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UNIVERSITY OF OKLAHOMA
GRADUATE COLLEGE

**CORRELATES OF EXTRA-PAIR PATERNITY AND THE EFFECTS OF
ECTOPARASITES ON NESTLING GROWTH, PARENTAL PROVISIONING
AND REPRODUCTIVE SUCCESS IN THE HOUSE SPARROW**

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

Doctor of Philosophy

By

ROBIN R. WHITEKILLER
Norman, Oklahoma
2000

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ECTOPARASITES ON NESTLING GROWTH, PARENTAL PROVISIONING
AND REPRODUCTIVE SUCCESS IN THE HOUSE SPARROW**

**A Dissertation APPROVED FOR THE
DEPARTMENT OF ZOOLOGY**

BY

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Chapter 1

BADGE SIZE AND EXTRA-PAIR FERTILIZATIONS IN THE HOUSE SPARROW

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Abstract. For House Sparrows, *Passer domesticus*, it has been proposed that the size of a male's throat badge correlates with his success in avoiding cuckoldry as well as obtaining extra-pair copulations (EPCs), and that females gain indirect (genetic) benefits from EPCs with large-badged males.

Alternatively, female House Sparrows may engage in EPCs as a guard against their social mate's infertility. We used multi-locus DNA fingerprinting to examine paternity and found that among 41 broods and 136 offspring, 20% of the offspring were attributable to extra-pair fertilizations (EPFs). Forty-one percent of the 34 males were cuckolded; however, large-badged males were as likely to be cuckolded as small-badged males. Moreover, we found no evidence that large-badged males were inherently superior to small-badged males in terms of survivorship. We compared the prevalence of unhatched eggs in broods with and without extra-pair offspring to determine whether EPFs are associated with hatching failure. Although we detected no association between hatch failure and EPFs, enhanced fertility remains a plausible EPC benefit to females, but experimental approaches may be required to evaluate its significance.

Key words: *cuckoldry, extra-pair copulation, extra-pair fertilization, fertility insurance, House Sparrow, Passer domesticus, sexual selection.*

INTRODUCTION

Conspicuous ornaments could be favored under sexual selection if they provide some advantage in male-male competition for mates and/or are attractive to females. In the latter case, two types of benefits to females have been proposed. Females might gain direct (nongenetic) benefits (Trivers 1972, Kirkpatrick and Ryan 1991) if ornamented males provide more parental care, possess better territories, or better guard the female from predators or the harassment of conspecifics. Alternatively, conspicuous traits might indicate indirect (genetic) benefits (Fisher 1930, Hamilton and Zuk 1982, Kirkpatrick and Ryan 1991), thereby conferring greater fitness on the female's offspring.

Research on House Sparrows (*Passer domesticus*) indicates that females of this species may gain direct benefits from pairing with highly ornamented males. In a Danish population, Møller (1988) showed that males with large throat badges were more likely to acquire mates than small-badged males; large-badged males, in turn, tended to occupy areas with better nesting sites. In an Oklahoma population, Voltura (1998) found that large-badged males do a greater share of nestling feeding than small-badged males.

Male ornamentation additionally has been suggested to play a role in the extra-pair mating system of House Sparrows. Although the species is considered mainly monogamous, females solicit extra-pair copulations (EPCs) and are targets for forced extra-pair copulations (Møller 1987). Møller (1990) reported that large-badged males performed more EPCs than small-badged

males, and he suggested that females may gain indirect benefits by choosing large-badged males as EPC partners.

Møller's perspective (1990) emphasizes the potential role of badge size as a true indicator of male genetic quality; he proposed that the trait is under strong directional sexual selection by virtue of its importance in female mate choice and in the context of sperm competition. In addition to finding that male badge size is related to EPC participation, Møller (1990) also found that large-badged males copulate more often with their own mates than small-badged males, and that they appear to guard their mates more intensely than do small-badged males (Møller 1987). These behavioral observations, along with the larger testes size of large-badged males (Møller and Erritzoe 1988), led Møller (1990) to predict that such males have greater success at siring extra-pair offspring while simultaneously avoiding cuckoldry.

Using DNA fingerprinting techniques, Wetton and Parkin (1991a) found that 13.6% of the offspring in a British population were sired by extra-pair males. However, subsequent research on both that population as well as a Spanish population showed no support for Møller's prediction that large-badged males would be cuckolded less often than small-badged males (Cordero et al. 1999). Instead, Wetton and Parkin's (1991b) results have led to an alternative hypothesis for why female House Sparrows engage in EPCs. They found a striking association between the number of unhatched eggs in a clutch and the presence of extra-pair offspring in the brood: the extra-pair fertilization (EPF) rate in broods with at least some hatching failure was roughly twice as high as in

broods where all eggs hatched successfully. This result prompted them to suggest that females may use EPCs more as a guard against a mate's potential infertility, than as a means to upgrade the genetic quality of their offspring.

We examined the frequency of extra-pair offspring in House Sparrows using multi-locus DNA fingerprinting. We also used video image analysis to measure digitized photographs of male badges, and we used those measurements to investigate whether variation in male badge size is related to loss of paternity to extra-pair matings, as Møller (1990) predicted, or to male survival. By comparing the prevalence of unhatched eggs among broods with and without extra-pair offspring, we also tested the generality of Wetton and Parkin's (1991b) finding that female production of offspring sired by EPFs is associated with hatching failure.

House Sparrows are semi-colonial passerines that begin breeding in central Oklahoma in March and continue through early August, producing two to three clutches of approximately four to five eggs each. This species readily uses nest boxes (Summers-Smith 1963); both parents participate in nest building, incubation, and feeding of the nestlings. Incubation lasts approximately 11 days and most young fledge about 14 days after hatching.

METHODS

STUDY SITE AND GENERAL FIELD METHODS

We erected 100 nest boxes at two sites (North Base and South Base, University of Oklahoma, Norman, Oklahoma) in 1993 and 1994. One hundred and

nineteen additional nest boxes were erected at four additional sites near North and South Bases in 1995 and 1996. We censused nest boxes at least twice weekly during the 1994-1997 breeding seasons to determine the date the first egg was laid, clutch size, number of eggs that hatched, number of young that fledged, and inter-brood interval. When the date the first egg was laid was not observed, it was calculated assuming that a female lays one egg per day.

Adults were captured in ground traps, mist nets, or in wire corridors attached to the nest box (Mock et al. 1999). We weighed individuals on an electronic balance (± 0.1 g) and then banded each with U.S. Fish and Wildlife aluminum bands plus a unique combination of plastic color bands for field identification. A scaled close-up photograph of each male's badge was taken at the time of his capture using a 0.5 X 0.5-cm grid in the background. All badge area estimates were from males captured during the breeding season, which minimizes the effects of feather tip abrasion on visible badge size (Griffith et al. 1999b). The badge area was quantified using video image analysis. In a separate sample, we found that area estimates obtained from photographs were highly correlated with estimates for the same individuals based on video-taped images of their badge sizes (Whitekiller et al., *in review*). Badge sizes were scored independently by R. Whitekiller and K. Voltura. Badge size for each male was scored "blind" as to his identity. The areas obtained by the two scorers were highly correlated ($r = 0.99$, $n = 65$, $P < 0.001$). Cordero et al. (1999) reported a similar technique for measuring badge size and found that it produced similar

measures as that of Møller (1990). Mean values for the two sets of scores are used in all analyses.

To examine the relationship between badge size and adult male survival, we compared the badge size of males banded as adults in 1994 or 1995 that were resighted within the next two years with the badge size of males that failed to return. Individuals were considered to have survived if they were resighted at any nest boxes, during ground trapping, or at any other location.

BLOOD COLLECTION AND MULTI-LOCUS DNA FINGERPRINTING

A 70-100 μ l blood sample was collected (from putative parents and offspring) from the brachial vein into heparinized capillary tubes, placed on ice in the field, and transported back to the laboratory. We expelled the sample into microcentrifuge tubes filled with 500 μ l of lysis buffer (Applied Biosystems Inc., Foster City, California) and stored it at 4°C until processed. Adults were bled at the time of capture and most chicks were bled on day 11 when they were banded; this routine reduced the amount of handling.

We analyzed parentage of 136 nestlings (14 broods, 42 offspring in 1994; 19 broods, 63 offspring in 1995; and 8 broods, 31 offspring in 1996, collectively representing the offspring of 34 different males) using multi-locus DNA fingerprinting. DNA was extracted from blood samples using the procedure described by Westneat (1990, 1993).

Approximately 15 μ g of DNA was digested with the restriction enzyme *HaeIII* following standard procedures (e.g., Westneat 1990). The concentration

of each sample was determined with a spectrophotometer and adjusted to 6 µg DNA per lane in 20 µl TE. Each sample was electrophoresed in a 0.8% agarose gel for 48 hr at 1.5 V cm⁻¹. Each gel was then stained with ethidium bromide, photographed under UV illumination, and washed following procedures in Westneat et al. (1988). The DNA was transferred to a nylon membrane (Zetabind) using a vacuum blotter. The membrane was rinsed briefly with 2XSSC and baked for 2 hr at 80°C. The membranes were placed in pre-hybridization mixture (Westneat et al. 1988) for 24 hr.

The membranes were hybridized with a ³²P-labeled PCR-amplified fragment of wild-type M13 (Vassert et al. 1987) at 60°C for 24 hr. Washes followed the protocols in Westneat et al. (1988) and Westneat (1990). After exposure to film, the membranes were stripped and rehybridized with a second multi-locus probe, 19.6 (equivalent to 33.6; Jeffreys et al. 1985).

FINGERPRINT SCORING AND PARENTAGE ANALYSES

Scoring followed the methods outlined in Westneat (1990, 1993). Bands on the autoradiographs were marked on acetate sheet overlays with permanent markers. We compared banding patterns between two individuals (putative parent and offspring) using the statistic $D = 2N_{AB}/(N_A + N_B)$ where N_A and N_B are the number of fragments in individual A (putative parent) and individual B (offspring), and N_{AB} is the number of bands shared by both (Wetton et al. 1987). Putative parents were run in lanes directly adjacent to offspring for scoring

accuracy. For each offspring, we also determined the number of novel bands present.

The number (\pm SD) of scorable bands for probe M13 averaged 14.7 ± 5.6 ($n = 135$), whereas the number of scorable bands for 19.6 averaged 24.7 ± 4.5 ($n = 132$). The proportion of bands shared between adults in the local population averaged 0.31 ± 0.10 for M13 and 0.42 ± 0.10 for 19.6. Average (\pm SD) band sharing between random adults for both probes was 0.37 ± 0.07 ($n = 22$). All fragments that were found in 81 nestling fingerprints were present in at least one of the putative parents' fingerprints. The remaining offspring ($n = 55$) contained at least one fragment not found in the fingerprint of either putative parent.

Novel bands can result from mutation, extra-pair fertilizations, intraspecific brood parasitism, or scoring errors. Scoring errors were unlikely given that scoring was performed independently by two individuals and only those bands that were clearly distinguishable were marked. If novel bands arose from mutation, then the number observed should fit that expected from a low rate of random events. The expected number of novel bands arising from mutation is dependent on the number (\pm SD) of bands scored for both probes, which averaged 38.6 ± 9.5 . To determine mutation rates, we assumed that nestlings with one or two novel bands were not likely to have misassigned parents. We found a mutation frequency of 0.31 per individual, with a mutation rate per fragment = 0.008 (0.31/39). Therefore, the expected probability of observing three novel bands from mutation alone was $0.31^3 = 0.03$, four novel bands was $0.31^4 = 0.009$, and five novel bands was $0.31^5 = 0.003$. Given that we analyzed

136 nestlings, we expected 4, 1, and < 1 nestlings to have three, four, and five novel bands, respectively. The observed values for three and four novel bands were close to or below that expected, whereas the observed number with five was much greater than expected. We concluded that offspring with fewer than four novel bands were likely to be descendent from both putative parents; those with five or more novel bands were unlikely to be descendent from at least one of the putative parents.

For nestlings with four novel bands, we used band-sharing values to help determine parentage. For all excluded offspring, we also used band-sharing to determine whether exclusions were the result of extra-pair fertilizations or intraspecific brood parasitism. Nestlings with zero or one novel band shared 0.62 ± 0.09 of their bands with each parent. The lower, one-tailed, 95% confidence limit of this distribution was 0.47 [$0.62 - (0.09 \times 1.65)$], which indicates that the probability is less than 0.05 that offspring would have a band-sharing coefficient less than 0.47 with a genetic parent. Individuals having a higher band-sharing than this level might not be relatives. We used the band-sharing of random adults as an estimate of the expected band-sharing between the male and offspring if the offspring was from an EPF. The upper, one-tailed, 95% confidence limit on the distribution of band-sharing values between random adults is [$0.37 + (0.07 \times 1.65)$] or 0.49. Thus the two distributions overlap sufficiently that we expected some nestlings to fall within this uncertain intermediate zone.

