

## Parental Feeding Rates in the House Sparrow, *Passer domesticus*: Are Larger-Badged Males Better Fathers?

Karen M. Voltura, P. L. Schwagmeyer & Douglas W. Mock

*Department of Zoology, University of Oklahoma, Norman, OK, USA*

### Abstract

Elaborated secondary sexual characteristics may reflect genetic quality or good health, either of which may be associated with an individual's competence as a parent. We examined whether female house sparrows (*Passer domesticus*) paired to large vs. small-badged mates gain benefits in the form of increased parental care or improved nestling welfare. House sparrow nests where the male had been trapped and banded were observed for 1 h on at least 5 d during the peak growth period of nestlings. Male feeding shares, measured as the proportion of total feeds per chick made by the male, were marginally positively correlated with male badge size. Moreover, higher male shares of nestling feeding were associated with improved prospects for offspring survival, and a greater proportion of chicks fledged from the nests of larger-badged males. These results suggest that females paired to large-badged males gain direct benefits in the form of enhanced nestling survival, which presumably stem from factors associated with increases in the proportion of nestling feeding contributed by their mates.

Corresponding author: P. L. Schwagmeyer, Department of Zoology, University of Oklahoma, Norman, OK 73019, USA. E-mail: [plsch@ou.edu](mailto:plsch@ou.edu)

### Introduction

The degree of elaboration of male secondary sexual traits has been found to be associated with mating advantages in many taxa (Andersson 1994). Sexual selection theory predicts that such exaggerated male traits should be associated with either genetic or material benefits to females or their offspring (Andersson 1994), regardless of whether the traits are subject to direct female choice or are indirectly favored by aspects of female behavior, morphology, or physiology that shape male mating competition (Wiley and Poston 1996). Females may gain genetic (indirect) benefits from mating with males with exaggerated traits if the traits are associated with male genetic quality and thereby enhance the survival or reproductive success of their offspring. Alternatively, non-genetic benefits that females might gain include increased fecundity (e.g. because of food provided by

her mate during courtship or incubation), increased parental care of offspring by her mate, access to better food sources on the male's territory, and a potentially lower risk of predation or lower levels of harassment from other males (Andersson 1994).

In birds, both behavioral and morphological male secondary sexual characteristics have been examined for their associations with genetic and non-genetic benefits. Examples of species where empirical evidence has suggested the existence of genetic benefits include the great reed warbler, *Acrocephalus arundinaceus* (Hasselquist et al. 1996), where the song repertoire size of extra-pair mates predicted offspring survival; the great tit, *Parus major* (Norris 1993), where a cross-fostering experiment showed that the breast stripe size of putative genetic fathers was positively correlated with the number of surviving sons; and the peacock, *Pavo cristatus* (Petrie 1994), where the sons of males with larger tail eye-spots had higher survivorship, and offspring of both sexes showed developmental advantages.

Evidence supporting the existence of direct benefits to females mating with males possessing exaggerated traits has been found, as well. In red-winged blackbirds (*Agelaius phoeniceus*), older males have larger song repertoires and lengthier courtships than younger males (Searcy and Yasukawa 1981) and males with these attributes have better territories. Territory quality may also vary with degree of male plumage elaboration: in blue grosbeaks (*Guiraca caerulea*) aspects of male plumage coloration were found to correlate positively with both the size of male territories and the abundance of prey within them (Keyser and Hill 2000).

In addition to studies relating elaborated male traits to territory quality, previous research also has examined whether such traits are associated with male parental quality. Whether male sexual signals are predicted to correlate positively or negatively with male parenting contributions can hinge on a variety of factors, including the extent to which males could profit from allocating more effort towards extra-pair matings and polygynous matings (Kokko 1998). The empirical studies often have focused on testing two opposing predictions. First, several 'good-parent' models have predicted that females are selected to choose males that increase their fecundity (Kirkpatrick 1985), and that traits that females find more attractive can evolve as honest signals of male parental quality (Hoelzer 1989). Alternatively, the 'sexy-son' hypothesis (Weatherhead and Robertson 1979) predicts that attractive males contribute less than less attractive males to parental care of offspring and thus may decrease the number of young a female produces, but the sons of females mated to attractive males inherit the attractive trait from their father and thus have higher reproductive success than sons of less attractive males. The differential-allocation hypothesis (Burley 1986) makes a similar prediction, that more attractive males will contribute relatively less to parental care than less attractive males, in this case because the mates of attractive individuals are expected to invest more heavily in the offspring. In support of the 'good-parent' models, female house finches were shown to gain direct benefits from pairing with more brightly colored males as a result of higher courtship feeding rates by brighter males (Hill 1991), and positive correlations between male

