

RESEARCH PAPERS

Different Reproductive Tactics in House Sparrows Signalled by Badge Size: Is There a Benefit to Being Average?

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Abstract

Sexual selection models usually predict directional selection for ornamental traits because of intra- as well as inter-sexual selection. Animals frequently face reproductive trade-offs, such as between mating and parental effort. Provided that both are essential and have opposite effects on ornament expression, we may however not necessarily expect directional selection for ornament size. The house sparrow is an ideal species to study such a trade-off, as the size of the male ornament, the black throat badge, seems to be inversely related to mating and parental effort. It has been suggested that large-badged males invest more in female attraction and territory defence, while small-badged males may invest more in parental care. In a nest-box study, we show that females started to breed earliest and produced the largest clutches when mated to males with average-sized badges that invested in paternal care more than other males. These results are discussed in view of inter- as well intra-sexual selection. Overall, average-badged males experienced the highest hatching failures, their chicks were in the poorest physical condition and they did not fledge more chicks than other males. It is therefore unlikely that the mating advantages that we observed could by themselves lead to stabilizing selection for badge size. Our results rather suggest that badge size in male house sparrows signals different reproductive tactics, which are adapted flexibly according to their physical condition and socio-ecological situations.

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Introduction

Many sexual selection models predict directional selection for ornamental traits (see Andersson 1994). In fact, males displaying most conspicuous

ornaments were found to have higher mating success (Andersson 1982; Endler 1983; Hill 1991), start to breed earlier (Alatalo et al. 1984; Norris 1990; Johnsen et al. 1998), have larger clutches (Rintamaki et al. 1998) and fledge more offspring (Møller 1994; McGraw et al. 2001). Higher mating success of conspicuous males is supposed to be an outcome of intra- and/or inter-sexual selection (see Andersson 1994). As larger or brighter ornament may by itself be attractive (Weatherhead and Robertson 1979) or indicate better immune defence (Dufva and Allander 1995; Møller 1997; Figuerola et al. 1999), females are thought to benefit from their choice by rearing more attractive sons (Saino et al. 1997) or viable progeny (Norris 1993; Møller 1994). Male–male competition can also assure a selective advantage for more ornamented males, as these are often more competitive and of higher social status (Rohwer 1982; Veiga 1996; McGraw and Hill 2000). More ornamented males often breed at higher quality nesting sites (Røskoft and Rohwer 1987; Wolfenbarger 1999) and invest in parental care more than other males (Hill 1991; Palokangas et al. 1994). Hence, females may prefer to pair with conspicuous males also because of the direct benefits they provide (Price et al. 1993).

Animals often face reproductive trade-offs, for instance, between mating and parental effort (Davies and Hatchwell 1992; Smith 1995; Magrath and Elgar 1997; De Ridder et al. 2000). Given that behaviours involved in mate attraction, territory defence or parental care are traded against ornament expression (Gustafsson et al. 1995; Griffith 2000), males may not be able to perform them all without changing their conspicuousness. Thus, instead of directional selection for more ornamented males, we may expect conditional mating strategies, depending on the value of these male behaviours in different environments (Qvarnström 2001). Consequently, females can prefer males with larger or brighter ornaments in some environments but not necessarily in all (Endler 1988). Male–male competition in variable socio-ecological environments may also lead to different reproductive consequences relative to ornament expression. For example, if territory defence becomes less important, it might pay some males to avoid male–male competition and reduce the costs of displaying large ornaments in favour of providing parental care (e.g. nest building or incubation of incomplete clutches). Consequently, less ornamented males may start to breed earlier and fledge more offspring because they are able to construct nests faster and provide more parental care than more ornamented males that spend more time defending territory. Nonetheless, if males cannot completely diminish parental care or territory defence, this may lead to non-directional ‘stabilizing’ selection for average ornament size.

The house sparrow *Passer domesticus* is an ideal species for investigating such a system. First, the species is biparental, with approximately equal amounts of parental care provided by both partners (Summers-Smith 1963). Secondly, the house sparrow is a territorial passerine and its reproductive success strongly depends upon territory quality (Møller 1988). In addition, the black throat patch (badge) varies widely among males (see, e.g. Møller 1987a). Several studies have shown that the badge is an honest indicator of condition (Møller 1987a; Møller

et al. 1996; Veiga and Puerta 1996; but see Gonzales et al. 1999; Buchanan et al. 2001). Although Møller (1989) suggested that there is a genetic basis to badge size, a cross-fostering study by Griffith et al. (1999a) showed the importance of environmental rather than genetic components of badge size. So far, results of the relationships between female preference, reproductive success and badge size are also controversial (see Møller 1988, 1989, 1990, 1992; Griffith et al. 1999b). Nevertheless, experimental studies did not find any support for female mate preference (Kimball 1996), nor for reproductive success (Veiga 1993) being based on badge size.