We found that 22 of the offspring were excluded as descendents of the male under both criteria (4+ novel fragments and band-sharing < 0.47; Fig. 1a, b). All but 20 of the remaining offspring had fewer than four novel bands as well as band-sharing coefficients > 0.47 with both putative parents. Ten nestlings had a band-sharing coefficient with the male slightly lower than 0.47 and fewer than two novel bands (Fig. 1a). Four other nestlings had a coefficient with the female of just under 0.47 and zero novel bands (Fig. 1b). We assigned these nestlings as descendant from both putative parents. One nestling had a band-sharing coefficient of 0.49 with the male and four novel bands. To be conservative, we assigned this nestling to the male. Five nestlings had band-sharing coefficients above 0.47 and five to eight novel bands. Because the probability of getting so many novel bands from mutation alone was very low (considerably lower than the probability of having a band-sharing of between 0.5 and 0.6 without being a descendant), and the band-sharing with the female in each case was higher than for the male, we excluded these offspring as descendant from the male. We ran statistical analyses with these five nestlings considered as within-pair fertilizations and found only slight differences in the outcomes.

STATISTICAL ANALYSES

Parametric analyses were used when variables were normally distributed; otherwise nonparametric tests were used. Means and standard deviations are

reported unless otherwise indicated. Alpha levels of 0.05 were considered significant.

RESULTS

EXTRA-PAIR PATERNITY AND GENERAL TRENDS

Overall, we concluded that 27 of the 136 offspring (20%) in 15 of 41 broods (36.5%) came from matings between the female and an extra-pair male and none came from intraspecific brood parasitism. Of 42 offspring in 1994, 8 were extra-pair (19%). Out of 63 offspring in 1995, 23.8% were extra-pair; and of 31 in 1996, 12.9% were extra-pair. Heterogeneity among years in percent extra-pair offspring was not significant ($G_2 = 2$, $P = 0.44$). In 1994, 1995, and 1996, 29, 47, and 25% of the broods respectively contained extra-pair offspring.

BADGE SIZE AND EXTRA-PAIR PATERNITY

Overall, 14/34 (41%) of the males were cuckolded. In 1994, 33% (3/9) of the males were cuckolded. In 1995 and 1996, 53% (9/17) and 25% (2/8) of the males were cuckolded, respectively. Badge size ranged from 174 to 609 mm² and averaged 361 ± 105 mm²; male badge size was not related to male body mass ($r = 0.02$, $n = 33$, $P = 0.90$).

We found no relationship between a male's badge size and the percentage of extra-pair offspring in his own brood (Fig. 2). Assigning the five questionable offspring as within-pair, does not change the relationship ($r_s = -0.10$, $n = 33$, $P = 0.58$). We also found no relationship when comparing the proportion

of extra-pair offspring in the nests of males with smaller ($\bar{x} = 0.3 \pm 0.4$, $n = 13$) versus larger than average badges (0.2 ± 0.3 , $n = 20$; Mann-Whitney *U*-test, $z = 0.7$, $P = 0.57$). Categorizing males as large vs. small-badged based on the median, rather than the mean, did not change the outcome of this latter analysis. Similarly, the badge size of cuckolded males ($\bar{x} = 339 \pm 87 \text{ mm}^2$, $n = 14$) did not differ from the badge size of non-cuckolded males ($378 \pm 116 \text{ mm}^2$, $n = 19$, independent sample $t_{31} = 1.1$, $P = 0.30$). The results of a logistic regression analysis also indicated that badge size was not a good predictor of whether a male was cuckolded (Likelihood ratio $\chi^2 = 1.2$, $n = 33$, $P = 0.28$).

BADGE SIZE AND SURVIVAL

We found no difference in the badge sizes of males that survived at least one season post-capture ($\bar{x} = 369 \pm 158 \text{ mm}^2$, $n = 15$) and the badge sizes of males that failed to return ($357 \pm 101 \text{ mm}^2$, $n = 20$; Mann-Whitney *U*-test, $z = 0.1$, $P = 0.96$). An additional analysis, using logistic regression, also indicated that male badge size was not a good predictor of adult male survivorship (Likelihood ratio $\chi^2 = 0.1$, $n = 35$, $P = 0.78$).

CUCKOLDRY AND HATCHING SUCCESS

The 41 broods used in the fingerprinting analysis developed from a total of 191 eggs. Eleven percent (21/191) of eggs laid failed to hatch; only 1% (2/191) contained embryos that clearly died during the hatching process. We found no relationship between time in breeding season and proportion of unhatched eggs

($r_s = -0.09$, $n = 41$, $P = 0.59$). Eleven of 26 (42%) legitimate broods (those with no extra-pair offspring) contained at least one unhatched egg, whereas 7 of 15 (47%) broods with at least one extra-pair offspring contained at least one unhatched egg. Thus, presence of extra-pair young in a brood was not associated with hatch failure ($\chi^2 = 0.1$, $P > 0.50$). Reanalyzing those data with the assumption that the five questionable offspring might be within-pair did not change the results of this analysis.

DISCUSSION

We found that 41% of the socially monogamous female House Sparrows copulated with an extra-pair male and produced at least one extra-pair offspring. The overall frequency of extra-pair fertilizations we observed (20%) is comparable to that found by Wetton and Parkin (1991a) in a British population (13.6%) and Cordero et al. (1999) in a Spanish population (10.4%). However, the size of the conspicuously sexually dimorphic throat patch of males was not associated with paternity. Our results agree with those of Cordero et al. (1999) in finding no support for Møller's (1990) prediction that EPCs would be a source of sexual selection on male badge size.

Cordero et al. (1999) also found no relationship between badge size and extra-pair paternity in both Spanish and British populations. All three studies show weak trends toward males with larger badges being cuckolded somewhat less, but combining the P -values for these three independent tests does not approach significance (Fisher's combined probabilities test: $\chi^2_6 = 5.9$, $P > 0.3$;

Sokal and Rohlf 1981). Overall, these results suggest that if badge size influences extra-pair sexual activity, that effect is weak.

Møller had based his prediction about EPCs on three findings: large-badged males copulate more frequently with their mates than small-badged males (Møller 1990), they guard them more intensely than small-badged males (Møller 1987), and they have larger testes (thus presumably produce more sperm) than small-badged males (Møller and Erritzoe 1988). The absence of a relationship between paternity and male badge size in these subsequent studies suggests that one or more of Møller's findings do not apply to these populations or that, if they do, they are mitigated by other factors that affect cuckoldry independently of a male's badge size.

A candidate for such mitigation would be female multiple mating that is driven primarily by fertility insurance, and we explored this possibility. Wetton and Parkin (1991b) had found a greater proportion of unhatched eggs in House Sparrow nests with EPFs, lending support for the fertilization insurance hypothesis. We examined this possibility in the Oklahoma population and found no association between extra-pair offspring in a brood and hatch failure. However, without examining each egg, it is difficult to determine whether unhatched eggs have been fertilized, and hatch failure may be more likely to represent embryo mortality, rather than infertility (Lifjeld 1994).

A technique for distinguishing between early embryo mortality and infertility was implemented recently to address this problem. Birkhead et al. (1995) used microscopic examination of the perivitelline layers of House Sparrow

eggs to discriminate between early embryo mortality and infertility; from their results, they estimated that 15% of hatch failures in a Spanish colony were attributable to infertility. Thus, if hatch failure occurs at about a 10% rate, as in both the Spanish and Oklahoma populations, the overall infertility risk is roughly 1.5% per egg. Although this may seem trivially low, it could be sufficient to promote female multiple mating if EPCs are not especially costly to females. Unless EPCs are highly costly to females, the observed infertility rate is likely to underestimate the rate that would occur if females did *not* engage in EPCs. Rather than simply using measures of the associations between hatch failure and EPFs, a fertility insurance advantage may be most readily detected via experimental manipulation of the number of female mating partners and/or female mating frequency. Only recently have such experimental approaches been used for non-domesticated bird species (Sax et al. 1998), and they may be feasible for House Sparrows.

Despite no evidence that male badge size affects paternity losses, large-badged males in this population may be favored by sexual selection, on several counts. First, they may have an advantage in male-male competition for breeding resources (e.g., nesting sites) as suggested by both Møller (1988) and Veiga (1993, 1996). We made no attempt to assess this, but note that such competition might be expected to be relatively relaxed in our study population given the abundance of both natural and artificial nest sites. Second, there is evidence that in this population, a male's badge size is positively correlated with both the relative share of nestling feeding he performs and with the proportion of

hatched young that fledge (Voltura 1998). Females therefore would have ample incentives for basing their choice of pair-mates on male ornamentation, because of the direct benefits in doing so. Whether there also exist genetic benefits from pairing with or engaging in EPCs with a large-badged male is less certain.

Although Møller (1989) found relatively high heritability of badge size (0.60) in a Danish population, a recent cross-fostering study has revealed that a male's badge size resembles that of his foster father much more than it resembles his genetic father's badge size (Griffith et al. 1999a). Additionally, we found no effect of male badge size on adult survivorship and, if badge size is an indicator of male genetic quality, we would have predicted that large-badged males would have higher survivorship. For example, in Belgian Blue Tits (*Parus caeruleus*), "attractive" males, those that are preferred as EPC partners (mates) and are able to avoid lost paternity at their own nests, had greater over-winter survivorship (Kempenaers et al. 1992). Finally, large-badged males may well sire more offspring through EPFs than small-badged males, as Møller (1990) predicted. We were unable to assign paternity of offspring produced through EPFs in this study, so we cannot evaluate this directly.

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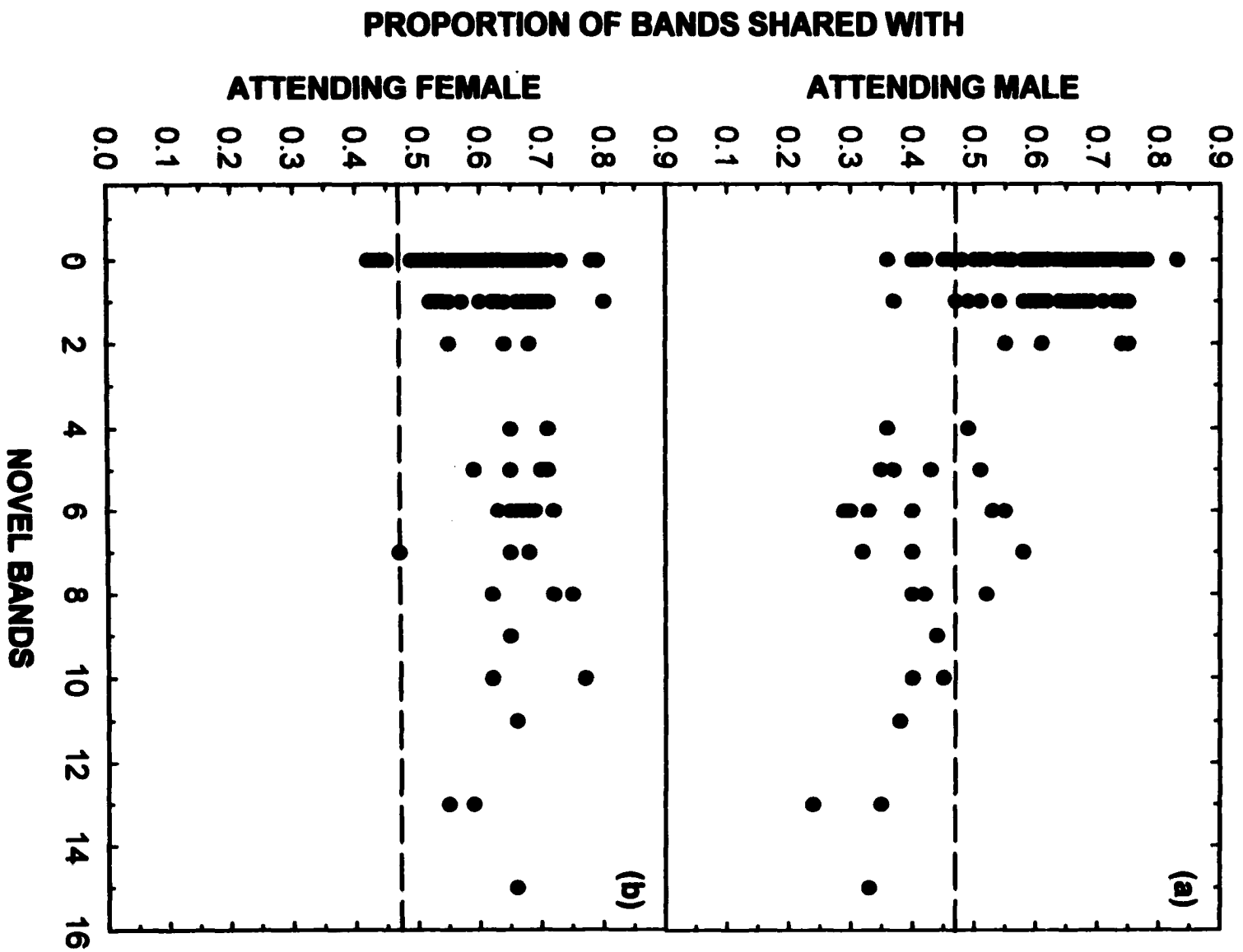
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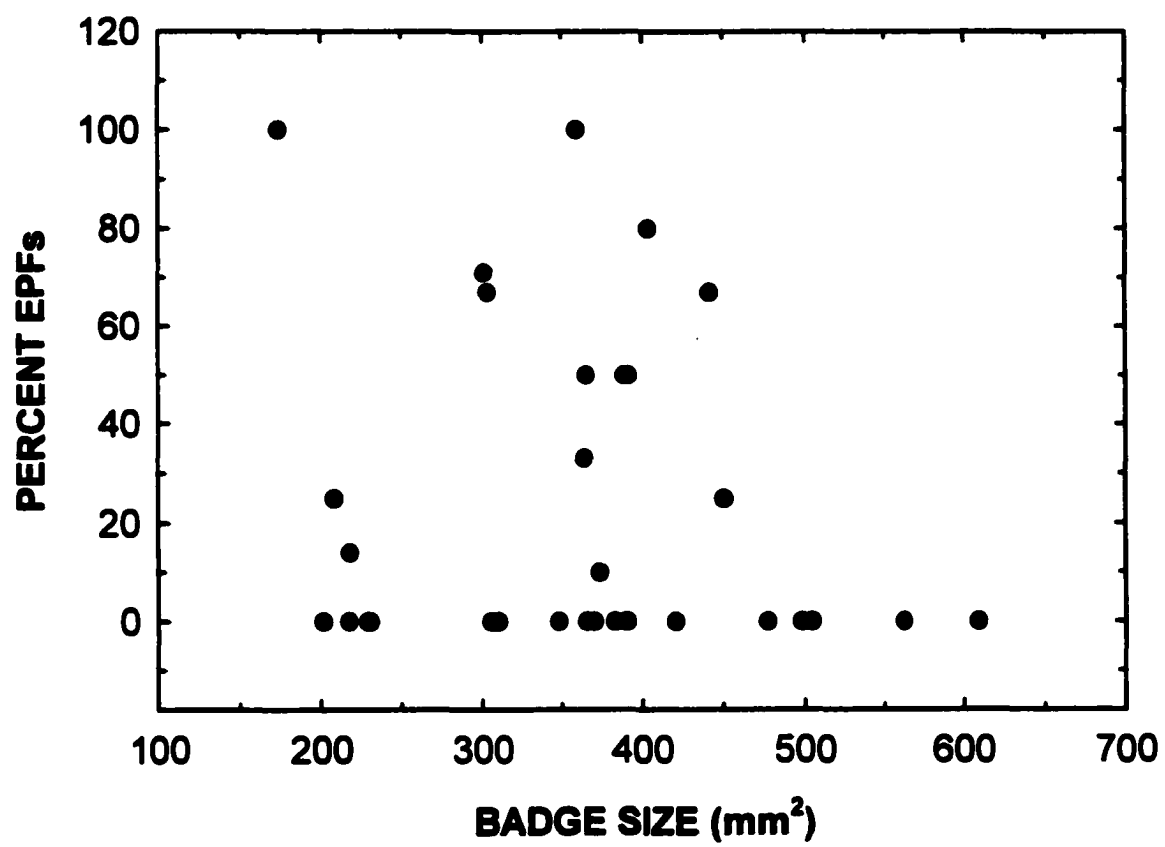
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FIGURE 1. Relationship between the proportion of bands shared with the attending parent and the number of novel bands for each nestling House Sparrow. Band sharing with (a) the attending male and (b) the attending female. The dotted line represents the lower, one-tailed, 95% confidence limit for band sharing between attending parents and offspring. Some of the data points are hidden from view.