plumage characteristics and nestling provisioning have been found in the pied flycatcher, *Ficedula hypoleuca* (Sætre et al. 1995), American kestrel, *Falco sparverius* (Wiehn 1997), and northern cardinal, *Cardinalis cardinalis* (Linville et al. 1998). On the other hand, several studies have revealed no association between nestling provisioning and various male plumage characteristics, [e.g. forehead patch size in the Norwegian pied flycatcher, *F. hypoleuca*: Dale et al. (1999); breast streaking in the yellow warbler, *Dendroica petechia*: Lozano and Lemon (1996); plumage reflectance in the bluethroat, *Luscinia svenicus*: Smiseth et al. (2001)] or a negative relationship [e.g. brightness in the yellowhammer, *Emberiza citrinella*: Sundberg and Larsson (1994)]. Studies of how male song characteristics correlate with parental care have produced similarly mixed results, with some showing positive associations [song rate and relative shares of nest defense and nestling provisioning in the stonechat, *Saxicola torquata*: Grieg-Smith (1982); dawn song output, nest defense and nestling provisioning in the willow tit, *P. montanus*: Welling et al. (1997); repertoire size and nestling provisioning in the sedge warbler, *A. schoenobaenus*: Buchanan and Catchpole (2000)], and others showing no relationship [e.g. repertoire size, incubation, and nestling provisioning in the starling, *Sturnus vulgaris*: Mountjoy and Lemon (1997)].

In the house sparrow (*Passer domesticus*), males have conspicuous black badges on their throats that are absent in females. We examined whether the badge size of male house sparrows is associated with increased parental care to nestlings, thus increasing offspring survival. Previous studies of the relationship between male house sparrow badge size and various aspects of breeding success suggest that badge size may correlate with direct benefits in interesting ways. House sparrows do not defend feeding territories, thereby eliminating the possibility that badge size correlates with territory quality, but Møller (1988) suggested that large-badged males possessed higher quality nest sites than small-badged males, which would provide one possible direct benefit to females from pairing with larger-badged males. Conversely, Griffith et al. (1999a) found higher annual reproductive success of small-badged males on Lundy Island, which they attributed to female choice for small-badged partners and to potential direct benefits provided by small-badged males. Finally, Reyer et al. (1998) have shown that large-badged males perform a greater share of those nest defense behaviors which are likely to be riskiest, indicating another potential direct benefit to females from pairing with larger-badged males. By observing the parental behavior of males of known badge size and examining feeding rates and nestling survival in relation to male badge size, we tested the hypothesis that male badge size is associated with direct benefits in the form of increased nestling care and enhanced offspring survival.

### Methods

Four nestbox populations of house sparrows in Norman, OK, were studied between 1994 and 1997. Known or suspected nest predators at these sites included European starlings (*S. vulgaris*), Loggerhead shrikes (*Lanius ludovicianus*), and

several species of snakes. Both shrikes and American kestrels have also been observed to frequent nest box areas sufficiently often to lead indirectly to chick death from starvation because of harassment of parents. Birds began building nests in mid-March and nestboxes were checked every 3–4 d to monitor laying. The first clutches hatched in early Apr. and birds continued breeding through the summer, laying three to four clutches over a single breeding season. Sampling of parental behavior of individuals tending successive broods has revealed that male rates of nestling provisioning show significant repeatability across broods (Schwagmeyer and Mock, unpubl. data). For the current study, variation among nests in offspring survival stemming from extraneous factors was reduced by avoiding sampling at the earliest nests of each year, when sudden episodes of inclement weather often cause heavy offspring mortality. The modal clutch sizes at these study sites are four and five; with one exception (a single six-egg clutch), this study included only males that currently were tending broods hatching from four or five egg clutches. Initial brood sizes at these nests ranged from two to six, and male badge size was not significantly correlated with initial brood size (Spearman rank correlation:  $r_s = 0.10$ ,  $n = 27$ ,  $p = 0.63$ ). All sampled pairs were socially monogamous.

