting in both experimental treatments.

example, seasonal fluctuations in the level of EPP may correlate with weather conditions during female fertility (see Valera and Hoi, 1999). It is possible that this relationship reflects the costs of females leaving their clutch unattended rather than the costs of engaging in EPCs.

Female house sparrows are subject to intense harassment by males, and forced copulations are common (Møller, 1987a; Summer-Smith, 1954). When the probability of harassment is high and resistance is costly, it would pay females to accept forced copulations rather than to be injured or killed (Westneat et al., 1990). If EPP is related to the degree of male harassment, we would expect that males incur higher paternity losses in habitats where they have to stay away from their mates longer. Our results seem consistent with this expectation, suggesting that male harassment might be one determinant of extrapair fertilizations.

As an alternative to the idea that females avoid EPCs when supplied with extra food, the lower levels of EPP may simply reflect that males were more able to control females when they spent more time together at the nest. Davies and Lundberg (1984) were able to change the social mating system in dunnocks *Prunella modularis* from polygynandry to polygyny by food supplementation. In our study, we altered the genetic mating system with food supplementation. Both studies are at a first glance consistent with the suggestion that ecological factors influence the abilities of males to control females. It is, however, questionable whether males actually can control their mates in these two species. In the dunnock, the change in mating system was due to a reduction in female territory size (Davies and Lundberg, 1984). In our study, males could stay longer with their mates only because females spent more time at the nests. Furthermore, the time house sparrow mates stay together at the nest seems to reflect male attractiveness rather than male mate guarding (Václav et al., 2002). In addition, our experiment shows that males did not respond to the increased risk of cuckoldry by increasing within-pair copulation frequency.

Female house sparrows appear to have ample opportunity when away from their mate to pursue EPCs. Several hypotheses have proposed constraints other than male control that could limit female promiscuity. Our study addresses three of these. First, by adding extra food to the nest sites, we should have reduced energetic costs preventing females from seeking EPCs (Slagsvold and Lifjeld, 1997). Contrary to the prediction, however, EPP was lower at nest sites supplied with extra food. Second, Gowaty (1996) hypothesized that females might be constrained from seeking EPCs because of the necessity of paternal care. Her prediction that females nesting in richer environments should produce more extrapair offspring is not supported by this study (but see Hoi-Leitner et al., 1999). Gowaty (1996) also predicted that high-quality females should have more extrapair young, presumably, consistently more in each breeding attempt. In our study, we found that EPP changed within a female from one breeding attempt to another as the food treatment shifted, a result not consistent with the prediction. Third, females may benefit from male mate guarding when extrapair males are aggressive (Gowaty and Buschhaus, 1998). This is unlikely in house sparrows because food supplementation should have decreased the exposure to harassment, yet EPP did not increase. We conclude that females did not take advantage of the improved habitat quality by seeking EPCs.

In conclusion, our study shows that ecological factors affecting the time budgets of males and females may have important consequences for extrapair paternity. Similarly, in a correlational study, Reyer et al. (1997) found that ecological factors determine the occurrence of extrapair fertilizations in water pipits *Anthus spinoletta*. We believe that it would be rewarding if more studies investigated the effects of ecological conditions on the dynamics of sexual conflict.

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