FIGURE 2. Relationship between male House Sparrow badge size and percent extra-pair fertilizations in his brood ($r_s = -0.18$, $n = 33$, $P = 0.33$). Some of the data points are hidden from view.





Chapter 2

Correlates of extra-pair paternity and mate-guarding in the house sparrow, *Passer domesticus*

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ABSTRACT

Extra-pair copulations (EPCs) are common among socially monogamous birds and are often initiated by the female. We examined the distribution of extra-pair offspring among broods of house sparrows, *Passer domesticus*. We then examined extra-pair paternity and male mate-guarding in relation to male attractiveness, breeding synchrony, and the proximity of male neighbors. Some males were more likely to be cuckolded than others: extra-pair offspring were more clustered within the broods of fewer males than expected by chance. Parentage analyses further revealed that males that spent more time mate-guarding had more extra-pair offspring in their nests. In this population, male badge size was unrelated to both paternity and mate-guard duration. Heavier males tended to spend less time in proximity to their mates. Moreover, heavier males tended to be cuckolded less than smaller males. Density was somewhat predictive of whether a male would be cuckolded; however, we did not find a relationship between breeding synchrony and the incidence of extra-pair fertilizations. Mate-guarding duration was not correlated with either density or breeding synchrony, but males showed a tendency to mate-guard more intensively when their nearest male neighbor was likely to be engaged in sexual display. Overall, these results indicate that males adjust their mate-guarding according to their risk of being cuckolded, but the degree to which increased mate-guarding investment is triggered by the behavior of their mates versus the behavior of their male neighbors remains unknown.

INTRODUCTION

Studies of parentage using molecular techniques have shown that copulations outside the pair bond are prevalent among socially monogamous bird species and are often initiated by females (Kempenaers and Petrie, 1998). Females may seek extra-pair copulations (EPCs) to protect against temporary or permanent infertility of their mates, to gain better genes for their offspring, and/or to gain additional parental care (Westneat et al., 1990).

Several factors have been proposed as potential correlates of extra-pair paternity, including a male's ability to guard his mate and his relative attractiveness (Westneat et al., 1990; Birkhead and Møller, 1992). When males provide paternal care, they are expected to invest time and energy to protect their paternity (Trivers, 1972), and they often do so by mate-guarding (Møller and Birkhead, 1991). Male mate-guarding (defined as close following of a female during her fertile period: Beecher and Beecher, 1979; Birkhead, 1979) does not necessarily guarantee paternity, however. On the contrary, Gowaty and Bridges (1991) found that male eastern bluebirds, *Sialia sialis*, that had a greater percentage of extra-pair young in their nests had spent more time guarding their mates. Kempenaers et al. (1995) found that monogamous male blue tits (*Parus caeruleus*) that followed their fertile mates more frequently tended to have more extra-pair young in their broods than males that followed less frequently. Similarly, Wagner et al. (1996) determined that young purple martin (*Progne subis*) males, which are particularly vulnerable to cuckoldry, mate-guarded more intensely than older males.

These observations of a positive relationship between male mate-guarding effort and cuckoldry incidence led to the suggestion that males adjust mate-guarding intensity according to their perceived risk of paternity loss (Gowaty and Bridges, 1991), which may vary with their own attractiveness or quality (Kempnaers et al., 1992; Kempnaers et al., 1995; Krokone et al., 1996; Wagner et al., 1996). Indeed, male attractiveness has been shown experimentally to affect mate-guarding investment. Male bluethroats (*Luscinia svecica*) that were made less attractive experimentally guarded their mates more closely than control males (Johnsen and Lifjeld, 1995).

The ability of males to guard effectively may be compromised if they simultaneously attempt to acquire extra-pair fertilizations (EPFs). Westneat et al. (1990) suggested that breeding synchrony, which creates temporal overlap between male mate-guarding activities and the availability of EPC opportunities, should be inversely related to EPF rates. Alternatively, Stutchbury and Morton (1995) predicted a positive relationship between synchrony and EPF rates and Stutchbury's (1998) comparative analyses have supported this. She suggested that breeding synchrony allows females to compare potential extra-pair mates simultaneously while they are displaying, and therefore better assess male genetic quality. The display activity of neighboring males may well facilitate their ability to attract extra-pair partners. In great reed warblers (*Acrocephalus arundinaceus*), females appear to prefer extra-pair mates that are singing during the interval when the females are fertile and that have larger song repertoires than their social mates (Hasselquist et al., 1996). In house sparrows (*Passer*

domesticus), EPFs are primarily attributable to neighboring males, and male EPF success is especially high during their social mates' own fertile period (Wetton et al., 1995), which is one of the stages of the nesting cycle when males engage in singing and courtship behavior (Hegner and Wingfield, 1986).

Density of breeding individuals also may affect opportunities for EPCs (Westneat et al., 1990; Birkhead and Møller, 1992). Females frequently obtain extra-pair fertilizations from neighboring males (Wetton et al., 1995; Hasselquist et al., 1996; Kempenaers et al., 1997). Higher densities should present greater opportunities for EPCs; thus, extra-pair fertilizations are predicted to increase proportionately with breeding density (Westneat et al., 1990; Birkhead and Møller, 1992). If greater densities present more opportunities for EPCs, then mate-guarding should also increase proportionately with breeding density (Birkhead and Møller, 1992).

In an Oklahoma population of house sparrows, we found that 20% of the offspring were the result of extra-pair matings (Whitekiller et al., 2000). Males in this population are known to guard their mates during egg-laying (Hankinson, 1999). In this study, we first examined the incidence of extra-pair offspring among broods to determine if EPFs are randomly distributed. We then examined extra-pair paternity as well as male mate-guarding behavior in relation to male attractiveness, breeding synchrony, density, and the reproductive status of male neighbors.

METHODS

Study Site and General Field Methods

House sparrows are socially monogamous passerines that breed in central Oklahoma from March through early August, producing multiple clutches. Both parents incubate clutches of approximately 4-5 eggs each; incubation lasts 10-11 days. Both parents feed offspring and young typically fledge 14-17 days after hatching.

We used data from birds breeding in nest boxes at four study sites in Norman, Oklahoma. During the 1994-1997 breeding seasons, nest boxes were checked at least twice weekly from the nest building stage until young fledged. Adults were captured, weighed, and then banded with U.S. Fish and Wildlife aluminum bands plus color bands. Chicks were weighed and banded 11 days after hatching. Blood samples for multi-locus DNA fingerprinting were collected from offspring 9-11 days post-hatch and from putative parents upon capture. For a detailed description of the blood collection, DNA fingerprinting, fingerprint scoring, as well as those methods used for parentage analyses, see Whitekiller et al. (2000).

Pattern of Extra-Pair Paternity

We assessed whether extra-pair young were randomly distributed among broods by performing a chi-square test of broods with and without documented extra-pair offspring (Lifjeld et al., 1993).

Male attractiveness

We looked at two traits that females could use as indicators of male quality, badge size and body size. For most males, R. Whitekiller and K. Voltura quantified badge areas from close-up badge photographs using the procedure described in Whitekiller et al. (2000). In two cases, however, we had mate-guarding data from males that had been banded as nestlings the previous year, but we lacked badge photos for them. We filmed these two males at their nest sites using a Sony video camcorder, and then digitized the film images of their badges for badge area estimates. To verify that the video camera images were suitable for analyses, and to calibrate the video-image areas against the photographed area estimates, we took both photographs and video images of 8 males' badges from Oklahoma Museum of Natural History specimens and compared the badge area estimates. The photo and video images were highly correlated ($r = 0.99$, $P \leq 0.0001$). We used the regression equation [badgephoto area (mm^2) = $-0.0814 + (1.00043 \times \text{badgevcr area; mm}^2)$] to convert the video image badge areas prior to statistical analyses. All badge area estimates of males are based on breeding season plumage, which minimizes the seasonal variation in visible badge size that results from feather abrasion (see Griffith et al., 1999).

In a previous study, we found that badge size was not a good predictor of adult male survivorship (Whitekiller et al., 2000). To determine whether variation in adult male body mass and adult male survival are correlated, we compared the masses of males banded as adults in 1994 or 1995 that were resighted

within the next two years with those of males that failed to reappear (Whitekiller et al., 2000).

Mate-guarding

We conducted daily thirty-minute focal nest observations from March through early July in 1994, 1995, and 1997 on 15 banded breeding pairs during the egg-laying period. Observations were conducted from a vehicle approximately 20-30 m from the nest box using a telescope. All behavioral sampling was done between 0700 and 1100. To determine the amount of time males spent guarding their mates, we recorded the amount of time the pair spent together within 10 m. We also recorded the number of arrivals and departures of the pair, which member initiated flight, and whether the other member followed within 30 s. Due to heavy rain, we had missing samples for one day on each of two pairs; in both cases we lack data for the day the third egg was laid. Results from observations of other pairs indicated that the amount of time males spent guarding their mates on the day the third egg is laid is highly correlated with, although greater than, the time spent guarding on the previous day ($r = 0.74$, $n = 13$, $p = 0.002$). Therefore, for analyses, we used the predicted amount of time these two males would have guarded had it not rained heavily [Day3sec = $21.7671 + (0.68025 * \text{Day2sec})$]. We also found that the percent of the total number of flights initiated by the female (FIF) on the day the third egg was laid was highly correlated with, but greater than, the percent (FIF) the day the first egg was laid ($r = 0.65$, $n = 13$, $p = 0.02$). Therefore, we used the regression

equation [Day3%FIF=16.764 + (1.124*Day1%FIF)] to predict the percent of the total number of flights initiated by the female for these two females. For the data on female-initiated flights followed by her mate and male-initiated flights followed by his female, we were unable to find any correlation between any days samples. Therefore, sample sizes for these analyses are reduced due to missing data on the day the third egg was laid for two pairs.