We captured adults with mist nets, ground traps or wire corridor traps and banded them with US Fish and Wildlife Service aluminum leg bands and unique combinations of plastic, colored bands. At the time of capture, we photographed males to obtain a standard picture of the black throat badge. We did not attempt to measure simultaneously any part of the male's badge which might still be 'hidden' by light-colored tips on the feathers, which abrade during the months after the autumn moult (Møller and Erritzoe 1992; Veiga 1996). Griffith et al. (1999a), however, have found that visible badge sizes during the breeding season are highly correlated with measures of the 'hidden' badge taken prior to the breeding season. In the present study, all males were captured and photographed at the peak of breeding (between mid-May and mid-Jul.), which should further reduce the possibility that individual differences in badge sizes were strongly affected by differences in the degree of abrasion of the light-colored feather tips.

For the photograph, males were held immobile with their beaks pointing upwards, at a 90° angle to the ground. They were photographed with a 0.5 × 0.5 cm grid in the background which was later used to scale the photos. Individual males were matched with their nestbox when they were resighted and identified after release. Later, we scanned the photographs into a computer and digitized the perimeter of the badge. Using the background grid to scale each photo, the area of the badge was calculated. Each photograph was digitized three times and the average of the three area measurements was used in the analysis. To eliminate potential scoring biases, we coded the photographs by the birds' US Fish and Wildlife Service band numbers and matched males to their nests after the badges were measured. The date of capture and the hatch date of the brood were measured as the number of days after the first egg hatched at any of the study sites. This date was April 8 in 1994, April 7 in both 1995 and 1996, and April 12 in 1997.

We sampled feeding rates for each male during the breeding cycle at the time of his capture. Thus, only feeding rates measured in the same year that a male's badge was photographed were used in the analysis; male badge size shows poor between-year consistency (Griffith et al. 1999b). Focal nest observations were made over days 3 through 11 of the nestling period (where day 0 is the day hatching began). We recorded feeding rates at each nest, distinguishing between maternal and paternal feeding visits. At least five 60-min focal nest observation samples were collected for each nest over the 9-d period. The onset of sampling at nests varied, and is a potential source of bias in our estimates of male provisioning behavior given that male house sparrow shares of feeding decline at about day 9 or 10 post-hatch (Hegner and Wingfield 1987; Veiga 1990). However, male badge sizes were not significantly correlated with the earliest day post-hatch that a nest was observed (Spearman rank correlation:  $r_s = -0.08$ ,  $n = 27$ ,  $p = 0.68$ ), the number of days across the nestling period that a nest was sampled (Spearman rank correlation:  $r_s = 0.15$ ,  $n = 27$ ,  $p = 0.45$ ), or the last day of sampling for each nest (Spearman rank correlation:  $r_s = 0.27$ ,  $n = 27$ ,  $p = 0.17$ ). This last variable was necessarily constrained in cases where all chicks died prior to day 11 post-hatch; the positive nature of the observed relationship indicates that, if anything, our sampling may have yielded underestimates of the provisioning behavior of large-badged males. Observations were staggered throughout the day such that no nests were consistently sampled during just the morning or afternoon time periods. For 13 nests we quantified the type of food delivered in each visit as large ( $> 2$  cm in length), medium (approx. 1 cm in length), small (approx. 0.6 cm in length), or seed or bread. In some cases (an average  $\pm$  SD of  $21.4 \pm 16.28\%$  of male visits;  $31.9 \pm 12.32\%$  of female visits) we failed to identify size of prey delivered for each visit to the nest. We consequently calculated prey size variables as the proportion of visits where prey size was identified.

We weighed chicks on day 11 and banded them with US Fish and Wildlife Service aluminum bands and colored, plastic leg bands. Nests were checked after day 17 to identify any chicks that had not fledged and were dead in the nestbox.

Statistical analyses were performed using JMP 3.2 (SAS Institute Inc., Cary, NC, USA) and SAS 6.0 statistical software. Behavioral samples of parental provisioning were converted to a single average for each pair. All variables were checked for normality, and in cases where they were not normally distributed we used either non-parametric analyses or transformed the variable to achieve normality when required by the particular test. To examine factors predicting nestling survival we used the events/trials syntax for logistic regression on SAS, such that the number of offspring that fledged at each nest was weighted by the number of chicks that had hatched at that nest. The effects of hatch date (time within season) on provisioning rates, offspring mass, and offspring survival were evaluated in preliminary analyses, and subsequent analyses corrected for variation in hatch dates when necessary. Probability values are two-tailed, and mean values are presented with standard deviations.