In this study, we show that males with average-sized badges started to breed earliest, had the largest clutches and invested in parental care performed early in the breeding cycle more than other males. Nevertheless, average-badged males suffered the highest egg losses and their offspring were in the worst physical condition. Overall, fledgling numbers and fledging success were not significantly related to male badge size.

Material and Methods

Study Area and Population

Our study was conducted in the Schönbrunn Zoo in Vienna, Austria, during the breeding seasons 1999 and 2000. In these 2 yr, house sparrows nested in 80 and 71 nest-boxes, respectively. We found a significant between-years difference in clutch size (t-test: $t = 2.84$, $df = 28$, $p = 0.008$) but not in brood size (t-test: $t = 1.51$, $df = 28$, $p = 0.13$), fledging numbers (t-test: $t = 0.56$, $df = 28$, $p = 0.58$) and fledging success (residuals from a regression of fledgling numbers on clutch size) (t-test: $t = 0.06$, $df = 231$, $p = 0.95$). Hence, to overcome a year effect, data for clutch size were standardized for the year. Birds were usually trapped after they completed their clutches. We measured badge size in males as this trait was found to be important for female mate choice in some previous studies (Møller 1988, 1989; Griffith et al. 1999b). Condition is represented by residuals from a regression of body weight on tarsus length (linear regression model: $r = 0.21$, $p = 0.012$, $n = 30$ males).

Badge size estimates vary among studies (Møller 1987a; Veiga 1993; Cordero et al. 1999; Griffith et al. 1999b) but these measurements are highly repeatable (Cordero et al. 1999; Griffith et al. 1999b). Therefore, we have chosen the original method by Møller (1987a) who assessed male badge size using a regression equation: $\text{Badge size (mm}^2\text{)} = 166.7 + 0.45 \times \text{badge length (mm)} \times \text{badge width (mm)}$.

Badge size increases with time because of the abrasion of white feather tips concealing the badge (Møller 1987a; Veiga 1996). Although we measured badge size from April onwards when it should be almost fully developed (Møller and Eritzøe 1992), to avoid seasonal variation of its size, we measured the total badge size including visible black patch and the black area beneath the white tips. These two measures were found to be highly correlated (Griffith et al. 1999b).

Estimates of Male Attractiveness and Reproductive Success

In both breeding seasons, we started to observe activity around the nest-boxes several months before the first eggs were laid (on 25 March in both years). To avoid influence from the number of breeding attempts on the condition of males, we included only pairs with three breeding attempts, using mean values to avoid pseudo-replication (see below). With this restriction, we analysed 30 different pairs (16 in 1999 and 14 in 2000).

We used the start of egg-laying for the first clutch as a measure of male attractiveness, which assumed that more attractive males were chosen earlier and had earlier laying females (see Price et al. 1988). The start of egg-laying refers to the number of days relative to 1 April when the first egg was laid. In this analysis, we included only pairs that were observed defending nest-boxes at least 1 month before they laid their first egg ($n = 26$ pairs). The latest day of clutch initiation for these pairs was 15 April and we therefore set this date as a limit for the analysis. The four remaining pairs started to defend nest-boxes during the first third of April and started to lay eggs at the end of April. As it is possible that these four pairs may have attempted to breed somewhere else before they settled in our nest-boxes, they were excluded from the analysis.

As females may invest in reproduction differentially in relation to male attractiveness (Burley 1986, 1988), we also examined clutch size and female investment in parental care (incubation). Clutch size was regularly monitored in all nest-boxes at least every second day during the whole breeding season. We recorded behaviour of both parents daily during the whole incubation period in 1999. Every nest site was monitored during 15 min when we recorded the presence of birds inside and around nest-boxes every 30 s. Birds were assumed to be incubating if they spent >1 min in the nest-box. In these tests, we analysed 16 different pairs for which we collected both morphological and behavioural data.

