Badge size, paternity assurance behaviours and paternity losses in male house sparrows

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Male quality may influence both the outcome of sperm competition and female faithfulness. In male house sparrows Passer domesticus, the size of the black throat patch (badge) signals dominance and perhaps attractiveness. So far, however, no study has reported any significant relationships between badge size, paternity and paternity assurance behaviours in this species. We found that the time mates spent together at the nest was positively correlated with badge size. Furthermore, although paternity losses were influenced by both the time spent at the nest and within-pair copulation frequency, we found no relationship between copulation rate and badge size. It seems therefore that copulation frequency served as a paternity assurance behaviour, whereas the time mates stayed together at the nest may have reflected male attractiveness. Alternatively, females may have decided to stay with large-badged males because they were better able to protect them from harassment by strange males. We suggest that average-badged males cuckolded were more often than males with smaller or larger badges. We also found that paternity losses were related to male badge size; average-badged males cuckolded were more often than males with smaller or larger badges. We suggest that average-badged males suffered higher paternity losses because they had different time allocation strategies than other males.
One important determinant of paternity is male quality. High quality males are often more successful in intra-
sexual competition for mates and limiting resources, as
well as in sperm competition (e.g. Birkhead 1998; see
Møller 1988, Watton et al. 1995 for house sparrow
Passer domesticus). Furthermore, females mated to
such males may be more faithful to their mates than
those mated to males of lower quality (e.g. Johnsen et
al. 1998). In male house sparrows, the size of the black
throat patch (badge) seems to signal individual quality.
The size of the badge is controlled by testosterone levels
(Evans et al. 2000), and Møller (1988) found that males
with large badges are more competitive and defend high
quality resources. In the same Danish population
Møller (1988) also found that male attractiveness was
positively correlated with badge size. However, in a
study of an island population of house sparrows in the
UK, Griffith et al. (1999a) reported that females tended
to prefer males with small badges as mates. Møller (1990, 1992) showed that male badge size
influences extra-pair behaviour in both sexes. Large-
badged males participate more often in both solicited
and forced extra-pair copulations than other males, and
females mated to large-badged males engage in fewer
extra-pair copulations (both forced and solicited) than
females mated to other males. Other studies have found
that male badge size does not influence paternity in
house sparrows (Cordero et al. 1999, Veiga and Boto
2000, Whitekeller et al. 2000), but so far no study has
combined behavioural and genetic data when examin-
ing the role of male badge size for sperm competition in
this species.

Here, we investigate paternity assurance behaviours
and extra-pair paternity in relation to male badge size.
Specifically, we test whether within-pair copulation fre-
cuency and the time mates stay together at the nest
influence paternity losses in house sparrows.

**Methods**

**Field work**

We studied a population of house sparrows in the
Schönbrunn Zoo, Vienna, in March–July 1999. In to-
tal, 45 pairs were breeding in 80 nest-boxes placed on
stable walls. Most of these pairs (80%) produced three
broods within the breeding season. Birds were trapped,
colour-ringed, measured and bled during incubation and
chick feeding throughout the breeding season. All
measurements were taken by R.V.

We obtained morphological and behavioural data for
14 pairs. To avoid seasonal variation in badge size, we
measured its total area (i.e. visible black patch plus
the black area concealed beneath the white feather tips)
and then calculated size as described by Møller (1987a).
Griffith et al. (1999b) found that expression of the
badge is mainly influenced by environmental factors
(see also Veiga and Puerta 1996). In the present house
sparrow population, however, male badge size was
positively correlated with body size, i.e. tarsus length
(linear regression, $R^2 = 0.24$, $P = 0.018$, $n = 23$, includ-
ing all measured males).

We studied behaviour at the nest-boxes from nest
building until chick feeding. Because temporal patterns
of copulation are supposed to reflect intensity of sperm
competition (Birkhead and Møller 1992), and copula-
tion activity in house sparrows peaks a few days before
the start of laying and remains high until the last egg is
laid (Møller 1987b, Tost 1994, R. Václav unpubl.), we
only analysed behaviours from the day before the first
egg was laid until clutch completion (in total 5–7 days,
depending on clutch size). We used 15-min observa-
tional protocols, recording copulations and whether the
birds stayed alone or with their mates at the nest every
30 s. At all nesting sites, birds were observed from 7 to
10 a.m. (because copulation frequency is highest during
that time; Tost 1994, R. Václav unpubl.), following a
rotating scheme. We recorded 57 copulations in total
(mean ± se: 4.1 ± 1.8 copulations per pair). On average,
each pair was observed during 93 ± 2.6 (se) min. We
used mean values when the same pair was recorded
nesting more than once.

**Genetic parentage**

We examined genetic parentage of 67 chicks from 16
pairs with multi-locus DNA fingerprinting. Lab pro-
cedures followed those previously described by Kroken
et al. (1996). We used band-sharing ($< 40\%$) and the
number of novel bands ($> 2$) when excluding putative
parents (R. Václav, H. Hoi and D. Blomqvist unpubl.).
To avoid pseudo-replication, we used mean values of
paternity losses for males breeding more than once.
Within broods, the proportion of chicks sired by extra-
pair males varied between 0 and 100% (mean ± se:
$32 ± 8.2\%$, $n = 16$). Combining the genetic and be-
avioural data, our sample consisted of 12 pairs.

**Results**

Before testing the relationships with badge size, we first
had to control for body size for the following reasons.
We found a significant positive correlation between
badge size and tarsus length (see Methods), which may
confound the relationships between badge size, pater-
nity assurance behaviours and paternity losses. Taking
body size into account can also be important because it
may affect how females perceive badge size, either
directly or indirectly through its relationship with domi-
nance (see Møller 1987a). We therefore used the resid-

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uals from the regression of badge size on tarsus length in the analyses.