### Results

Badge size ranged from 177 to 693 mm<sup>2</sup> and was not significantly correlated with date of capture of the male (Spearman rank correlation:  $r_s = 0.21$ ,  $n = 27$ ,  $p = 0.28$ ). The proportion of feeding performed by individual males ranged from 0.066 to 0.688. There were no differences among years of this study in male feeding visits/nestling/h (Kruskal–Wallis test:  $\chi^2 = 3.41$ ,  $n = 27$ ,  $p = 0.33$ ), female feeding visits/nestling/h ( $\chi^2 = 4.50$ ,  $n = 27$ ,  $p = 0.22$ ), nor in the proportion of feeds by fathers ( $\chi^2 = 0.74$ ,  $n = 27$ ,  $p = 0.86$ ) and data for all 4 yr were combined for the remainder of the analyses.

In general, mean ( $\pm$ SD) female feeding rates ( $2.82 \pm 1.37$  feeding visits/nestling/h) were higher than male feeding rates ( $2.12 \pm 0.98$ ) for nests in this study (paired  $t$ -test:  $t = 3.02$ ,  $n = 27$ ,  $p = 0.006$ ). Male and female feeding rates were positively correlated with each other (Fig. 1), and the relationship remained positive with the effects of hatch day partialled out (Spearman rank correlation:  $r_{s(xy)z} = 0.44$ ,  $n = 27$ ,  $p = 0.02$ ).

The total feeds per nestling for each nest, after controlling for hatch day, was unrelated to male badge size (log male badge size, Pearson partial correlation:  $r_{(xy)z} = 0.06$ ,  $n = 27$ ,  $p = 0.78$ ). Similarly, the mean mass of nestlings at day 11 post-hatch was not correlated with male badge size once hatch day was controlled for (log male badge size, Pearson partial correlation:  $r_{(xy)z} = -0.13$ ,  $n = 24$ ,  $p = 0.56$ , with nests with no surviving nestlings at day 11 post-hatch eliminated from analyses). The proportion of total feeds made by the male at a nest (which was not associated with hatch day:  $p > 0.50$ ) tended to be positively correlated with the size of his badge (Fig. 2). However, the mean feeds per nestling for fathers with hatch day controlled for was not significantly related to badge size (log badge size, Pearson partial correlation:  $r_{(xy)z} = 0.21$ ,  $n = 27$ ,  $p = 0.32$ ), and similarly, the mean female feeds per nestling was not significantly related to her

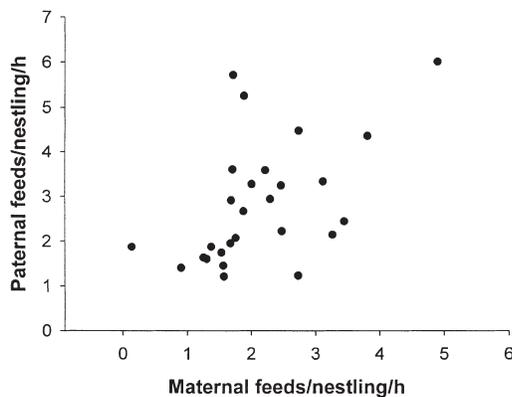


Fig. 1: The mean number of feeding visits/nestling/h for mothers and fathers. Spearman rank correlation:  $r_s = 0.60$ ,  $n = 27$ ,  $p = 0.001$

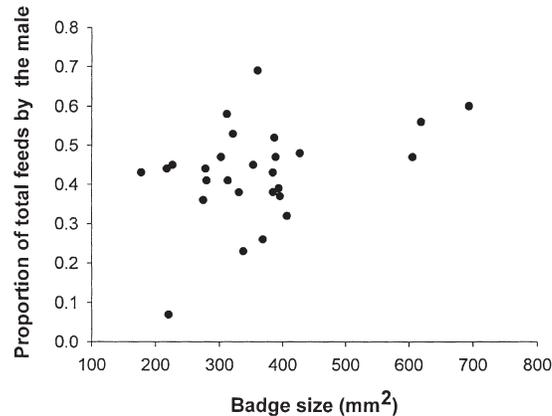


Fig. 2: The correlation between the proportion of total feeds made by the male at a nest and his badge size. Pearson correlation with log-transform of badge size:  $r = 0.36$ ,  $n = 27$ ,  $p = 0.06$

mate's badge size (log female feeds/chick and log badge size, Pearson partial correlation:  $r_{(xy)z} = -0.12$ ,  $n = 27$ ,  $p = 0.54$ ).