Reproductive success was measured as the total number of chicks at fledging (fledgling numbers) and mean chick condition during three breeding attempts (see below). In addition, we present fledging success as the residuals from a regression of the number of chicks at fledging (reaching the age of 10–14 d) on the clutch size. To assess chick condition we first determined the residual variation in body weight not explained by tarsus length using chicks at the age of 10–14 d (linear regression model with tarsus as the independent variable: $r^2 = 0.78$, $p < 0.001$, $n = 438$ chicks). We then calculated the mean of these residuals for each brood and derived new residuals using the relationship between these values and brood size (i.e. brood size was the independent variable: $r^2 = 0.12$, $p < 0.001$, $n = 143$ broods). Finally, we calculated the mean value for three broods of each pair ($n = 26$ pairs). Four pairs did not succeed in fledging their chicks. As we were unable to take morphological measurements of these chicks, offspring condition of these four pairs was not included in the analysis.

Statistical Analyses

Parametric tests were used in our analyses only when the requirements for these tests were met. We wanted to evaluate whether the relationships between badge size and other variables are linear or curvilinear. In the latter case, we aimed to test whether males with average-sized badges are doing better or worse than the rest of males. Therefore, instead of curve fitting (e.g. using quadratic or other polynomial regression), we tested the relationships between different reproductive parameters and absolute deviations from the mean badge size. Hence, positive linear relationships between absolute deviations and another trait implied that the average-badged males were doing worse than other males. All relationships were examined with Spearman rank correlations. To prevent type-I errors, without greatly increasing the chance of type-II errors, we performed Bonferroni adjustments following suggestions by Rice (1989) and Chandler (1995).

Results

Mating Patterns and Parental Effort in Relation to Badge Size

We did not find significant relationships between the start of breeding and deviations from the mean badge size (Fig. 1a). However, the relationship between absolute deviations from the mean badge size and the start of breeding, as illustrated in Fig. 1b, suggests that females initiated clutches earliest with average-badged males. Differential allocation in reproduction by females in relation to male badge size may be most obvious in relation to clutch size. Although clutch size seemed to decrease with badge size ($r_s = -0.36$, $p = 0.049$, $n = 30$; Fig. 2a), this was not significant after Bonferroni adjustment. Importantly, a negative relationship between clutch size and absolute deviations from the mean badge size suggest that average-badged males had clutches significantly larger than other males (Fig. 2b).

Female reproductive effort relative to badge size seemed to change in a later phase of reproduction. In particular, female investment in incubation was not highest when paired to average-badged males (using absolute deviations from the mean badge size: $r_s = 0.23$, $p = 0.39$, $n = 16$) as expected from investment in clutch size but instead tended to increase linearly with the size of the partner's badge (using relative deviations from the mean badge size: $r_s = 0.51$, $p = 0.04$, $n = 16$; the relationship was not significant after the Bonferroni adjustment at the significance level $\alpha = 0.025$). Interestingly, male investment in incubation did not significantly increase with badge size (Fig. 3a), but instead peaked in average-badged males (Fig. 3b). This is supported by the negative relationship between absolute deviations from the mean badge size and male participation in incubation (Fig. 3b).

