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BADGE SIZE AND EXTRA-PAIR FERTILIZATIONS IN THE HOUSE SPARROW[1]

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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.

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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 ($\pm$ 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 $\times$ 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, unpubl. data). Badge sizes were scored independently by R. 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 μl 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 μl 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 μg of DNA was digested with the restriction enzyme *Hae*III 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 ^{32}P-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 (± 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 (± 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, extrapair 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 (± 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 × 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 × 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.

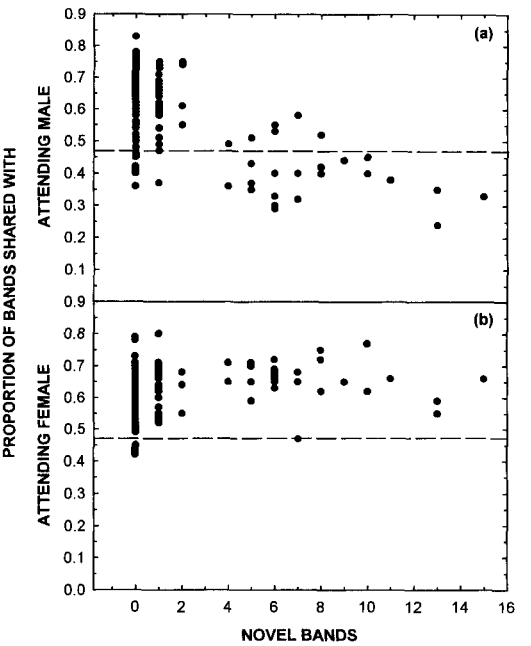

FIGURE 1. Relationship between the proportion of bands shared with the attending parent and the number of novel bands for each nestling House Sparrow. Band sharing with (a) the attending male and (b) the attending female. The dotted line represents the lower, one-tailed, 95% confidence limit for band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

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

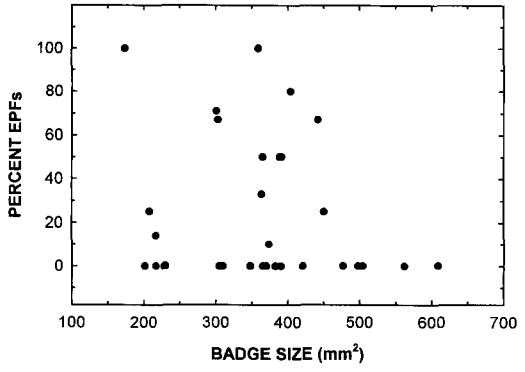

FIGURE 2. Relationship between male House Sparrow badge size and percent extra-pair fertilizations in his brood. Some of the data points are hidden from view.

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 mm^2 and averaged 361 ± 105 mm^2; 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 ($r_s = -0.18$, $n = 33$, $P = 0.33$; 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 ($\bar{x} = 339 \pm 87$ mm^2, $n = 14$) did not differ from the badge size of non-cuckolded males (378 ± 116 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 ($\bar{x} = 369 \pm 158$ mm^2, $n = 15$) and the badge sizes of males that failed to return (357 ± 101 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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