Of the 113 total chicks hatched to parents in this study, 23 failed to survive to fledge. When the proportion of feeding performed by males, the total number of feeds per chick, and hatch date were considered as alternative predictors of nestling survival, only the proportion of feeding performed by males was significantly associated with hatchling survival to fledging (Logistic regression: Wald  $\chi^2 = 4.39$ ,  $n = 27$ ,  $p = 0.035$ ): when males did a greater share of feeding, the risk of losing nestlings declined. Furthermore, although larger-badged males did not have broods with heavier nestlings, they did fledge a greater proportion of the chicks that hatched in their nest: male badge size had a strong positive relationship to nestling survival (Logistic regression: Wald  $\chi^2 = 7.18$ ,  $n = 27$ ,  $p = 0.007$ ).

For the 13 nests with data on size of prey delivered to the nest, the proportion of feeds by either fathers or mothers that were large prey items was not correlated with male badge size (Table 1). For males, though, the proportion of feeds that were medium-sized prey was negatively correlated with badge size. The proportion of small prey items fed by males increased with increasing badge size, and their mates showed a similar tendency (Table 1).

### Discussion

In our study populations, larger-badged male house sparrows fledged a markedly higher proportion of the young in their nests than smaller-badged males. Yet, total parental delivery rates were not associated with male badge size, nor was there an association between male badge size and the mass of offspring that survived to day 11 post-hatch. Instead, the parental division of labor tended

*Table 1:* The mean and SD proportion of prey of different size category delivered by parent house sparrows, and the Pearson partial correlations of male badge size with the proportion of feeds of a given prey size after controlling for the effects of hatch day ( $n = 13$ )

Prey size	Parent							
	Mother				Father			
	$\bar{x}$	SD	$r_{(xy)-z}$	p value	$\bar{x}$	SD	$r_{(xy)-z}$	p value
Small	0.53	0.204	0.56	0.06	0.56	0.130	0.64	0.02*
Medium	0.27	0.105	-0.31	0.33	0.24	0.081	-0.78	0.002*
Large	0.14	0.128	-0.34	0.29	0.13	0.095	-0.20	0.53

\* $p < 0.05$ .

Proportions were based on total numbers of prey delivered that were of identifiable size; proportions for each sex total  $< 1.0$  because data on the least common prey type, seed or bread used in conjunction with ground-trapping, were not subjected to analyses.

to vary with male badge size, with large-badged males doing proportionately more provisioning and their mates less. The male share of feeding, in turn, was a better predictor of nestling survival than was the total per-chick provisioning rate. The combination of proportionately higher feeding rates and improved offspring survival suggests that females gain direct benefits from pairing with large-badged males; this proposition agrees with other studies showing that more ornamented males are better parental providers (e.g. Wiehn 1997; Linville et al. 1998).

Our results for male badge size and provisioning shares parallel those obtained by Reyer et al. (1998) on badge size and nest defense in house sparrows: they found that the main effect of badge size on nest defense behavior was not in terms of absolute levels of male defense, but in the relative allocation of defense behavior within pairs. Reyer et al. (1998) argued that the greater share of risky nest defense shown by large-badged males may stem from the presumed greater paternity of such males. This explanation would not apply to our study sites, and may, indeed, be of limited generality, given that male badge size has not been found to correlate with paternity in Oklahoma (Whitekiller et al. 2000) or in Britain or Spain (Cordero et al. 1999).

These aforementioned correlational field studies uniformly yield results where causal relationships are difficult to disentangle. One question that deserves future study is whether female quality and male badge size covary, such that the improved offspring survival of large-badged males is at least partially attributable to superiority of their mates. The lack of a relationship between badge size and female feeding rates observed in the current study might argue against this. However, the strong positive correlation between male and female feeding rates within pairs suggests that mates have similar provisioning profiles, which certainly could be the result of assortative pairing based on factors influencing parental competence.

Why the division of provisioning effort within house sparrow pairs should be strongly related to nestling survival also merits further study, particularly given

that food deliveries by large-badged males were biased toward small items, and those of their mates tended to be so as well. Additional aspects of both male and female parental care that we did not measure may contribute to the relationships we found among male badge size, feeding shares, and nestling welfare. The increased proportion of nest defense by large-badged males, as discovered by Reyer et al. (1998) for *P. domesticus* in Switzerland, could potentially have improved the survivorship of the offspring of large-badged males at our study sites. Some of the chick losses occurring in the nests we sampled did indeed appear to result from predation (e.g. when the largest chick in the nest was suddenly discovered missing). If badge size is similarly related to male nest defense in Oklahoma, and if males are more effective at nest defense than females, anti-predator behavior may provide links among badge size, male feeding share, and offspring survival. Alternatively, increased feeding shares by males may be associated with increased time females spend vigilant near the nest or increased time females are able to spend brooding during the early part of the nesting cycle (e.g. Johnson et al. 1993; Johnson and Kermott 1993).

