

## Importance of colony size and breeding synchrony on behaviour, reproductive success and paternity in house sparrows *Passer domesticus*

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**Abstract.** Several comparative studies have previously identified breeding density and synchrony as potential determinants of reproductive success and extra-pair mating. However, the mechanisms and interaction of these two factors are poorly known. Here, we examined the effects of breeding density and synchrony on the behaviour, reproductive success and paternity losses in house sparrows. In order to test the effects of colony size, we created nest sites with varying numbers of nest-boxes. Our results show that there is an interaction between breeding synchrony and density, namely that breeding synchrony decreased with colony size. Neither colony size nor breeding synchrony seemed to influence brood size at fledging, although birds in larger colonies laid larger clutches. Moreover mate guarding behaviour was not influenced substantially by these two factors. Only nest guarding was significantly related to colony size and breeding synchrony. Paternity losses were not significantly related to colony size but they appeared to decrease with increasing synchrony. This finding supports the idea that extra-pair fertilisations are under male rather than female control.

**Key words:** breeding density, synchrony, house sparrows, reproductive success, paternity

### Introduction

Ecological factors like food availability, weather or predator pressure are well known to influence life history and reproductive success of a species (L a c k 1968). In addition, they were recognised to effect parental effort (H o i et al. 1995), mating system (E m l e n & O r i n g 1977, H o i et al. 1995), sexual strategies (see B i r k h e a d & M ø l l e r 1992) and paternity (H o i & H o i - L e i t n e r 1997). In respect of the latter two, colony size and breeding synchrony have been recently suggested as important socio-ecological determinants (B i r k h e a d & B i g g i n s 1987, B i r k h e a d & M ø l l e r 1992). Both factors may determine intraspecific competition for resources such as food, nest sites or mates (W i t t e n b e r g e r & H u n t 1985, B r o w n 1987). In this way, breeding density and synchrony may directly influence breeding success, but may also effect sexual strategies like extra-pair behaviour or paternity guards and consequently the realised reproductive success. M ø l l e r & B i r k h e a d (1993) reported that cuckoldry is higher in colonial than solitary breeding bird species. They suggested that this might be due to insufficient mate guarding or increased possibility to encounter sexual partners. W a g n e r (1993) hypothesised that females may even promote breeding in higher densities in order to facilitate extra-pair matings. Nevertheless, only some studies support this prediction (e.g. M ø l l e r

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1985, Birkhead et al. 1987, Hill et al. 1994, Møller & Ninni 1998). A comparative study by Westneat & Sherman (1997) did not provide general support for this idea between species (but see Møller & Ninni 1998) although the authors showed that cuckoldry increases with density within species. Westneat & Sherman (1997) further suggested that density might perhaps be linked with additional factors such as habitat structure, female behaviour affecting encounter rate with extra-pair males or breeding synchrony. Indeed, breeding synchrony was found to favour extra-pair mating in some species (Stutchbury et al. 1994). However, the role of synchrony for extra-pair behaviour is still controversial (see Weatherhead 1997). Namely, it is not clear whether extra-pair paternity (EPP) should increase (Stutchbury & Morton 1995) or decrease with synchrony of breeding (Birkhead & Møller 1992). A recent comparative study by Møller & Ninni (1998), however, suggests that among species paternity decreases with breeding asynchrony.

Most of the non-comparative studies on extra-pair paternity tend to examine only one factor at the time, whether it is breeding density or synchrony (Thuis et al. 2001). In this study, therefore, we try to investigate simultaneously the importance of both colony size and breeding synchrony on reproductive success, paternity assurance, nest guarding behaviours and paternity losses in house sparrows *Passer domesticus*. The house sparrow is an ideal species for such a study because it nests solitarily as well as in colonies of variable sizes (Summer-Smith 1954, Cramp 1994, Tost 1994). Moreover, sperm competition is intense in this species as indicated by high within-pair copulation frequency (Møller 1987) and occurrence of EPP (e.g. Wetton & Parkin 1991, Cordero et al. 1999, Václav et al., in press). In order to study the effect of colony size and breeding synchrony, we offered house sparrows breeding situations in the plots with varying number of nest-boxes and experimentally altered start of egg-laying.