Density and Breeding Synchrony

To examine the relationships among local breeding density, mate-guarding, and extra-pair fertilizations, we measured the distance from the focal nest to the nearest occupied nest box and determined the reproductive status of the male resident. To examine the relationships among synchrony of breeding, mate-guarding, and extra-pair fertilizations, we calculated the breeding synchrony at each study site during each female's fertile period using the breeding synchrony index Langefors et al. (1998):

$$SI_p = \left(\frac{\sum_{i=1}^{t_p} f_{i,p}}{t_p (F - 1)} \right) \cdot 100$$

where SI_p = the breeding synchrony for the p th female over her fertile period, F = the total number of breeding females at the study site, $f_{i,p}$ = the total number of fertile females other than female p , in the study site on day i , t_p = the number of fertile days for the p th female. We conservatively assumed each female was fertile during the 5 days before she laid her first egg through laying of the penultimate egg (Møller, 1987). The mean presumed fertile period for this

population of house sparrows was 9 days.

Statistical analyses

We used SAS version 6.08 (SAS Institute, Cary, NC) and SigmaStat version 2.0 (SPSS Inc., Chicago, IL) statistical packages. Means \pm standard deviations are reported unless otherwise indicated. When variables were not normally distributed, non-parametric tests were used.

RESULTS

Patterns of Extra-Pair Paternity

Twenty percent of the offspring came from extra-pair matings (Whitekiller et al., 2000), so the probability that any one offspring is illegitimate is 0.20. The broods of 20 males contained no extra-pair offspring (EPO), while the broods of 14 males contained one or more. The expected number of broods without EPFs was calculated as $\sum N_i(1 - P)^i$, where P is the probability that any offspring is illegitimate ($P = 0.20$) and N_i is the number of broods of size i (Lifjeld et al., 1993). With broods from 34 males (multiple-broods from the same male were treated as one large brood), the expected number of broods with no EPO would be 12; therefore, the expected number with one or more illegitimate young would be 22. Comparison of the observed and expected number of broods with and without EPFs showed that extra-pair offspring were not distributed randomly (Fig. 1), but instead were more clustered within fewer broods than expected by chance.

Mate-guarding, Extra-Pair Paternity, Male Badge Size and Male Body Size

Males spent on average from 34 to 827 s per sample ($\bar{x} = 317 \pm 212.55$) guarding their mates. Mean duration of guarding, in turn, was significantly correlated with the proportion of the total female-initiated flights followed by her mate ($r = 0.59$, $n = 13$, $p = 0.03$). Thus, males that spent more time in proximity to their mates also were more likely to follow their mates when they departed the nest area. There was no evidence, however, that females being guarded more intensively departed from their mates or nests especially often: the mean proportion of all departures from the nest area initiated by the female was unrelated to mate-guarding duration ($r_s = 0.07$, $n = 15$, $p = 0.79$). There also was no indication that females that were being guarded more intensively were any more or less inclined than other females to maintain contact with their mates when the latter departed from the nest area: the proportion of the total number of flights initiated by the male in which the female followed was not related to male mate-guarding duration ($r = -0.02$, $n = 13$, $p = 0.95$).

DNA fingerprinting was conducted for broods of six males whose mate-guarding behavior had been sampled. The parentage analyses revealed a positive significant relationship between the amount of time these males spent guarding their mates and percent extra-pair fertilizations (Fig. 2). Thus, on average, males that spent more time guarding their mates had more extra-pair offspring in their nests.

As reported elsewhere (Whitekiller et al., 2000), male badge size is not

strongly related to paternity in this population. There apparently also exists no relationship between male mate-guarding tenacity and badge size: mean duration of guarding during the laying period was not correlated with male badge size (Fig. 3). However, there was a trend for mate-guarding duration to be negatively associated with male body mass (Fig. 4): heavier males tended to spend less time in proximity to their fertile mates. Furthermore, heavier males tended to have lower percentages of extra-pair offspring in their nests than smaller males (Fig. 5). Badge size and adult male mass are not correlated (Whitekiller et al., 2000).

Adult Male Mass and Survival

We found no difference in the body masses of adult males that survived at least one season post-capture ($\bar{x} = 28.38 \pm 1.0$ g, $n = 18$) and the masses of males that failed to return ($\bar{x} = 27.9 \pm 1.7$, $n = 16$, $t = 1.031$, $df = 32$, $p = 0.31$). An additional analysis, using logistic regression, also indicated that male mass was not a strong predictor of adult survivorship (likelihood ratio $\chi^2 = 0.30$, $n = 34$, $p = 0.30$).

Local Breeding Density, Extra-Pair Paternity, and Mate-Guarding

Nearest neighbor distances for pairs whose broods were fingerprinted ranged from 4.5 to 63 m with an average of 23.09 ± 14.76 m. We found no correlation between distance to nearest neighbor (i.e., nearest occupied nest box) and percent EPFs (Fig. 6). This analysis may be confounded by season effects,

however: EPFs tended to be more frequent early in the season ($r_s = -0.23$, $n = 41$, $p = 0.14$) when density was highest ($r_s = 0.26$, $n = 41$, $p = 0.10$). After performing a partial correlation to remove the effects of season, the relationship between density and extra-pair paternity did not change ($r_s = -0.14$, $n = 41$, $p = 0.38$). Notably though, no EPFs occurred in any of the 9 focal nests that were located more than 33 m from any male neighbor's nest. Using logistic regression, we found that distance to nearest neighbor may be somewhat predictive of whether a male will be cuckolded (likelihood ratio $\chi^2 = 2.265$, $n = 41$, $p = 0.13$). The mean time a male spent guarding his mate and proximity of the nearest neighbor were not related (Fig. 7).

Nearest male neighbors were further categorized according to their reproductive status to determine the influence of neighboring male display behavior on mate-guarding. Males whose nearest male neighbor was likely to be calling or courting (either unpaired, presumably guarding his own fertile mate, or feeding nestlings in the last 1/3 of the nestling cycle: Hegner and Wingfield, 1986) tended to spend more time guarding their mates ($\bar{x} = 434.90 \pm 266.41$ s; $n = 6$) than males whose nearest male neighbor was unlikely to be engaged in sexual display (incubating or feeding nestlings in the first 2/3 of the nestling cycle, i.e., days 1-9: Hegner and Wingfield 1986: $\bar{x} = 238.33 \pm 131.60$ s; $n = 9$, $t = 1.914$, $df = 13$, $p = 0.08$).

Breeding Synchrony, Extra-Pair Paternity, and Mate-Guarding

Breeding became somewhat more asynchronous within study sites as the

season progressed ($r = -0.23$, $n = 41$, $p = 0.14$). Breeding synchrony was not a good predictor of whether a male was cuckolded (Logistic Regression likelihood ratio $\chi^2 = 0.607$, $n = 41$, $p = 0.44$). We also found no relationship between breeding synchrony and percent EPFs with season removed using a partial regression ($r = 0.08$, $n = 41$, $p = 0.63$), nor was there a significant relationship between breeding synchrony and male mate-guarding duration ($r_s = 0.33$, $n = 15$, $p = 0.22$).

DISCUSSION

Analyses of the incidence of EPFs among and within broods indicate that paternity losses in this population are not randomly distributed among males: extra-pair offspring are more clustered within the broods of certain males than expected by chance, as Wetton and Parkin (1991) found in a British population. Thus, some males' mates are more prone to engage in EPCs than others' mates or the EPC activity of these females more frequently leads to fertilization.

The paternity analyses revealed one factor that may place individual males at higher risk of cuckoldry: low body mass. This raises the possibility that larger males are of higher quality than smaller males, and that their social mates are accordingly less likely to seek or accept EPCs than the mates of smaller males. Whether females obtain genetic benefits from pairing with larger males is unclear, however. We found no effect of male body size on adult survivorship, and if adult male mass were suggestive of male genetic quality, we would expect larger males to have higher survivorship. However, power analysis indicates that

our sample size may be too small to address this question adequately (power = 0.25-0.30).

Alternatively, perhaps at least some of the variation in paternity between small and large males arises from differences in their competence during sperm competition, rather than differences in their mates' EPC activities. We cannot rule out the possibility that females seek EPCs simply as fertility insurance (Wetton and Parkin, 1991; Whitekiller et al., 2000), in which case variation across males in paternity may be primarily related to success in sperm competition. Larger males have larger testes in Bengalese finches (Birkhead, 1992) and perhaps in house sparrows (Møller and Erritzoe, 1988). Furthermore, Birkhead et al. (1994) have shown that house sparrow male testes mass is positively correlated with number of spermatozoa in the seminal glomera.

In addition to male mass, we also examined two aspects of the social environment that could potentially influence male vulnerability to cuckoldry: breeding synchrony and density. While breeding became more asynchronous as the season advanced, we could demonstrate no relationship between breeding synchrony over the fertile period of each female and whether her mate was likely to be cuckolded. However, density may be somewhat predictive of extra-pair paternity: no extra-pair offspring were produced in nests where the nearest male neighbor was more than 33 m from the focal nest.

Overall, then, the two most promising correlates of extra-pair paternity that we have been able to detect in this population are adult male mass and the proximity of male neighbors. Small males may be at relatively high risk of

cuckoldry, and males with close male neighbors tend to be more vulnerable. The mate-guarding behavior of males suggests that they may track their cuckoldry risks fairly closely. First, among the small sample of males for which we had both paternity data and mate-guarding data, we found a clear positive relationship between mate-guarding and extra-pair paternity; males that spent more time in close proximity to their mates had a higher percentage of extra-pair offspring in their broods. Second, males whose phenotype apparently places them in greater risk of cuckoldry may guard their mates more intensively, male mass being negatively correlated ($p = 0.08$) with mate-guarding intensity. By contrast, we found no effect of male badge size on mate-guarding, which parallels our earlier finding that in this population, large-badged males are cuckolded as often as small-badged males (Whitekiller et al., 2000). Third, of the two features of the social environment that we examined as potential predictors of cuckoldry, only proximity of the nearest male neighbor appeared promising. While we did not find a relationship between mate-guarding duration and density, our sample size may too small to address this question adequately (power = 0.15-0.20). It is also quite possible that some of the tacit assumptions on which these trade-off predictions were based – most notably that effective mate-guarding is necessarily incompatible with a male's ability to seek EPC opportunities – simply do not hold for some (e.g., heavier) or all males in this population. In addition, a more profitable approach may be to consider the reproductive status of the nearest male neighbor in combination with his proximity: males whose nearest male neighbor was likely to be actively engaged

in sexual display appeared to guard their mates more than males whose nearest male neighbor was not ($p = 0.08$).

Collectively, these findings suggest that males 'tune' their investment in mate-guarding according to their cuckoldry risk. The greater the risk, the more intensively they guard. This is consistent with Gowaty and Bridges' (1991) suggestion that a male may adjust his mate-guarding after his female has behaved in some way that appears to jeopardize his paternity. Unlike Gowaty and Bridges (1991), however, we were unable to identify any differences in the behavior of fertile females that were being guarded more versus less tenaciously. Perhaps male mate-guarding investment in house sparrows is influenced more strongly by male interactions with male neighbors than by interactions with their social mates.

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Figure Legends

Figure 1

Frequency distribution of the percent of within-pair and extra-pair offspring for thirty-four males ($\chi^2 = 8.24$, $df = 1$, $p < 0.005$).

Figure 2

Relationship between time a male spent guarding his mate and percent extra-pair fertilizations (EPFs) in his brood ($r_s = 0.85$, $n = 6$, $p = 0.03$).

Figure 3

Relationship between male badge size and time a male spent guarding his mate ($r = -0.12$, $n = 15$, $p = 0.68$).

Figure 4

Relationship between adult male body size and time a male spent guarding his mate ($r = -0.51$, $n = 13$, $p = 0.08$). Only 13 of the 15 males whose mate-guarding behavior was sampled were used in the analyses because current-year masses were not available for two males.