Our results are consistent with the hypothesis that female house sparrows could use male badge size as an indicator trait to assess the quality of their mate as a provider for offspring. Previous work on house sparrows indicated that badge size is heritable, based on a significant father-son regression with a sample size of 13 (Møller 1989). Correlations among genetic quality, badge size, and male parental investment may thus provide one means by which badge size could serve as an indicator of paternal effectiveness. More likely, badge size reflects male condition: several studies have shown badge size to be condition-dependent (Veiga and Puerta 1996; Cordero et al. 1999; Griffith 2000), and investigations of how male house sparrow badge size affects male dominance status uniformly have found a positive relationship (Møller 1987; Veiga 1993; Solberg and Ringsby 1997; Liker and Bara 2001). General condition may well correlate with paternal competence. An alternative possibility stems from the effects of rearing environment on badge size. In a direct test of badge size heritability, Griffith (1999b) found that the badge sizes of cross-fostered males more closely resembled that of their foster father than that of their genetic father, suggesting strong paternal or maternal effects. Wolf et al. (1997) modeled the evolution of indicator traits for parental quality. They showed that, in cases where the amount of parental investment that mothers and fathers provide during the period of parental care affects the expression of an indicator trait in male offspring, a phenotypic correlation can evolve between the amount of paternal care a male will provide and the expression of an indicator trait. The degree to which the male trait and the amount of parental care males provide are correlated determines the honesty of the trait: the stronger the correlation, the more reliable the signal (Wolf et al. 1997). This requires heritability of parental investment patterns, however, and we know of no such data for the house sparrow.

Badge size in male house sparrows has been shown to be related to age as well as to indices of body condition in free-living individuals (Veiga 1993; Veiga and Puerta 1996, Cordero et al. 1999; but see Møller 1989; Lifjeld 1994). Yearling

males generally have smaller badges than older males (Veiga 1993; Cordero et al. 1999; Griffith et al. 1999b). If smaller-badged males are likely to be less experienced breeders (and/or to mate with less experienced breeders), the correlations among badge size, paternal feeding shares, and offspring survival could be explained largely in terms of parental experience: positive correlations among male age, parental care, and either male song features (e.g. Searcy and Yasukawa 1981; Yasukawa et al. 1990) or male plumage (e.g. Wiehn 1997) occur in several species. Sampling of nests very early in the season, when yearling males have had no previous breeding opportunities, should yield even more pronounced relationships among offspring survival, parental behavior, and badge size if this is the case.

While we have shown that there are plausible means by which females gain directly from pairing with large-badged males, this does not rule out the possibility that they might also gain indirect benefits. However, the preponderance of evidence argues against badge size being strongly heritable, and the between-year inconsistency of a male's badge size (Griffith et al. 1999b) suggests that it would serve poorly as a marker of male genetic quality. Furthermore, there is no evidence that male badge size affects adult survivorship at Oklahoma study sites (Whitekiller et al. 2000), and the Griffith et al. (1999b) cross-fostering experiment revealed no relationship between badge size of the biological father and offspring survival to 6 mo.

Finally, although the provisioning results presented here provide no indication that females increase their care of nestlings when paired to large-badged mates, as predicted by Burley (1986, 1988), differential investment by females in relation to the quality of their mate can occur in multiple ways (Sheldon 2000). In Oklahoma, female house sparrows paired to large-badged males produce more male-biased broods at hatching than females mated to small-badged males (Voltura 1998). Regardless of whether male badge size is heritable, as has been suggested by Møller (1989), or shows a strong paternal effect (Griffith et al. 1999b), the sons of large-badged males would have badges resembling those of their fathers. The results of the current study indicate that those sons would experience improved survival as nestlings. The effect of paternal badge size on nestling survival would consequently amplify the sex ratio bias present at hatching, such that larger-badged males and their mates would produce disproportionately greater numbers of fledgling sons with larger badges.

#### Acknowledgements

We thank R. Whitekiller, A. Skypala, K. Montague, L. Cline, M. Howell, G. Wang, and C. Weddle for assistance with nestbox censusing, capturing and photographing males and nest observations of feeding behavior. C. McCallister developed and printed many of the badge photographs and image analysis and badge measurements were carried out in the lab of J. N. Thompson Jr., O. M. Fincke, J. N. Thompson, Jr. and J. L. Rogers reviewed various drafts of the manuscript and provided very useful comments. Funding was received through a GAANN Fellowship administered by the Department of Zoology at the University of Oklahoma and grants from the G. M. Sutton Scholarship Foundation to KMV, NSF grant IBN9408148 to DWM and PLS and from the

Department of Zoology at the University of Oklahoma. The research reported in this manuscript complies with the laws of the USA and was approved by the Institutional Animal Care and Use Committee at the University of Oklahoma (Animal Welfare Assurance #73-R-100).