## Material and Methods

Our study was conducted in the Schönbrunn Zoo in Vienna, Austria during the breeding seasons 1999 and 2000. In these two years, house sparrows nested in 80 and 69 nest-boxes, respectively. Five to ten nest-boxes were hung on buildings in 1999 and three nest-boxes in 2000. In this way, we created four plots with five nest-boxes and ten plots with ten nest-boxes in 1999 and 15 plots with three nest-boxes in 2000. All plots were occupied in 1999 but eight plots were unsettled or settled only during one breeding attempt in 2000. The nest-boxes were placed 1-1.5 m apart in all plots. Birds were usually trapped after completing their clutches. We weighed all birds and measured the length (mm) of tarsus, wing and tail. We found no difference in the size of the male ornament (mean badge size: 379.7 mm<sup>2</sup> in 1999 and 386.4 mm<sup>2</sup> in 2000; t-test:  $t = 0.39$ ,  $p = 0.70$ ,  $n = 16, 14$ ). Since badge size is considered to be a condition-dependent trait (Griffith 2000), we think that the phenotype of birds did not markedly influence breeding patterns between years.

In both breeding seasons, we started to observe activity around nest-boxes several months before the first eggs were laid (25 March in both years). Clutch and brood size were regularly monitored in all nest-boxes at least every second day during the whole breeding season. Brood size at fledging refers to an estimate of fledging numbers when chicks were 10-14 days old. Accordingly, fledging success was calculated as the number of chicks in the

nest reaching the age of 10-14 days divided by the number of laid eggs. We analysed the behaviour of 28, 29 and 25 pairs during three consecutive breeding attempts during the egg laying in 1999. Every nest site was observed daily during 15 min when we recorded the presence of birds inside and around nest-boxes, the time mates stayed together and within-pair copulation frequency.

In 2000, we manipulated breeding synchrony experimentally. To achieve asynchrony, we swapped up to the half of nest contents from the nest of a focus pair to the nest of a neighbouring pair that was at a similar stage of breeding. On the other hand, we attained synchrony by equalising nest contents between pairs at apparently different breeding stages. The focus pair was, in this case, one that nested formerly at a later breeding stage. This was not the most suitable technique in the second and mainly third breeding attempt when the volume of nest material was more or less stable and was hence an unreliable estimate of breeding stage. For this reason, we used behavioural observations to estimate breeding stage and manipulated nest contents in the same logic as described above. Moreover, in the third breeding attempt, we delayed more advanced breeders by reducing their clutch size by taking up to two eggs and hence extending their laying period by laying additional eggs. In this way, we could increase synchrony between pairs with reduced clutches and focus pairs by more than 40% (mean clutch size in our study was 4.6 eggs in 1999 and 4.3 in 2000). Consequently, synchrony refers in this part of the results to the cases when we achieved either full or at least 80% breeding synchrony, whereas asynchrony means that the focus and neighbouring pairs did not overlap their laying periods. Synchrony from the correlational part of results refers to the proportion of the laying period that overlapped between pairs within a nesting site.

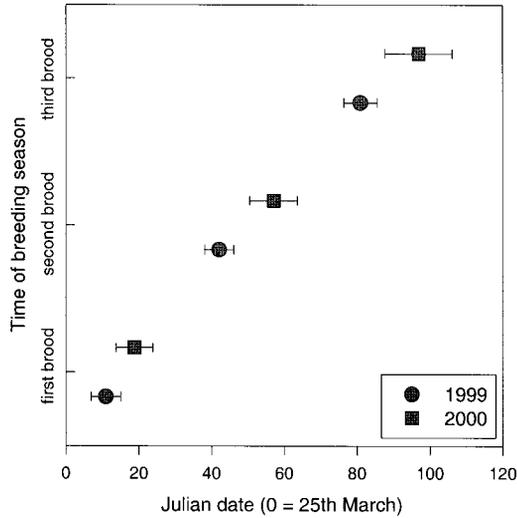
For analysing paternity losses, we used multi-locus DNA fingerprinting. We examined genetic parentage of 34 families. Laboratory procedures followed those previously described by Kroken et al. (1996). We used band-sharing and number of novel bands (i.e. bands present in chicks but not in the putative parents) when excluding parents (e.g. Kroken et al. 1996). The method and assumptions for paternity exclusion are presented in more detail in Wetton et al. (1987) and Westneat (1990). Paternity losses refer for each pair to the proportion of extra-pair young in the brood.

Parametric tests were used in our analyses only when the requirements for these tests were met. Normality was tested with the Liliefors and Shapiro-Wilk tests. In order to achieve normality, data on paternity losses were log transformed. In parametric tests, post hoc comparisons were calculated with the Newman-Keuls test. If not stated otherwise, presented values are means and standard errors. The majority of studied pairs (94 % in 1999 and 93 % in 2000, respectively) contributed more than one clutch within breeding season. Hence, in order to avoid pseudo-replication, we examined seasonal and annual variation of reproductive success and behaviour with repeated ANOVAs. In addition, since the number of pairs at nest sites fluctuated between breeding cycles, variation of different behaviours was analysed using mean values for each nest site. Synchrony decreased with increasing size of colony (multiple regression:  $r^2 = 0.22$ ,  $F_{2,27} = 3.83$ ,  $p = 0.034$ , effect of colony size –  $\beta = -0.47$ ,  $p = 0.011$ , effect of set-up –  $\beta = -0.02$ ,  $p = 0.90$ ). To control for this interrelationship and the effect of nest-box set-up, we included in multiple regression analyses all of the three factors. Hence, colony size, breeding synchrony and the type of set-up (5 and 10 nest-box sites) were entered as independent variables and reproductive success, behaviour and paternity losses as dependent variables.