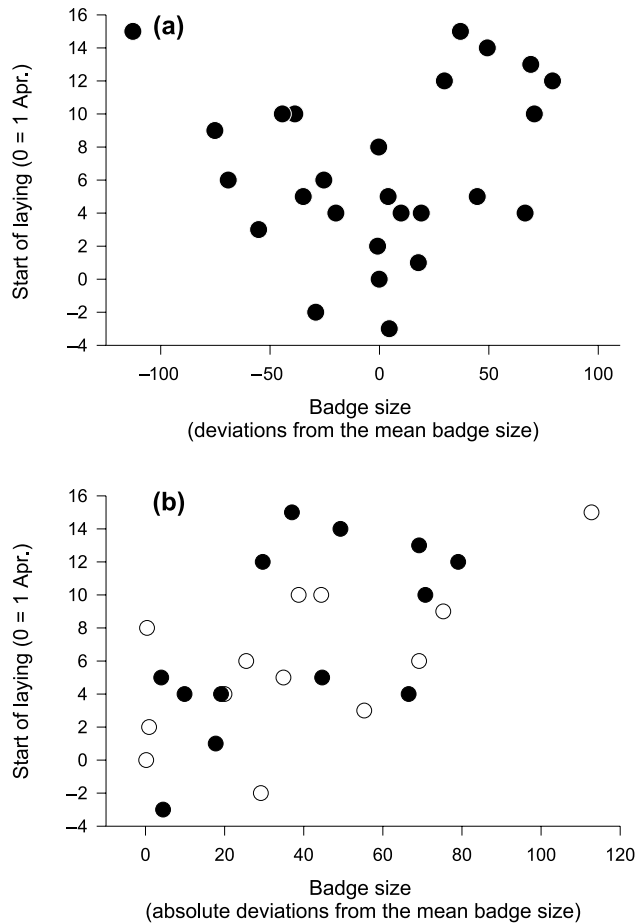


Fig. 1: Relationship between start of egg laying and badge size as (a) deviations from the mean badge size ($r_s = 0.15$, $p = 0.46$, $n = 26$) and (b) absolute deviations from the mean badge size ($r_s = 0.61$, $p = 0.001$, $n = 26$). Open circles and filled circles indicate that original values were smaller or larger than the mean, respectively. Note that significance levels are $\alpha = 0.025$ as a result of the Bonferroni correction

Badge Size and Annual Reproductive Success

Although average-badged males had the largest clutches, annual fledgling numbers were neither related to relative ($r_s = 0.26$, $p = 0.17$, $n = 30$) nor to absolute ($r_s = 0.001$, $p = 0.99$, $n = 30$) deviations from the mean badge size. In contrast, fledging success seemed to increase linearly with the badge size of social fathers ($r_s = 0.38$, $p = 0.038$, $n = 30$), although not significantly after the Bonferroni adjustment at $\alpha = 0.025$. Likewise, fledging success was not related to absolute deviations from the mean badge size ($r_s = 0.13$, $p = 0.50$, $n = 30$).

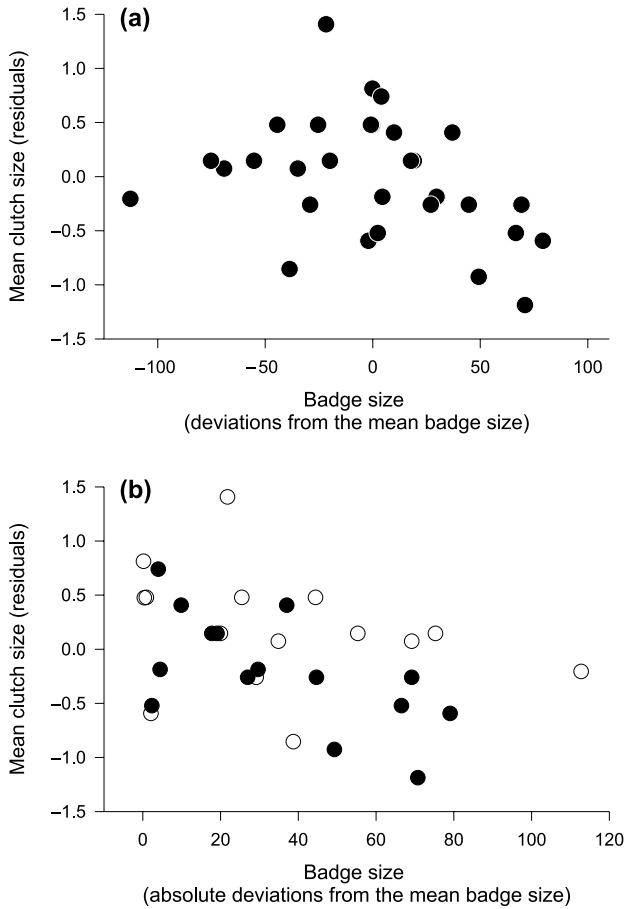


Fig. 2: Relationship between mean clutch size and badge size as (a) deviations from the mean badge size ($r_s = -0.36$, $p = 0.049$, $n = 30$) and (b) absolute deviations from the mean badge size ($r_s = -0.46$, $p = 0.01$, $n = 30$). Open circles and filled circles indicate that original values were smaller or larger than mean, respectively. Mean clutch size was calculated from three breeding attempts; clutch size was controlled for the year effect. Note that significance levels are $\alpha = 0.025$ as a result of the Bonferroni correction

The reason why there was ultimately no relationship between annual fledgling numbers and badge size seems to be related to failures in hatching and rearing young. Although we found that hatching failures tended to decrease linearly with male badge size (Fig. 4a), the highest failures occurred in the nests of average-badged males (Fig. 4b). In addition, chicks reared by average-badged males were in poorer condition than chicks reared by other males (Fig. 5b), without any significant relationship between chick condition and relative deviations from the mean badge size (Fig. 5a).