### Literature Cited

- Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton.
- Buchanan, K. L. & Catchpole, C. K. 2000: Song as an indicator of male parental effort in the sedge warbler. *Proc. R. Soc. Lond. B* **267**, 321–326.
- Burley, N. 1986: Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* **127**, 415–445.
- Burley, N. 1988: The differential allocation hypothesis: an experimental test. *Am. Nat.* **132**, 611–628.
- Cordero, P. J., Wetton, J. H. & Parkin, D. T. 1999: Extra-pair paternity and male badge size in the House Sparrow. *J. Avian Biol.* **30**, 97–102.
- Dale, S., Slagsvold, T., Lampe, H. M. & Sætre, G.-P. 1999: Population divergence in sexual ornaments: the white forehead patch of Norwegian pied flycatchers is small and unsexy. *Evolution* **53**, 1235–1246.
- Grieg-Smith, P. W. 1982: Song-rates and parental care by individual male stonechats (*Saxicola torquata*). *Anim. Behav.* **30**, 245–252.
- Griffith, S. C. 2000: A trade-off between reproduction and a condition-dependent sexually selected ornament in the house sparrow *Passer domesticus*. *Proc. R. Soc. Lond. B* **267**, 1115–1119.
- Griffith, S. C., Owens, I. P. F. & Burke, T. 1999a: Female choice and annual reproductive success favour less-ornamented male house sparrows. *Proc. R. Soc. Lond. B* **266**, 765–770.
- Griffith, S. C., Owens, I. P. F. & Burke, T. 1999b: Environmental determination of a sexually selected trait. *Nature* **400**, 358–360.
- Hasselquist, D., Bensch, S. & von Schantz, T. 1996: Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature* **381**, 229–232.
- Hegner, R. E. & Wingfield, J. C. 1987: Effects of brood-size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. *Auk* **104**, 470–480.
- Hill, G. E. 1991: Plumage coloration is a sexually selected indicator of male quality. *Nature* **350**, 337–339.
- Hoelzer, G. A. 1989: The good parent process of sexual selection. *Anim. Behav.* **38**, 1067–1078.
- Johnson, L. S. & Kermott, L. H. 1993: Why is reduced male parental assistance detrimental to the reproductive success of secondary female house wrens? *Anim. Behav.* **46**, 1111–1120.
- Johnson, L. S., Kermott, L. H. & Lein, M. R. 1993: The cost of polygyny in the house wren *Troglodytes aedon*. *J. Anim. Ecol.* **62**, 669–682.
- Keyser, A. J. & Hill, G. E. 2000: Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behav. Ecol.* **11**, 202–209.
- Kirkpatrick, M. 1985: Evolution of female choice and male parental investment in polygynous species: the demise of the “sexy son”. *Am. Nat.* **125**, 788–810.
- Kokko, H. 1998: Should advertising parental care be honest? *Proc. R. Soc. Lond. B* **265**, 1871–1878.
- Lifjeld, J. T. 1994: Do female house sparrows copulate with extra-pair males to enhance their fertility? *J. Avian Biol.* **25**, 75–76.
- Liker, A. & Bara, Z. 2001: Male badge size predicts dominance against females in house sparrows. *Condor* **103**, 151–157.
- Linville, S. U., Breitwisch, R. & Schilling, A. J. 1998: Plumage brightness as an indicator of parental care in northern cardinals. *Anim. Behav.* **55**, 119–127.
- Lozano, G. A. & Lemon, R. E. 1996: Male plumage, paternal care and reproductive success in yellow warblers, *Dendroica petechia*. *Anim. Behav.* **51**, 265–272.
- Møller, A. P. 1987: Variation in badge size in the house sparrow *Passer domesticus*: evidence for status signalling. *Anim. Behav.* **35**, 1637–1644.
- Møller, A. P. 1988: Badge size in the house sparrow, *Passer domesticus*. Effects of intra- and intersexual selection. *Behav. Ecol. Sociobiol.* **22**, 373–378.
- Møller, A. P. 1989: Natural and sexual selection on a plumage signal of status and on morphology in house sparrows, *Passer domesticus*. *J. Evol. Biol.* **2**, 125–140.