Figure 5

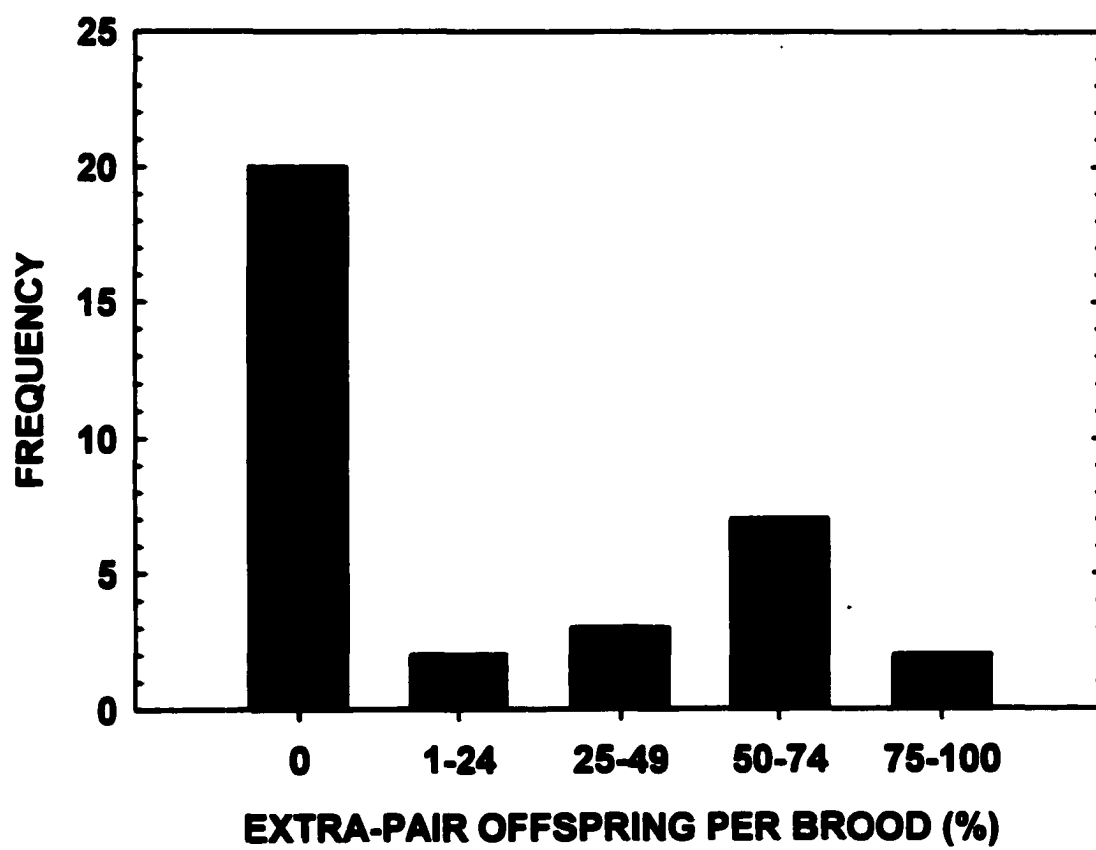
Relationship between adult male body size and percent extra-pair fertilizations (EPFs) in his brood ($r_s = -0.27$, $n = 34$, $p = 0.12$). Some of the solid circles (i.e., data points) are hidden from view.

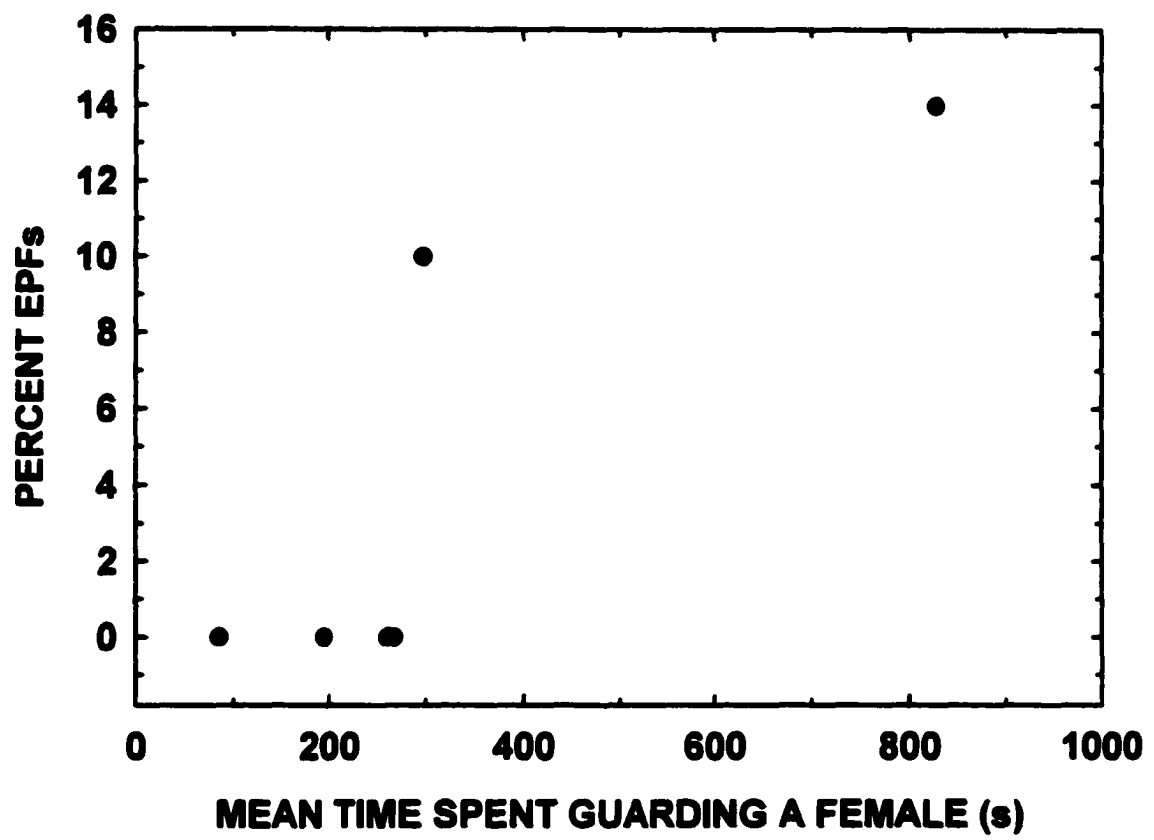
Figure 6

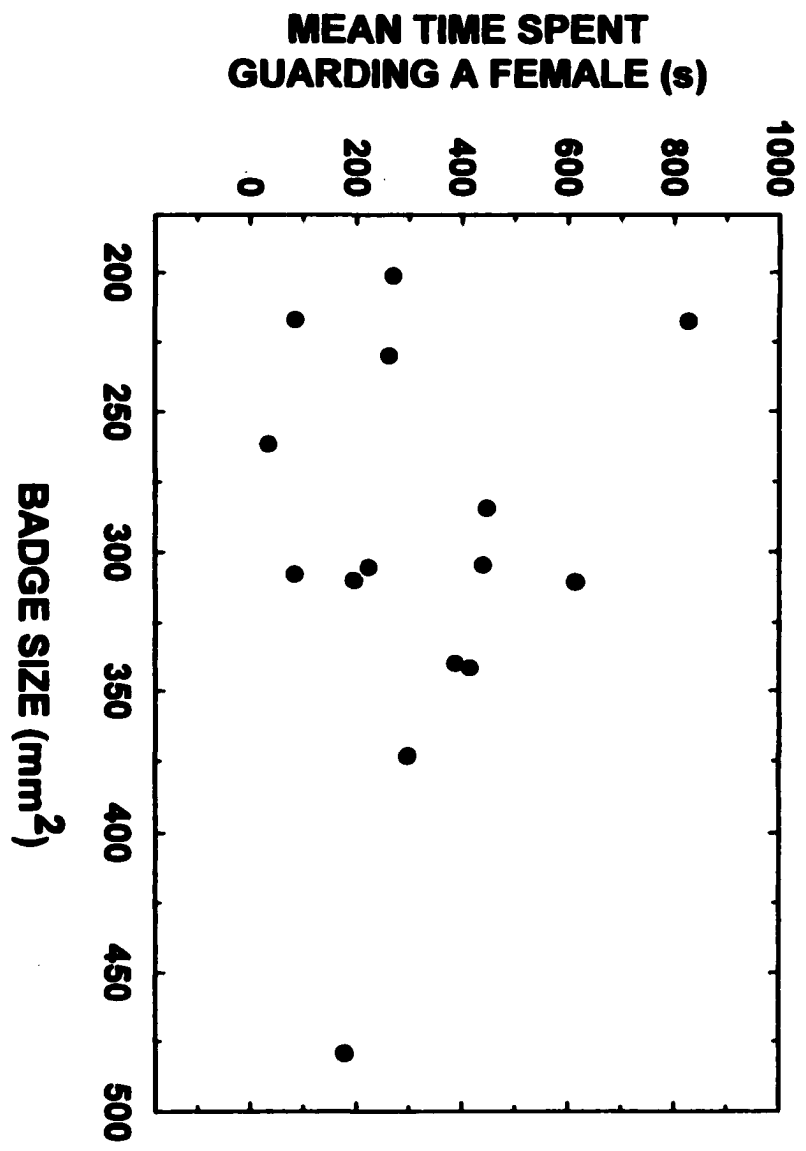
Relationship between density (i.e., distance to nearest neighbor from focal nest box) and percent extra-pair fertilizations (EPFs) in the brood ($r_s = -0.18$, $n = 41$, $p = 0.26$). Some of the solid circles (i.e., data points) are hidden from view.

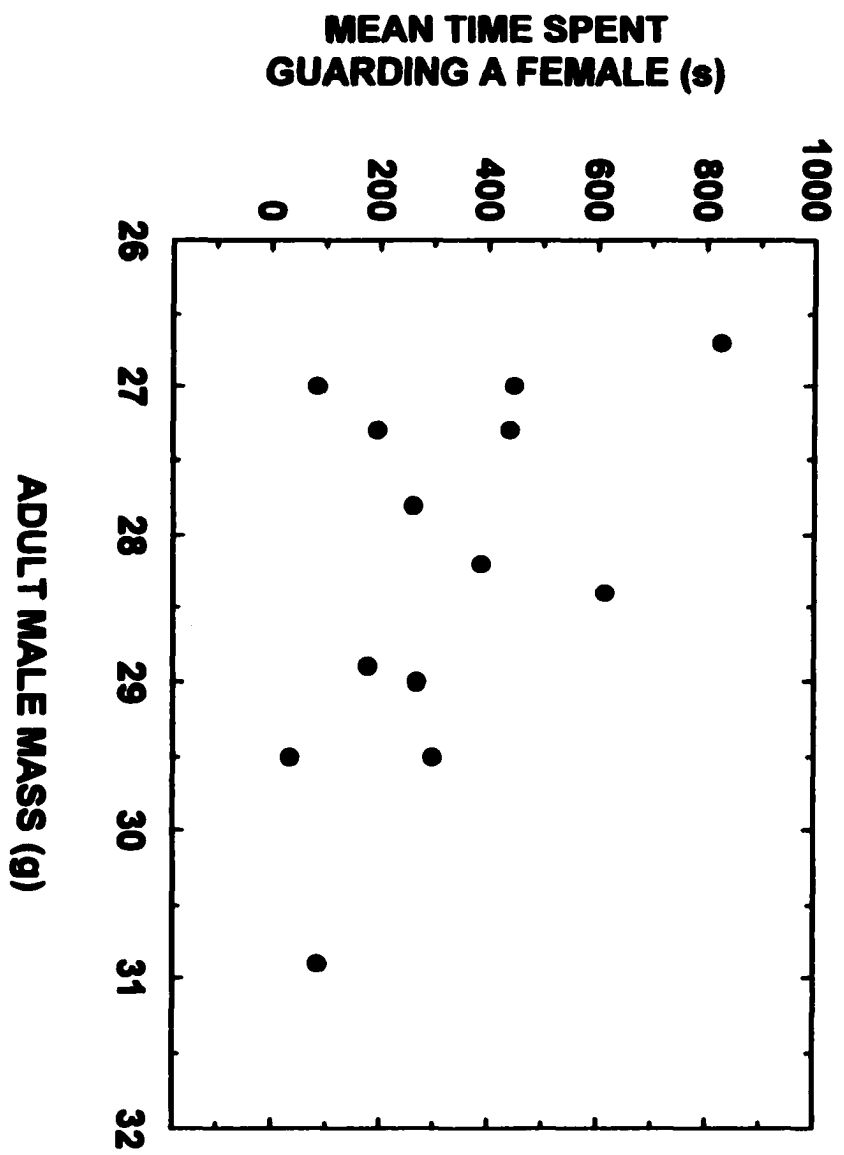
Figure 7

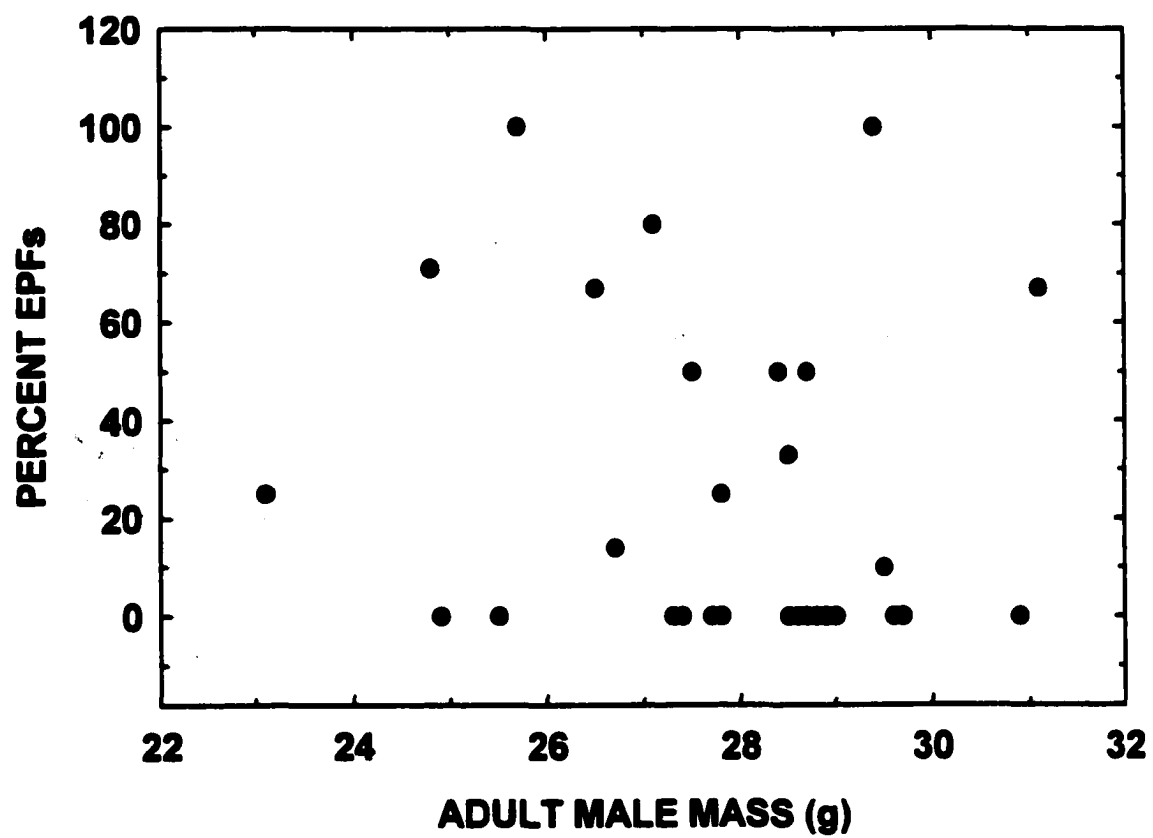
Relationship between time a male spent guarding his mate and density (i.e., distance to nearest neighbor from focal nest box; $r = -0.29$, $n = 15$, $p = 0.29$).