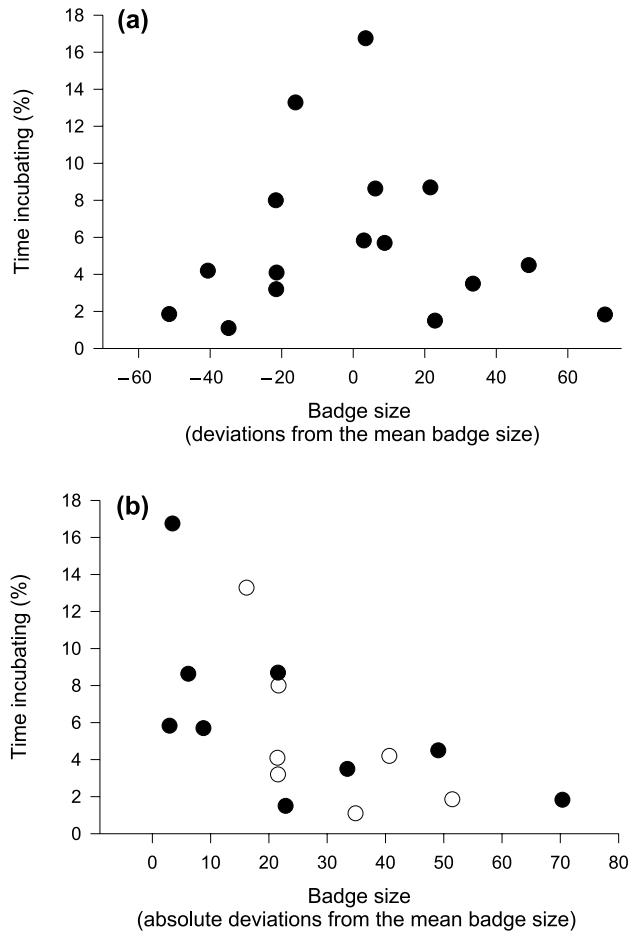


Fig. 3: Relationship between the proportion of time males incubated during 15-min long protocols and badge size as (a) deviations from the mean badge size ($r_s = 0.06$, $p = 0.83$, $n = 16$) and (b) absolute deviations from the mean badge size ($r_s = -0.69$, $p = 0.003$, $n = 16$). Open circles and filled circles indicate that original values were smaller or larger than mean, respectively. Note that significance levels are $\alpha = 0.025$ as a result of the Bonferroni correction

Discussion

By examining relationships between badge size, estimates of male attractiveness, and parameters of parental care and reproductive success, we consistently detected non-linear associations. Curvilinear relationships between the start of breeding, clutch size and male badge size suggest that females preferred to mate with average-badged males. Moreover, we found that average-badged males expended more parental effort in terms of incubation than males with smaller and larger badges. These results suggest that in our population males with average-sized badges experienced a mating advantage compared with males with a more