- Møller, A. P. & Erritzoe, J. 1992: Acquisition of breeding coloration depends on badge size in male house sparrows *Passer domesticus*. *Behav. Ecol. Sociobiol.* **31**, 271–277.
- Mountjoy, D. J. & Lemon, R. E. 1997: Male song complexity and parental care in the European Starling. *Behaviour* **134**, 661–675.
- Norris, K. 1993: Heritable variation in a plumage indicator of viability in male great tits *Parus major*. *Nature* **362**, 537–539.
- Petrie, M. 1994: Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**, 598–599.
- Reyer, H.-U., Fischer, W., Steck, P., Nabulon, T. & Kessler, P. 1998: Sex-specific nest defense in house sparrows (*Passer domesticus*) varies with badge size of males. *Behav. Ecol. Sociobiol.* **42**, 93–99.
- Sætre, G.-P., Fossnes, T. & Slagsvold, T. 1995: Food provisioning in the pied-flycatcher: do females gain direct benefits from choosing bright-coloured males? *J. Anim. Ecol.* **64**, 21–30.
- Searcy, W. A. & Yasukawa, K. 1981: Does the “sexy son” hypothesis apply to mate choice in red-winged blackbirds?. *Am. Nat.* **117**, 343–348.
- Sheldon, B. C. 2000: Differential allocation: tests, mechanisms and implications. *Trends Ecol. Evol.* **15**, 397–402.
- Smiseth, P. T., Ornborg, J., Andersson, S. & Amundsen, T. 2001: Is male plumage reflectance correlated with paternal care in bluethroats? *Behav. Ecol.* **12**, 164–170.
- Solberg, E. J. & Ringsby, T. H. 1997: Does badge size signal status in small island populations of house sparrows, *Passer domesticus*? *Ethology* **103**, 177–186.
- Sundberg, J. & Larsson, C. 1994: Male coloration as an indicator of parental quality in the yellowhammer *Emberiza citrinella*. *Anim. Behav.* **48**, 885–892.
- Veiga, J. P. 1990: Sexual conflict in the house sparrow: interference between polygynously mated females versus asymmetric male investment. *Behav. Ecol. Sociobiol.* **27**, 345–350.
- Veiga, J. P. 1993: Badge size, phenotypic quality, and reproductive success in the house sparrow: a study on honest advertisement. *Evolution* **47**, 1161–1170.
- Veiga, J. P. 1996: Permanent exposure versus facultative concealment of sexual traits: an experimental study in the house sparrow. *Behav. Ecol. Sociobiol.* **39**, 345–352.
- Veiga, J. P. & Puerta, M. 1996: Nutritional constraints determine the expression of a sexual trait in the house sparrow, *Passer domesticus*. *Proc. R. Soc. Lond. B* **263**, 229–234.
- Voltura, K. 1998: Parental investment and offspring sex ratios in house sparrows, *Passer domesticus* and cattle egrets, *Bubulcus ibis*. PhD Thesis, Univ. of Oklahoma, Norman, OK.
- Weatherhead, P. & Robertson, R. J. 1979: Offspring quality and the polygyny threshold: the “sexy son hypothesis”. *Am. Nat.* **113**, 201–208.
- Welling, P. P., Rytönen, S. O., Koivula, K. T. & Orell, M. I. 1997: Song rate correlates with paternal care and survival in willow tits: advertisement of male quality? *Behaviour* **134**, 891–904.
- Whitekiller, R. R., Westneat, D. W., Schwagmeyer, P. L. & Mock, D. W. 2000: Badge size and extra-pair fertilizations in the house sparrow. *Condor* **102**, 342–348.
- Wiehn, J. 1997: Plumage characteristics as an indicator of male parental quality in the American kestrel. *J. Avian Biol.* **28**, 47–55.
- Wiley, R. H. & Poston, J. 1996: Perspective: indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**, 1371–1381.
- Wolf, J. B., Moore, A. J. & Brodie, E. D. III. 1997: The evolution of indicator traits for parental quality: the role of maternal and paternal effects. *Am. Nat.* **150**, 639–649.
- Yasukawa, K., McClure, J. L., Boley, R. A. & Zanolco, J. 1990: Provisioning of nestlings by male and female red-winged blackbirds, *Agelaius phoeniceus*. *Anim. Behav.* **40**, 153–166.

*Received: February 7, 2002*

*Initial acceptance: May 18, 2002*

*Final accepted: July 14, 2002 (J.-G. Godin)*