The proportion of time mates spent together at the nest increased with residual male badge size (Spearman rank correlation test, $r_s = 0.69$, $P = 0.006$, $n = 14$; Fig. 1). Examining within-pair copulation frequency, we found no significant relationship with residual badge size ($r_s = 0.10$, $P = 0.73$, $n = 14$).

The relationship between paternity losses, i.e. the proportion of extra-pair chicks per brood, and residual badge size resembled an inverse U-shape, suggesting that average-badged males were cuckolded more than other males (Fig. 2a). Since paternity losses seemed to decrease in both directions from the average badge size, we took the absolute values of the residuals (cf. Shine et al. 1999). This resulted in a negative relationship between paternity losses and absolute residuals of badge size (Spearman rank correlation test, $r_s = -0.54$, $P = 0.031$, $n = 16$; Fig. 2b), supporting that males with average-sized badges were cuckolded more than males with smaller or larger badges. Using absolute deviations from mean badge size without controlling for tarsus length yielded a similar result ($r_s = -0.43$, $P = 0.10$, $n = 16$).

To examine whether the time mates stayed together at the nest and within-pair copulation frequency functioned as paternity assurance behaviours, we tested their relationship with paternity losses. We found that the proportion of extra-pair chicks per brood decreased with time spent at the nest ($r_s = -0.61$, $P = 0.037$, $n = 12$; Fig. 3), as well as with copulation rate ($r_s = -0.69$, $P = 0.013$, $n = 12$; Fig. 4). However, there was no significant correlation between these two behaviours ($r_s = 0.22$, $P = 0.49$, $n = 12$), suggesting that they had different functions.

**Discussion**

We found a positive correlation between male badge size and the proportion of time mates spent together at the nest. This behaviour may have been under male
control, i.e. mate guarding. However, Tost (1994) reported that copulation frequency and mate guarding by close following are correlated in house sparrows. Since we found no relationship between copulation frequency and the time mates stayed together at the nest, this suggests that the latter behaviour was not mate guarding. Paternity losses were influenced by both time at the nest and copulation frequency. Importantly, we found no relationship between copulation rate and badge size. It seems therefore that within-pair copulation frequency serves as a paternity assurance behaviour, independent of badge size, whereas the time mates spent together at the nest may reflect male attractiveness. Thus, in our study the time mates stayed together might have been determined by females rather than by males. Females may decide to stay with large-badged males because they are more attractive (Møller 1988, but see Griffith et al. 1999a), or better able to protect them from harassment by strange males (see Birkhead and Møller 1992).

This is the first study showing that paternity losses are related to badge size in house sparrows (cf. Cordero et al. 1999, Veiga and Boto 2000, Whitekiller et al. 2000). The relationship was curvilinear, suggesting that males with the smallest and largest badges were cuckolded less than those with average badges. The fact that small-badged males suffered similarly low paternity losses as large-badged males may seem like a paradox given that small-badged males should be least successful in sperm competition (see Møller 1992 for behavioural observations). Small-badged males have, however, relatively small clutches (Václav and Hoi in press). Thus, their relatively low proportion of extra-pair chicks may be due to a lower probability of detecting such chicks in small broods (Burley and Parker 1997). Furthermore, although small-badged males spent little time at the nest with their mates, they may have spent more time together with them away from the nest. If so, different time allocation strategies may be the reason why average-badged males suffered higher paternity losses than small-badged males. In particular, males with intermediate badges spend more time at the nest than other males (guarding and incubating incomplete clutches; Václav and Hoi in press), likely trading it against time spent guarding their females. In barn swallows *Hirundo rustica*, female mate choice is based on either male parental quality (nest building effort) or attractiveness (tail length) (Soler et al. 1998). If also female house sparrows use male parental effort and attractiveness as cues when selecting partners, our study shows that this choice may have different consequences for paternity losses.

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References


The cost of reproduction in birds is the sum of a number of expenditures: egg production, nest construction, incubation and chick rearing. Of these, the cost of nest construction is the least studied and yet could be substantial, particularly for species needing large amounts of specialised materials (Hansell 2000). Feathers are an important material for the insulation of nests of many small bird species, particularly in temperate latitudes (Collias and Collias 1984, Moller 1984). Such species rely on locating feathers scattered through the environment, so competition for feathers during the breeding season could force birds to search widely to locate them, perhaps at significant expense. This would be particularly true of species like the goldcrest *Regulus regulus* that may line its nest with several hundred feathers, or the long-tailed tit *Aegithalos caudatus* that typically uses around 1500 (Hansell 2000). However, we are aware of no previous study that has attempted to investigate the availability of feathers for nest builders. In this field study, natural availability of feathers was explored by monitoring the loss of marked feathers placed at fixed sites and their subsequent recovery from nests of birds found breeding in the vicinity.

**Materials and methods**

The study site was an area of about 650 × 270 m, which included mixed woodland, an overgrown garden, a rough lawn and a small lake (160 m across), situated 18 km SE of Glasgow (54°03′W, 55°47′N, Ordnance Survey ref. 738557). Within this area, twenty sites were chosen, each about 70 m from its two nearest neighbours. Patches of 50 marked feathers were placed directly on the ground each week at each of the 20 sites for a 16-week period from mid-March to mid-July in three successive years 1995–97. These were contour feathers from the breast and back of wood pigeons *Columba palumbus*. The feathers were 30–50 mm in length, predominantly white with greyish tips. Wood pigeon feathers were the second most common feather among those of 27 species found in a sample of 22 nests of long-