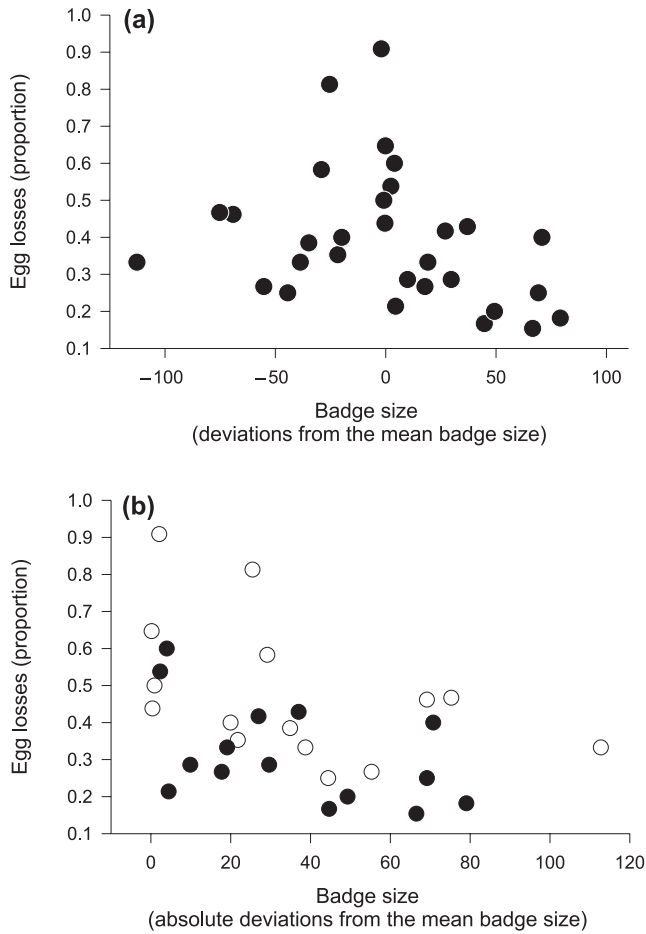


Fig. 4: Relationship between annual egg losses and badge size as (a) deviations from the mean badge size ($r_s = -0.42$, $p = 0.02$, $n = 30$) and (b) absolute deviations from the mean badge size ($r_s = -0.48$, $p = 0.008$, $n = 30$). Open circles and filled circles indicate that original values were smaller or larger than mean, respectively. Egg losses refer to the mean proportion of eggs that did not hatch during three breeding attempts. Note that significance levels are $\alpha = 0.025$ as a result of the Bonferroni correction

extreme expression of this ornament (cf. Møller 1988, 1989, 1990, 1992; Griffith et al. 1999b). However, despite the earlier start of breeding and larger clutches in the nests of average-badged males, fledging success was not significantly related to badge size.

As average-badged house sparrow males are in poorer physical condition and have weaker immune defence than more ornamented males (Møller et al. 1996; Veiga and Puerta 1996), a seeming mating advantage of such males might be interpreted in view of female preference for direct benefits. Nest defence in male house sparrows increases with the size of badge (Møller 1988; Reyer et al. 1998).

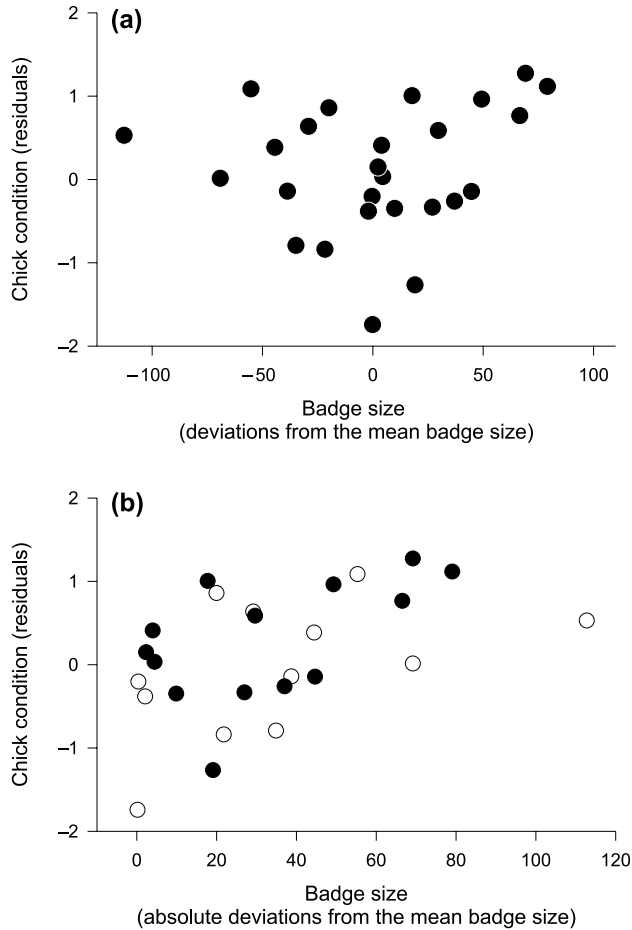


Fig. 5: Relationship between chick condition and badge size as (a) deviations from the mean badge size ($r_s = 0.21$, $p = 0.30$, $n = 26$) and (b) absolute deviations from the mean badge size ($r_s = 0.51$, $p = 0.007$, $n = 26$). Open circles and filled circles indicate that original values were smaller or larger than mean, respectively. The condition of chicks refers to the residuals of chick weight that was not explained by tarsus length and brood size. Residuals are means from three breeding attempts. Note that significance levels are $\alpha = 0.025$ as a result of the Bonferroni correction