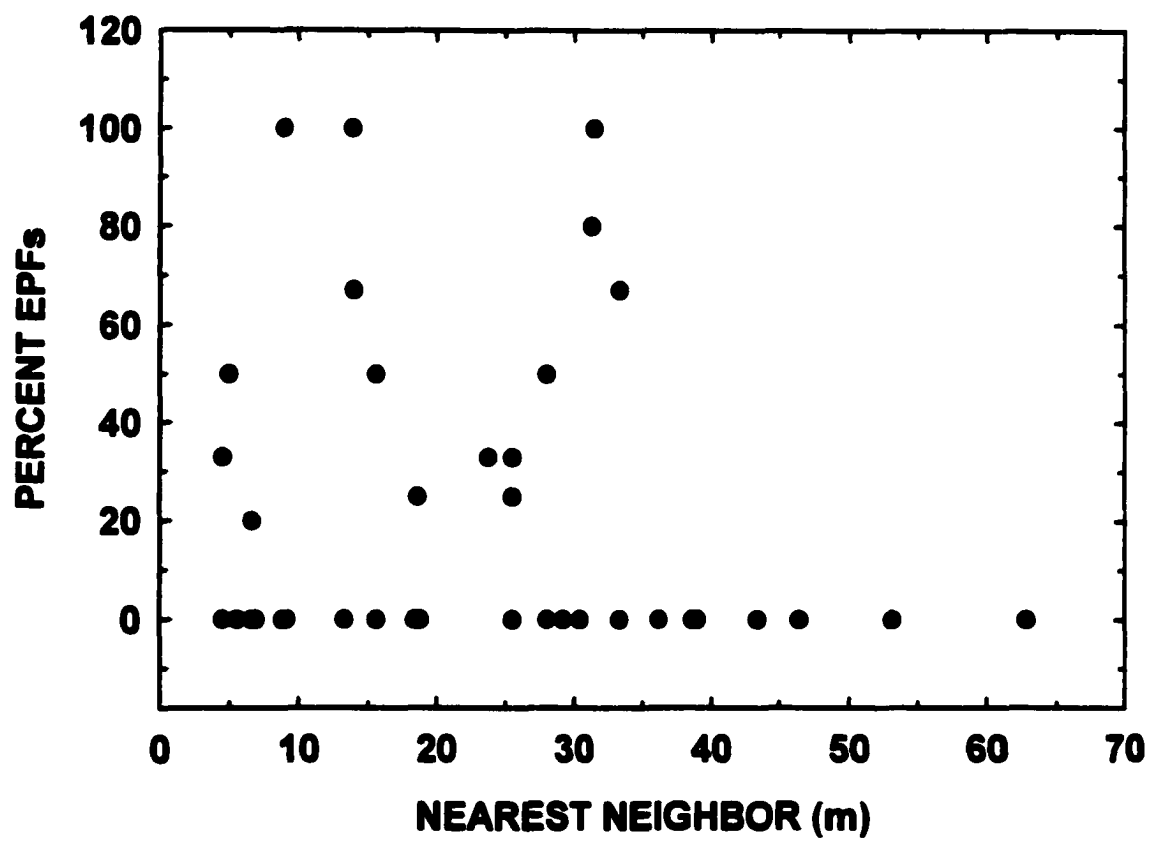


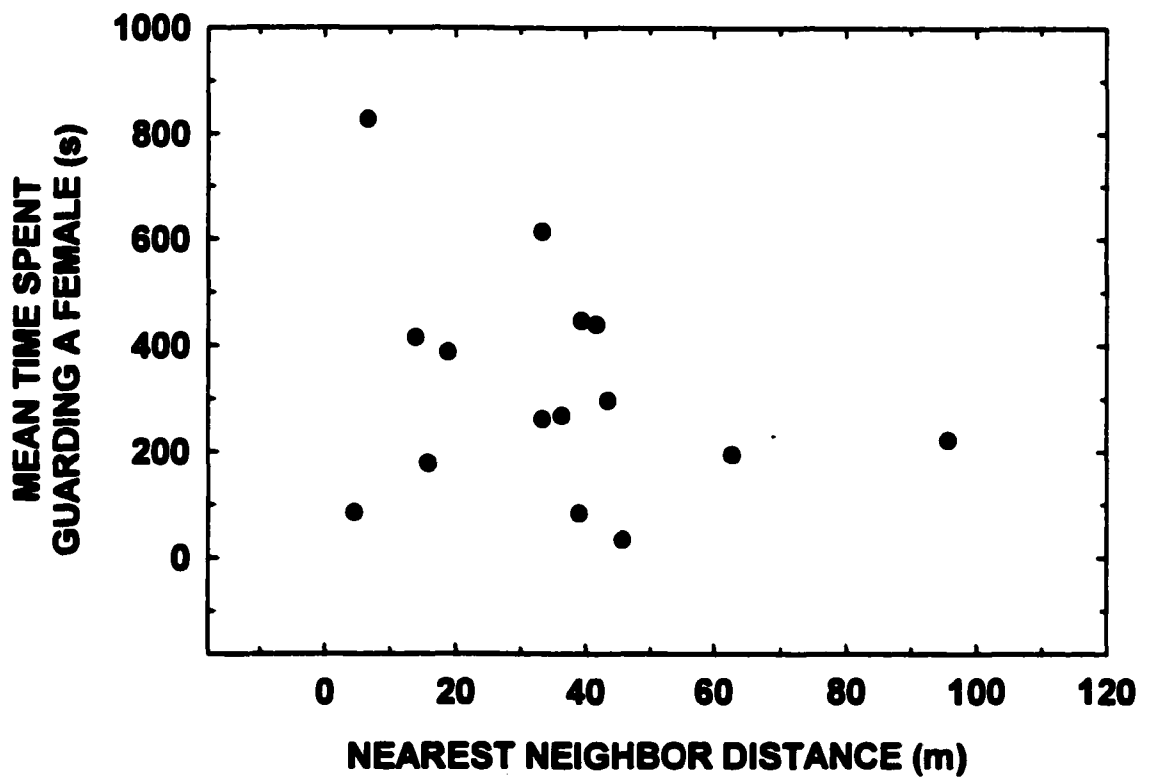












Chapter 3

Effects of ectoparasites on house sparrow nestling growth and fledging success

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This chapter is written in style for publication in the journal

Oikos.

Abstract

Ectoparasites have negative effects on the quality and quantity of offspring produced. To determine whether *Pellonyssus reedi*, a haematophagous mite, affects growth and reproductive success of house sparrows (*Passer domesticus*), I compared the mite loads of offspring in nests treated with a pesticide to that of young in sham-treated control nests. I assessed the effects of *P. reedi* by comparing mass, tarsus length, wing length, duration of the nestling period, and fledging success for nestlings between treatments. Nestlings in pesticide-treated nests had, on average, greater mass and tarsus lengths than nestlings in control nests. Nestlings in pesticide-treated nests also tended to have longer wings. Duration of the nestling period did not differ between the two treatments. I also found no effect of *P. reedi* on fledging success; however, it may affect juvenile survival. These results support the hypothesis that the mode of transmission for *P. reedi* is linked to its level of virulence. *P. reedi* is an intermediate-transmission parasite and exhibits medium virulence: it reduces nestling body mass, but does not appear to influence fledging success.

Introduction

Avian species serve as hosts to a variety of ectoparasites including lice, mites, ticks, flies, bugs, and fleas. Diverse effects of ectoparasites on host reproductive success have been documented (Møller 1997). Some studies have shown no effect of ectoparasites on nestling growth or survival (Darolova et al. 1997, Pacejka et al. 1998). However, other research indicates that ectoparasites have a negative impact on the quality and quantity of offspring produced. For example, in the pied flycatcher *Ficedula hypoleuca* (Merino and Potti 1995) and in blue tits *Parus caeruleus* (Hurtrez-Bousses et al. 1997) ectoparasites negatively influence offspring growth. In cliff swallows (*Hirundo pyrrhonota*), ectoparasites reduced both offspring growth and fledging success (Chapman and George 1991).

Clayton and Tompkins (1994) have suggested that some of the variation in the degree to which various ectoparasites harm nestlings originates from differences in ectoparasite transmission modes. In captive rock doves (*Columba livia*), they compared the effects of two different ectoparasites on nestling growth and host reproductive success. Mites (*Dermanyssus gallinae*) significantly reduced host fitness, whereas lice (*Columbicola columbae* and *Campanulotes bidentatus*) had no effect on reproductive success. While the transfer of lice is dependent on contact between parents and their offspring (i.e., lice are vertically transmitted to new hosts), *D. gallinae* can migrate independently of their hosts from one nest to another. These results, along with the results of a literature survey, led Clayton and Tompkins (1994) to conclude that avian ectoparasites

that are transmitted horizontally (i.e., among unrelated hosts) are more virulent than vertically transmitted parasites.

A common ectoparasite of house sparrow nestlings is a haematophagous mite, *Pellonyssus reedi* (formerly *P. passer*) of the family Macronyssidae. Clark and Yunker (1956) briefly described the mite's life cycle and morphology: the life cycle consists of an egg, larva, protonymph, deutonymph, and adult.

Pellonyssus reedi is found on adult hosts (Lindholm et al. 1998), nestlings, and in nesting material, indicating vertical transmission, however, *P. reedi* also has opportunities for horizontal transmission through at least two routes. First, non-parental birds, particularly juveniles, often visit occupied and unoccupied nests, and are hence vulnerable to mites residing in the nest material. Second, *Pellonyssus spp.* disperse to new habitats via their hosts (Simberloff and Wilson 1969, Radovsky 1998). Thus *P. reedi* presumably falls into the category of ectoparasites with 'intermediate' transmission (displaying both vertical and horizontal transfer to new hosts), consistent with Clayton and Tompkins (1994) characterization of two other macronyssids. Based on Clayton and Tompkins (1994), *P. reedi* would thus be expected to have higher virulence than ectoparasites that rely primarily on vertical transmission, but lower virulence than those that are primarily transmitted horizontally.

In Oklahoma, *P. reedi* is first observed on nestlings in late May, and from sampling mite loads of chicks just prior to fledging, Weddle (in press) found a negative correlation between chick mite load and chick body mass. This suggests that these mites may be detrimental to the fitness of host offspring.

The purpose of this study was to determine whether the mite *P. reedi* affects the growth and reproductive success of the house sparrow via experimental manipulations of mite loads. To assess the role ectoparasites play in growth, I compared mass, tarsus length, wing length, and duration of the nestling period of chicks in nests treated with a pesticide to that of chicks in sham-treated control nests. To evaluate the role that ectoparasites play on reproductive success, I compared fledging success in nests treated with a pesticide to that in sham-treated nests.

Methods

House sparrows are semi-colonial passerines. They begin laying clutches in central Oklahoma in late March and continue through early August, producing up to 4 broods. This species uses nest boxes readily (Summers-Smith, 1963); both parents participate in nest construction, incubation, and feeding of the nestlings. Most young fledge 13 to 16 days after hatching.

In July 1996, I erected nest boxes at two sites in Norman, Oklahoma. Because some ectoparasites can survive over the winter in nest material (Rendell and Verbeek 1996), all nest boxes were cleaned of prior nest material in early March 1997. During the 1997 season, I checked nest boxes at least twice weekly to determine the date the first egg was laid, clutch size, number of eggs that hatched, and number of young that fledged.