## Results

### Seasonal and annual variation in reproductive success and behaviour during egg laying

Although the first eggs were recorded on the same day, 25th March, pairs nesting in 2000 tended to initiate their clutches later than pairs in 1999 and this difference increased and was significant in the two subsequent breeding attempts (Fig. 1).



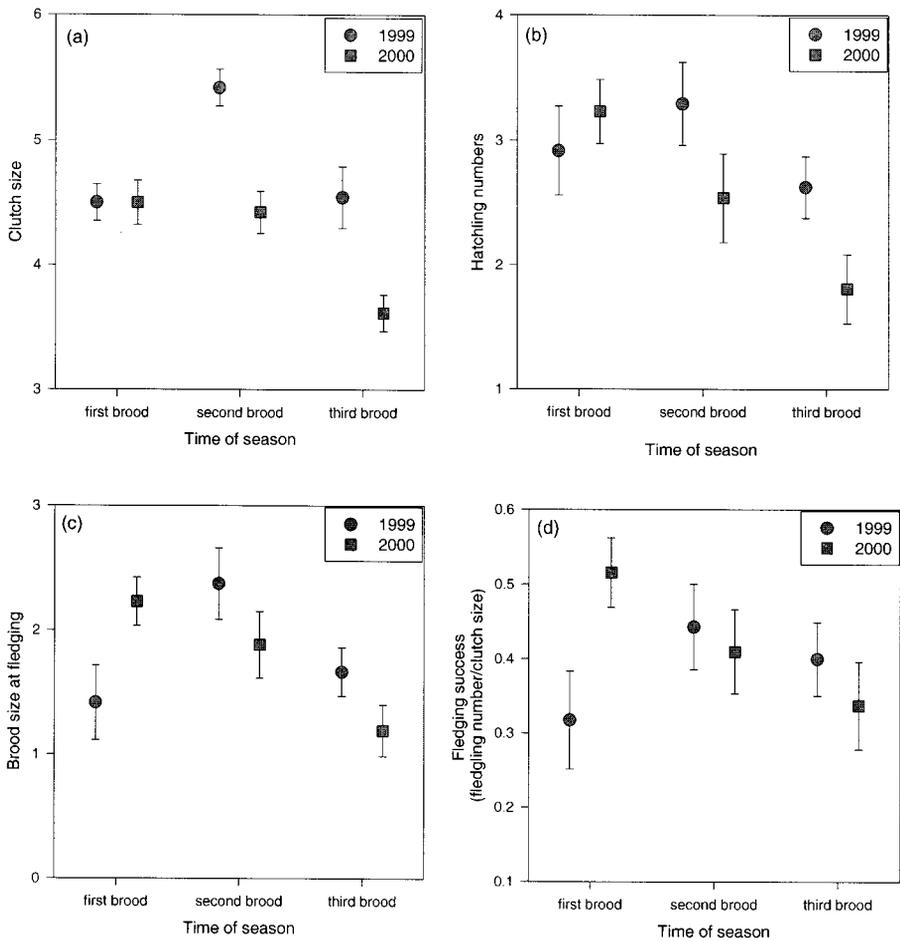
**Fig. 1.** Start of egg laying (means  $\pm$  s.e.) for the three breeding attempts in 1999 and 2000. Median-test of the annual difference between first breeding attempts:  $\chi^2 = 3.43$ ,  $p = 0.068$ ,  $n = 78$ ; second breeding attempts:  $\chi^2 = 12.36$ ,  $p < 0.01$ ,  $n = 81$ ; and third breeding attempts:  $\chi^2 = 20.13$ ,  $p < 0.01$ ,  $n = 73$ .

There was seasonal variation in reproductive success (Fig. 2). Clutch size, hatching size and brood size at fledging varied significantly among the three breeding attempts (Fig. 2a, b and c). Reproductive success in terms of brood size at fledging peaked in the second breeding attempt in 1999, whereas in 2000 it appeared to decline with the season. Importantly, when taking clutch size into account, efficiency of fledging chicks did not change significantly between the three breeding cycles (Fig. 2d).