However, males with conspicuous ornaments often participate least in parental care (see Møller and Thornhill 1998). Moreover, to maintain their large ornaments, male house sparrows may not allocate substantial effort in paternal care (Griffith 2000). It is therefore possible that male badge size could serve females as a cue of male reproductive effort. Depending on the costs and benefits of paternal investment, female preference for a certain component of male reproductive effort may vary across populations (Qvarnström 2001). Indeed, Møller (1988) and Reyer et al. (1998) found that male house sparrows with large

badges were likely to be preferred by females because of their superior defending behaviour. In contrast, Griffith et al. (1999b) found for an island population that female house sparrows preferred small-badged males, supposedly for their high parental effort. Consequently, average-badged males in our population could be assumed to have an advantage as a result of the female preference for intermediate levels of nest defence and paternal care. However, we showed that males with average-sized badges did not provide intermediate, but instead highest paternal care. In contrast, small-badged males initiated breeding late, scarcely invested in parental care and tended to experience low fledging success. It is possible that the relationship between male ornamentation and paternal care is unstable and may vary with mating opportunities (Kokko 1998; Qvarnström and Price 2001). Nonetheless, our results do not support a suggestion by Griffith et al. (1999b) that females should prefer small-badged males because of their superior paternal effort.

Alternatively to female preference, mating advantages of average-badged males might reflect consequences of male–male competition. It is known that male badge size signals status in house sparrows (Møller 1987b; Veiga 1993), whereas the likelihood of male–male conflicts increases with badge size (Møller 1987b). Hence, males developing average-sized badges may be able to accelerate breeding by reallocating their reproductive effort from male–male fights to parental care (e.g. nest building). This may happen on the basis of a time allocation, but it also is plausible at the proximate level because development of smaller badges requires lower amounts of testosterone than for large badges (Evans et al. 2000; Buchanan et al. 2001). Thus, aggressive behaviour of ‘lower testosterone males’ is stimulated less, while parental care is not suppressed to such an extent as in ‘high testosterone males’ (Hegner and Wingfield 1987). The honesty of status signalling in male house sparrows is maintained by means of time and energy consuming male disputes (Møller 1987b). Displaying an intermediate badge, suppressing competitiveness and elevating parental care may therefore represent a reproductive tactic by which some males attempt to maximize their fitness. A larger variation in the expression of behaviours of average-badged males also suggests that this reproductive tactic is more flexible than tactics of males with extreme ornaments. Nonetheless, despite the mating advantages of average-badged males early in the breeding cycle, this reproductive tactic did not lead to fledging more offspring. Moreover, it is unlikely that males with smaller badges could optimize reproductive success by extra-pair copulations (Møller 1987a). The high egg loss in pairs of average-badged males could have been an outcome of a low fertilization success as smaller badged males have smaller testes (Møller and Erritzøe 1988) and copulate with their mates less frequently than males with large badges (Møller 1990). However, as the majority of unhatched eggs in house sparrows contain dead embryos (Birkhead et al. 1995) and average-badged males reared chicks of worst condition, a low fledging success of such pairs might stress the importance of maternal care. The high egg losses could have also resulted from a weak protection of females from the harassment of aggressive males, or lower viability of the offspring sired by average-badged males. In contrast, despite

the late breeding start and the smallest clutches, males with large badges may increase their fitness through extra-pair fertilizations, perhaps through forced extra-pair copulations (Møller 1990). Our results hence suggest that badge size in male house sparrows might signal different reproductive tactics, similarly as found in collared flycatchers *Ficedula albicollis* (Qvarnström 1999). The chosen tactic and ornament expression may then be adopted according to male condition and socio-ecological contexts (Qvarnström 2001).

In conclusion, this study shows that average-badged males in our population experienced mating advantages over other males. As these males invested more in parental care, females could have benefited directly by preferring males signalling higher parental ability. Alternatively, accelerated breeding and large clutches of average-badged males may have occurred as a result of avoiding male–male competition and instead investing in early forms of parental care. We are unable to clearly explain whether it was because of inter- or intra-sexual selection, however these two mechanisms may not be mutually exclusive. Despite apparent mating advantages, average-badged males did not fledge more young than other males. Hence it is unlikely that the mating advantages we observed could by themselves lead to stabilizing selection for badge size.

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