During this study, I remained blind with respect to the treatment imposed on each nest. Two containers of powder, consisting of either talcum powder (as

a control) or powdered 5% Sevin (experimental) were labeled as 'A' or 'B' by a colleague, such that the contents of each container were unknown to me. I subsequently wore nose plugs during all nest treatments to reduce my detection of the pesticide's odor. On day 4 post-hatch, I removed chicks and manipulated mite loads by attempting to coat all nesting material, with the exception of that in the top 2.5 cm of the nests with powder A or B. The top portion of the nest was not treated to avoid direct exposure of the chicks to the pesticide (Pilar Hayes, Oklahoma City Zoo Veterinary Resident). To control for seasonal effects, I matched experimental and control nests for hatching date. Hatch date for all nests used in the experiment ranged from 5 June through 16 July. Experimental and control nests were also matched for clutch size.

On cycle day 11, I sampled the mite load for each chick in control and experimental nests by brushing seven areas of each chick's body (dorsal and ventral sides of each wing, dorsal and ventral sides of the body, and head) seven times each with a small makeup brush onto white paper for transfer (see Griffiths 1978; Weddle in press). Ectoparasites from each nestling were stored in labeled vials containing 70% ethyl alcohol. Both control and experimental nests were removed after the chicks fledged. I replaced each nest with an equivalent amount of dry grass for future occupants. Each collected nest was sealed in a labeled plastic bag, transported to the laboratory, and placed in a Berlese funnel within 48 h after collection.

The Berlese funnel was made of galvanized steel and had a diameter of 30.5 cm and a depth of 12.1 cm. Before placing a nest in the funnel, I placed a

jar with 70% ethyl alcohol beneath the funnel so that the spout of the funnel projected approximately 3-4 cm into the jar. The funnel was lined with a layer of cheesecloth to collect debris. The nest was removed from the plastic bag and placed on the cheesecloth. I positioned a goose neck lamp with a 100-watt light bulb approximately 15 cm above the nest. The light and heat drove the invertebrates down through the nest and into the jar of alcohol. After 12 h, the jar was sealed and labeled. The mite loads (i.e., the numbers of immature and adult mites) for each chick and nest were determined using a dissecting microscope.

Chicks were weighed on an electronic balance to the nearest 0.1 g on days 4, 6, 8, and 11 post-hatch. Left tarsus and wing lengths were also measured on day 11. Tarsus length was measured to the nearest 0.05 mm using digital calipers. Wing length (the outermost primary) was measured using a wing rule to the nearest mm. Chicks were banded on day 11 with U. S. Fish and Wildlife aluminum bands and a unique combination of plastic color bands for future field identification. I observed nest boxes twice daily after chicks were 11 days old to determine the length of the nestling period. I omitted data on duration of the nestling period for one pair of nests because in one of the two broods, a chick became entangled in the nest material and I had to free its leg before it was able to fledge.

I performed data analyses using SigmaStat 2.0 (SPSS Inc., Chicago, IL). Parametric analyses were used when variables were normally distributed; non-parametric tests were used when variables were not normally distributed. Means

are reported \pm standard deviations (SD). Alpha levels of 0.05 were considered significant.

Results

Twenty-eight broods (14 experimental and 14 control) were used in this study. One additional pair of broods was eliminated from analyses because the control nest had no mites. Nest mite load ranged from 8 to 8998 (mean: 1385.32 ± 1911.26). Although both experimental and control nests contained mites, there was a significant difference in the mean number of mites between treatments: nest mite load for pesticide-treated nests averaged 732.21 ± 1054.98 , whereas control nests averaged 2038.43 ± 2356.93 (Paired *t*-test: $t = 3.40$, 13 df, $p = 0.005$). Sevin was effective at reducing the number of mites in nests. Furthermore, the mean number of mites on the nestlings and the number of mites in the nests were positively correlated ($r_s = 0.55$, $n = 28$, $p = 0.002$), and there was a significant effect of treatment on mean mite load per nestling: the number of mites found on nestlings in experimental nests averaged 0.60 ± 0.70 versus an average of 19.66 ± 14.83 in control nests (Paired *t*-test: $t = 4.70$, 13 df, $p < 0.001$). No other ectoparasites were detected.

There was no difference between experimental and control treatments in mean chick mass on day 4 post-hatch, when nests were treated (Table 1). The effect of *P. reedi* on mean chick mass was also not significant on days 6 or 8 post-hatch (Table 1). Two way repeated measures ANOVA indicated no effect of nest treatment on mean chick mass ($F_{1,26} = 1.219$, $p = 0.28$); however, there

was a significant effect of post-hatch day on mean chick mass ($F_{2,26} = 662.270$, $p < 0.001$). Notably, I found no interaction between day post-hatch and nest treatment (Two way repeated measures ANOVA: $F_{2,26} = 1.151$, $p = 0.324$).

Day 11 mean chick mass was significantly greater in pesticide-treated nests than in control nests (Table 1). Similarly, mean tarsus length on day 11 was significantly greater in treated nests than control nests (Table 2). A wing length effect could not be demonstrated statistically, though chicks from experimental nests had longer wings on average than chicks from control nests (Table 2).

I found no difference in the proportion of chicks fledged (i.e., the brood size at fledging divided by the brood size on day 4 post-hatch, when nests were treated) from experimental versus control nests (Wilcoxon Signed Rank Test: $W = 6.00$, $p = 0.25$). Both pesticide-treated and control nests had very high proportions of chicks fledge: the proportion of chicks that fledged from experimental nests averaged 1.00 ± 0.00 ($n = 14$), whereas the proportion of chicks that fledged from control nests averaged 0.94 ± 0.12 ($n = 14$). I also found no difference in the nestling period (i.e., duration of time from hatching to fledging) for experimental and control nests (Wilcoxon Signed Rank Test: $W = 2.00$, $p = 0.88$). Chicks in experimental nests fledged on average 14.64 ± 0.20 ($n = 13$) days after hatching. Control nestlings fledged on average 14.54 ± 0.27 ($n = 13$) days post-hatch.

Discussion

This study demonstrates that *P. reedi* directly affects house sparrow offspring quality. Day eleven body masses and tarsus lengths were greater in pesticide-treated nests than control nests. Furthermore, broods reared in pesticide-treated nests tended to have longer wings pre-fledging. Nevertheless, I found no difference in fledging success between treatments. On average, pesticide-treated nests did not fledge more, or fewer, chicks than control nests; however, the proportion of chicks fledged from experimental and control nests was very high. Based on Clayton and Tompkins' (1994) criteria, *P. reedi* consequently would be considered to exhibit 'medium' virulence, wherein it reduces nestling body mass, yet has no discernible impact on fledging success. The observed effects of *P. reedi* on house sparrow nestlings are therefore qualitatively consistent with Clayton and Tompkins' hypothesis that avian ectoparasite virulence is directly proportional to the amount of horizontal transmission.

P. reedi's effects also resemble those of at least one other ectoparasite with intermediate transmission. Fauth et al. (1991) examined the effects of the northern fowl mite (*Ornithonyssus sylvarium*), an ectoparasite with both horizontal and vertical transmission, on European starling (*Sturnis vulgaris*) reproductive success. Chicks in insecticide-treated nests had greater body mass but were no more, or less, likely to survive 6-8 weeks after fledging. On the other hand, *Ornithonyssus bursa*, another mite classified as having 'intermediate' transmission, is highly virulent in some studies (Møller 1990), although other

studies have failed to detect an effect on fledging success (de Lope and Møller 1993).

The effects of these few intermediate-transmission parasites that have been studied experimentally are particularly instructive when compared against the effects of ectoparasites that are mainly vertically-or mainly horizontally-transmitted. That *P. reedi* has no discernible impact on house sparrow fledging success does not imply that it has no effect on survival prospects. To the contrary, *P. reedi* clearly affects the offspring mass of house sparrow chicks prior to fledging, and this seems likely to influence offspring survival: Ringsby et al. (1998) found that juvenile survival of *Passer domesticus* nestlings is positively related to fledging mass. From the parasite's perspective, to the extent that transmission opportunities are facilitated by transport out of the nest by fledglings, reduced virulence may be selectively advantageous. Quantitative comparisons of *P. reedi* transmission via mobile hosts (parents or juveniles) versus transmission from nesting material alone would be useful in defining more precisely the degree of this advantage. Theoretically, eliminating the mite's prospects for transmission via nesting material (i.e., increasing its reliance on host mobility) should select for lower virulence (Ewald 1983).

From the host's perspective, even moderate levels of ectoparasite virulence, such as observed here, may affect host reproductive strategies. When offspring quality affects post-fledging survival, ectoparasite load may influence population demographics as well as life history traits. For example, ectoparasites with both horizontal and intermediate transmission affect duration

of the nestling period: the nestling period was shorter for broods in parasite-infested nests of cliff swallows (Chapman and George 1991) and barn swallows (Møller 1990). In multi-brooded hosts such as the house sparrow, changes in duration of the nestling period have the capacity to influence the interbrood interval and thus, number of reproductive attempts per season. However, I did not find a difference in the duration of the nestling period for experimental and control nests. What variable, or set of variables, determines the length of the nestling period in house sparrows remains to be tested.

Other influences of *P. reedi* on house sparrow life history traits merit further study. Møller (1989) and others (Pacejka et al. 1998) suggested that by cleaning out nest boxes before the breeding season, researchers reduce ectoparasite loads. If mite load is indeed heavier in natural breeding sites, then the effect on host fitness could be much greater than what I found. Furthermore, even when parasite loads are relatively reduced, if house sparrows can assess accurately those loads, adults may attempt to find less parasite-infested breeding areas in which to raise offspring or they may adjust clutch sizes or parental investment to counter the increased risk of parasitism encountered during successive breeding attempts (Poiani 1993; Richner and Heeb 1995; Tripet and Richner 1997).

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thank H. Klompen at Ohio State University for identifying the mite species and G. A. Marvin for counting the mite loads for all chicks and nests. My research was supported by a George Miksch Sutton Scholarship in Ornithology, the University of Oklahoma Department of Zoology, and in part by NSF IBN-9408148 to P. L. Schwagmeyer and D. W. Mock.

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Table 1. Mean mass of chicks in experimental and control nests for days four, six, and eight post-hatch.

Day Post-hatch	Experimental (n = 14)	Control (n = 14)	Paired t-test	
			t	P
Four	12.01 ± 1.99	11.57 ± 1.12	0.856	0.41
Six	17.55 ± 2.41	17.01 ± 1.77	0.658	0.52
Eight	22.32 ± 2.17	21.17 ± 1.92	1.482	0.16

Table 2. Mass, tarsus length, and wing length of chicks in experimental nests and controls on day 11 post-hatch.

	Experimental (n = 14)	Control (n = 14)	Paired t-test	
			t	P
Mass (g)	24.71 ± 1.88	23.03 ± 1.83	2.186	0.05
Tarsus Length (mm)	21.99 ± 0.36	21.53 ± 0.53	2.711	0.02
Wing Length (mm)	46.94 ± 2.23	45.38 ± 2.21	1.793	0.10

Chapter 4

EFFECTS OF ECTOPARASITE DENSITY ON PARENTAL PROVISIONING OF NESTLING HOUSE SPARROWS

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**This chapter is written in style for publication in the journal *Condor*
and includes a co-author.**

Abstract. There is growing evidence that avian ectoparasites reduce host fitness. The purpose of this study was to determine whether density of the mite *Pellonyssus reedi*, a common ectoparasite of House Sparrow (*Passer domesticus*) nestlings, influences the rate at which parents feed their nestlings. Parents may feed infested nestlings more because they are especially needy and signal as much, or parents may decrease their investment in parasitized chicks because they are poor vehicles for parental fitness. To evaluate the effect of *P. reedi* on parental provisioning, we manipulated mite loads experimentally and then compared the total number of feeding visits, sizes of prey delivered, and divisions of parental workloads between pesticide-treated and sham-treated (control) nests. The application of pesticide lowered mite populations by 64% relative to control nests. Neither total feeding rate nor mean prey size delivered differed between experimental and control treatments, but the division of parental labor did. There were indications that male parents made the majority of deliveries in pesticide-treated nests; female parents made the majority of deliveries in control nests, but this difference could not be demonstrated statistically.

INTRODUCTION

Birds serve as hosts to a variety of ectoparasites, and suffer fitness consequences from the infestations (Loye and Zuk 1991, Clayton and Moore 1997). Richner et al. (1993) found that the hen flea (*Ceratophyllus gallinae*) negatively affects Great Tit (*Parus major*) offspring quality and quantity by demonstrating that chicks in parasite-free nests had greater masses, tarsus lengths, and fledging success than their counterparts in parasite-infested broods. Similarly, Møller (1990) found that a haematophagous mite, *Omithonyssus bursa*, reduced the fitness of Barn Swallows (*Hirundo rustica*) as measured by nestling tarsus length and body mass.

Because avian parents adjust their investment patterns to nestlings as a function of brood size (e.g., von Haartman 1953, Mock and Lamey 1991) and offspring condition (e.g., Smith and Montgomerie 1991, Kilner et al. 1999), it follows that the impact of ectoparasites on host fitness may be mediated by the parents in several ways. For example, to compensate for the parasite's effects on chick growth and/or survival, parents might accelerate food deliveries; conversely, if chick condition were to fall below a point where salvation were no longer cost-effective, parents might abandon the brood altogether (e.g., Kahl 1964). Johnson and Albrecht (1993) suggested that one reason field studies may fail to detect significant effects of ectoparasites on offspring quality and/or quantity may be the result of increased investment by the parents. In their study on the effects of blow fly larvae and mites on nestling House Wrens (*Troglodytes aedon*), they found little effect on nestling growth or survival even though the

ectoparasites consumed large amounts of blood. Tripet and Richner (1997) found that Blue Tit (*Parus caeruleus*) parents increased deliveries to nestlings that were parasitized by hen fleas and could detect no differences in mass, tarsus length, or body condition for nestlings raised in parasitized and parasite-free nests. By contrast, while Great Tit (*Parus major*) parents similarly increased feeds to young parasitized by hen fleas, their efforts did not compensate fully for the parasite's effects. Chicks in parasite-free nests had greater mass, tarsus length, and body condition than chicks in parasitized nests (Christe et al. 1996).

Parents may decrease parental investment to broods in parasite-infested nests if investment in the current brood negatively affects their likelihood of future reproduction and/or their post-reproductive survival. In House Martins (*Delichon urbica*) and Penduline Tits (*Remiz pendulinus*) parents reduced feeding rates to nestlings in parasitized nests (Møller et al. 1994, Darolova et al. 1997). The remaining possibilities are that parents may not adjust investment on the basis of ectoparasite presence and/or that only one member of the pair may do so.

A common ectoparasite of House Sparrow (*Passer domesticus*) nestlings is a haematophagous mite, *Pellonyssus reedi*, of the family Macronyssidae (Radovsky 1998). Both experimental (Whitekiller *in review*) and correlational (Weddle 2000) evidence indicates that *P. reedi* can have a significant impact on House Sparrow offspring quality. The purpose of this study was to determine whether the adverse effects of *P. reedi* on nestling quality are partially mediated through declines in parental provisioning at infested nests, or whether the negative effects occur despite increased investment in parasitized young. For

this purpose, we compared total feeding visits, size of prey delivered, and the division of labor between male and female parents at nests treated with a pesticide with those measures of performance at sham-treated control nests.

House Sparrows are semi-monogamous passerines. The adults are sexually dimorphic, and both sexes participate in construction of the nests, incubation, and feeding of the nestlings. At temperate latitudes, they can raise up to 4 broods per summer and their young typically fledge 13 to 16 days after hatching.

METHODS

Nest boxes were erected at two sites in Norman, Oklahoma, in July 1996. All boxes were cleaned of nest material just prior to the 1997 season. During the 1997 season (late March through early August), nest boxes were checked at least twice weekly to determine date of laying, clutch size, number of eggs that hatched, and number of young that fledged.

Nests were treated with either 5% Sevin (experimental) or talcum powder (control) as described in Whitekiller (*in review*). We controlled for seasonal effects by matching experimental and control nests for hatch date. We also matched experimental and control nests for clutch size.

On Days 6 through 10 of the nestling period (with 0 as the day hatching began), we conducted daily 1-hr observations of parental feeding behavior using a spotting scope from a car parked approximately 20-30 m from the nest.

Observations were conducted between 0700 and 1500 and staggered throughout

the day to reduce effects of diurnal variation in feeding rates. We recorded feeding visits made by each parent, during which we tried to categorize food items according to size as either 'small' (<13 mm in length = basically too short to protrude past the lateral edges of the bill), 'medium' (13-19 mm = protruding visibly by less than a bill's width), or 'large' (20+ mm). Occasionally, we were unable to determine the size of prey; therefore, we calculated prey size results using the proportion of visits at the nest in question where prey size was identifiable. All prey delivery data are corrected for brood size and presented as an hourly rate (e.g., deliveries per chick per hr). Prey size data are not included for one pair of nests because for one of the two broods, we were unable to clearly discern prey size for more than one 1-hr observation.

As described by Whitekiller (*in review*), we sampled the mite load for each chick in control and experimental nests on day 11. Ectoparasites thus dislodged from each nestling fell onto white paper and were easily transferred for storage to labeled vials containing 70% ethyl alcohol. Chicks were also weighed and banded on Day 11 with USFWS aluminum bands and unique combinations of plastic color bands (Hill 1992) for future field identification.

After chicks had fledged, experimental and control nests were removed from the boxes (replaced with an equivalent amount of dry grass for future occupants), sealed separately in labeled plastic bags, transported to the laboratory, and placed in a Berlese funnel within 48 hr after collection (see Whitekiller *in review*). The number of mites regardless of developmental stage (i.e., mite load) for each nest were counted using a dissecting microscope.

We performed data and power analyses using SigmaStat 2.0 (SPSS Inc. Chicago, IL). Means and standard deviations are reported unless otherwise indicated.

RESULTS

Although both experimental and control nests contained mites, the treatment lowered the mean nest loads by an average of 64%. The mean number of mites on the nestlings and the number of mites in the nests were positively correlated, and there was a significant effect of treatment on mean mite load per nestling (*Whitekiller in review*).

Parental feeding rates (deliveries per chick per hr) did not differ between treatments, averaging 5.46 ± 1.53 in control nests vs. 5.98 ± 1.24 in nests treated with a pesticide (Paired $t = 1.031$, $df = 11$, $P = 0.33$). Male visits tended to be more frequent at experimental nests (3.24 ± 1.10) than at controls (2.48 ± 1.47 ; Paired $t = 1.822$, $df = 11$, $P = 0.10$), whereas maternal visits were similar at experimental (2.73 ± 1.08) and control nests (2.98 ± 1.18 ; Paired $t = 0.621$, $df = 11$, $P = 0.55$). A two way repeated measures ANOVA showed no effect of gender ($F_{1,22} < 0.001$, $P = 0.98$) or nest treatment ($F_{1,22} = 0.810$, $P = 0.38$) on parental feeding rates. There was also no apparent interaction between gender and treatment ($F_{1,22} = 1.514$, $P = 0.23$). Maternal visits were somewhat negatively correlated with paternal feeds per chick per hour for both pesticide-treated nests ($r_s = -0.50$, $n = 12$, $P = 0.09$) and controls ($r_s = -0.55$, $n = 12$, $P = 0.06$).

The proportion of total feeds made by males and females was similar for all nests pooled (Paired $t = 0.260$, $df = 23$, $P = 0.80$), but males tended to deliver more at pesticide-treated nests (0.54 ± 0.15 , $n = 12$) than at control nests (0.44 ± 0.20 , $n = 12$; Paired $t = 1.781$, $df = 11$, $P = 0.10$).

The size of food delivered to experimental and control nests did not differ (Table 1). Furthermore, the size of prey delivered by males and females did not differ between treatments (Table 2).

DISCUSSION

Total feeding visits and size of prey did not differ between pesticide-treated and control nests. Furthermore, the size of prey delivered by males and females did not differ between treatments. If parents do not compensate behaviorally for the presence of mites, either by adjusting their feeding rates or the size of prey delivered, then we might predict differences in chick quality between pesticide-treated and control nests. Whitekiller (*in review*) showed that mites negatively affected House Sparrow nestling masses and tarsus lengths (and possibly wing lengths). A positive relationship between offspring mass at fledging and subsequent juvenile survival has been documented in other populations of this species (Summers-Smith 1963, Ringsby et al. 1998).

Several explanations have been offered for the lack of compensation by the parents (Saino et al. 1998), including that parents are either (1) unable to compensate for the effects of the mites because they are already feeding near their maximum rate or (2) they cannot detect any increasing needs of the

nestlings or that (3) parents are unwilling to compensate because they must weigh the costs of increased effort toward the current brood against future reproduction and/or post-reproductive survival. Explanations 1 and 2 seem unlikely. Although not significant, the proportion of feeds made by males tended to be greater in pesticide-treated nests, whereas the proportion of feeds made by females tended to be greater in control nests ($P = 0.10$). Despite the limitations of our behavioral data (power is low: $1-\beta = 0.27$), these trends imply that parents have the capacity both to monitor offspring condition and to modify their own performance.

Parental response may be due to the direct detection of the presence of the mites and/or differences in begging rates between pesticide-treated and control nests. Numerous field studies have shown that avian parents are sensitive and responsive to the begging stimuli from their broods (e.g., von Haartman 1953, Smith and Montgomerie 1991, Kacelnik et al. 1995, Kilner et al. 1999). It would be interesting to know whether experimental mite-reductions lead to measurable changes in the signals offspring provide to the House Sparrow parents: Christe et al. (1996) found that Great Tit broods that were infested with hen fleas spent more time begging than parasite-free broods.

In contrast to the results of this study, male Great Tits fed more often in parasite-infested than parasite-free nests, whereas there was no difference in female provisioning rates between treatments (Christe et al. 1996). These authors suggested that the differences between males and females may be explained by differences in the trade-off between current versus future broods

with females investing more in future broods and males investing more in current broods. In a study involving brood size manipulations, Moreno et al. (1995) also found sex differences in Pied Flycatcher (*Ficedula hypoleuca*) parental reactions to increased demands of their broods. Males made more feeding visits to enlarged broods whereas females did not adjust their feeding rates.

If ectoparasites affect the condition of the female parent indirectly (i.e., due to increased energy expenditure), then they may also affect future reproductive attempts (e.g., clutch size; Poiani 1993) and/or post-reproductive survival. Hegner and Wingfield (1987) studied the effects of the addition of nestlings to House Sparrow broods and found that the additional offspring resulted in an increase in maternal and paternal feeding visits along with a decrease in subsequent clutch size. The interbrood interval also lengthened following brood enlargement. For males, the additional parental provisioning affected nest site defense and mate guarding during the latter stages of the nesting cycle.

Studies that have looked specifically at the effects of parasites on host provisioning have found no effect of parasites on the adult hosts. Tripet and Richner (1997) found that increased parental provisioning by Blue Tit parents to chicks in parasitized nests had no effect on either adult male or female body condition. Christe et al. (1996) found similar results in Great Tits. There was no difference in adult body mass or tarsus length between parasite-infested and parasite-free nests.

Effects of brood size manipulations on post-reproductive survival have been documented in Kittiwakes (*Rissa tridactyla*; Jacobsen et al. 1995), Blue Tits (Nur 1984), and House Sparrows (Hegner and Wingfield 1987). Jacobsen et al. (1995) found that female Kittiwakes provisioning enlarged broods were less likely to return the next breeding season. No effect on male post-reproductive survival was documented. Nur's (1984) findings parallel those of Jacobsen et al. (1995). While Blue Tit adult female survival decreases as brood size increases, no effect on male survival was detected. Hegner and Wingfield (1987) found that the brood enlargements did not affect House Sparrow adult body condition or survival even though parents increased feeding rates. Whether mites indirectly affect male or female House Sparrow body condition and post-reproductive survival is yet to be tested.

Although we found no difference in the proportion of small, medium, and large prey items delivered to pesticide and control nests, perhaps identifying specific prey types may be more illuminating. Wright et al. (1998) found that European Starling (*Sturnis vulgaris*) parents did not adjust the amount of food delivered per chick per visit to varying experimental brood sizes; however, proportions of prey types did differ. Lower masses of starling chicks in enlarged broods could have been the result of the delivery of less digestible prey types or increased sibling competition.

The question remains as to why both parents do not respond to increased mite loads by increasing feeding visits and/or size of prey. Females may not respond positively to the presence of mites simply because males do (see

Winkler 1987, Wright and Cuthill 1989). Further research is needed to test for variation in parental response between and within years.

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Table 1. Proportion of small, medium, and large prey items delivered by both parents for both pesticide-treated and sham-treated control nests.

PREY SIZE	PESTICIDE TREATMENT ($\bar{x} \pm SD$)	CONTROL ($\bar{x} \pm SD$)	PAIRED T	DF	P
SMALL	0.61 \pm 0.16	0.63 \pm 0.20	0.331	10	0.75
MEDIUM	0.18 \pm 0.13	0.16 \pm 0.07	0.502	10	0.63
LARGE	0.21 \pm 0.13	0.21 \pm 0.19	0.128	10	0.90

Table 2. Proportion of small, medium, and large prey items made by males vs. females for pesticide-treated nests and sham-treated controls.

	PREY SIZE	PESTICIDE TREATMENT ($\bar{x} \pm SD$)	CONTROL ($\bar{x} \pm SD$)	PAIRED T	DF	P
MALES	SMALL	0.34 ± 0.16	0.30 ± 0.18	0.632	10	0.54
	MEDIUM	0.10 ± 0.12	0.09 ± 0.05	0.331	10	0.75
	LARGE	0.09 ± 0.07	0.09 ± 0.09	0.052	10	0.96
FEMALES	SMALL	0.26 ± 0.16	0.33 ± 0.23	1.027	10	0.33
	MEDIUM	0.08 ± 0.06	0.07 ± 0.03	0.308	10	0.77
	LARGE	0.12 ± 0.07	0.11 ± 0.11	0.274	10	0.79