Examining annual variation in reproductive success, we found that larger clutches were laid in 1999 but hatching size and brood size at fledging were similar between years (Fig. 2a, b and c). In addition, pairs achieved similar fledging success in both years (Fig. 2d). Interactions between the effect of year and the time of season for clutch and brood size at fledging, and mainly fledging success (Fig. 2a, c and d) suggest that pairs in 1999 allocated most reproductive effort to the second breeding attempt rather than the first as in 2000.

### Seasonal variation of colony size, synchrony and behaviour

Depending on the number of available nest-boxes in the plots (plots with 3, 5 and 10 nest-boxes), 87%, 77% and 46% of the nest-boxes were occupied (Fig. 3). While the number of breeding pairs did not differ between the plots with 5 and 10 nest-boxes, fewer pairs nested

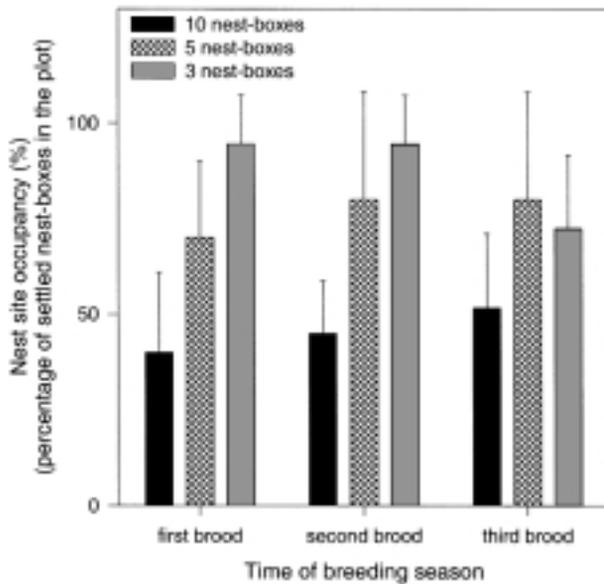


**Fig. 2.** Seasonal and annual variation in four measures (means  $\pm$  s.e.) of reproductive success. **(a)** Clutch size (2-way repeated measures ANOVA, seasonal effect:  $F_{2,96} = 13.54$ ,  $p < 0.001$ , year effect:  $F_{1,48} = 15.29$ ,  $p < 0.001$ , interaction:  $F_{2,96} = 5.90$ ,  $p < 0.01$ ), **(b)** Hatching size (seasonal effect:  $F_{2,96} = 5.51$ ,  $p < 0.01$ , year effect:  $F_{1,48} = 1.99$ ,  $p = 0.17$ , interaction:  $F_{2,96} = 2.67$ ,  $p = 0.07$ ), **(c)** Brood size at fledging (seasonal effect:  $F_{2,96} = 5.49$ ,  $p < 0.01$ , year effect:  $F_{1,48} = 0.04$ ,  $p = 0.84$ , interaction:  $F_{2,96} = 6.24$ ,  $p < 0.01$ ), **(d)** Fledging success (seasonal effect:  $F_{2,96} = 0.85$ ,  $p = 0.43$ , year effect:  $F_{1,48} = 0.35$ ,  $p = 0.55$ , interaction:  $F_{2,96} = 4.50$ ,  $p = 0.013$ ).

in the plots with 3 nest-boxes (the mean number ( $\pm$  se) of pairs in plots: with 10 nest-boxes:  $4.56 \pm 0.42$ ; 5 nest-boxes:  $3.83 \pm 0.34$ ; 3 nest-boxes:  $2.5 \pm 0.1$ ;  $F_{2,69} = 23.25$ ,  $p < 0.01$ ; post hoc 10-3\*\* and 5-3\*\*; \*\*  $p < 0.01$ ). In contrast to the set-ups with 5 and 10 nest-boxes, there was a seasonal decline in the colony occupancy with breeding season for the set-up with 3 nest-boxes (Fig. 3).

On average, 25% of the laying period (days) overlapped between pairs within a nesting site. We found no change in breeding synchrony between the three successive breeding attempts (first attempt:  $26.45\% \pm 5.31$ ; second attempt:  $21.09\% \pm 3.27$ ; third attempt:  $26.43\% \pm 7.51$ , Kruskal-Wallis:  $H_{2,30} = 0.51$ ,  $p = 0.75$ ).

We did not detect significant differences between three breeding attempts in the time that mates stayed at the nest together during the time of egg laying, although mate guarding



**Fig. 3.** Seasonal variation of nest site occupancy (means  $\pm$  s.e.) in relation to the number of installed nest-boxes. (10 nest-boxes: Kruskal-Wallis  $H_{2,18} = 1.83$ ,  $p = 0.40$ ; 5 nest-boxes:  $H_{2,12} = 1.18$ ,  $p = 0.55$ ; 3 nest-boxes:  $H_{2,42} = 6.02$ ,  $p = 0.049$ ).

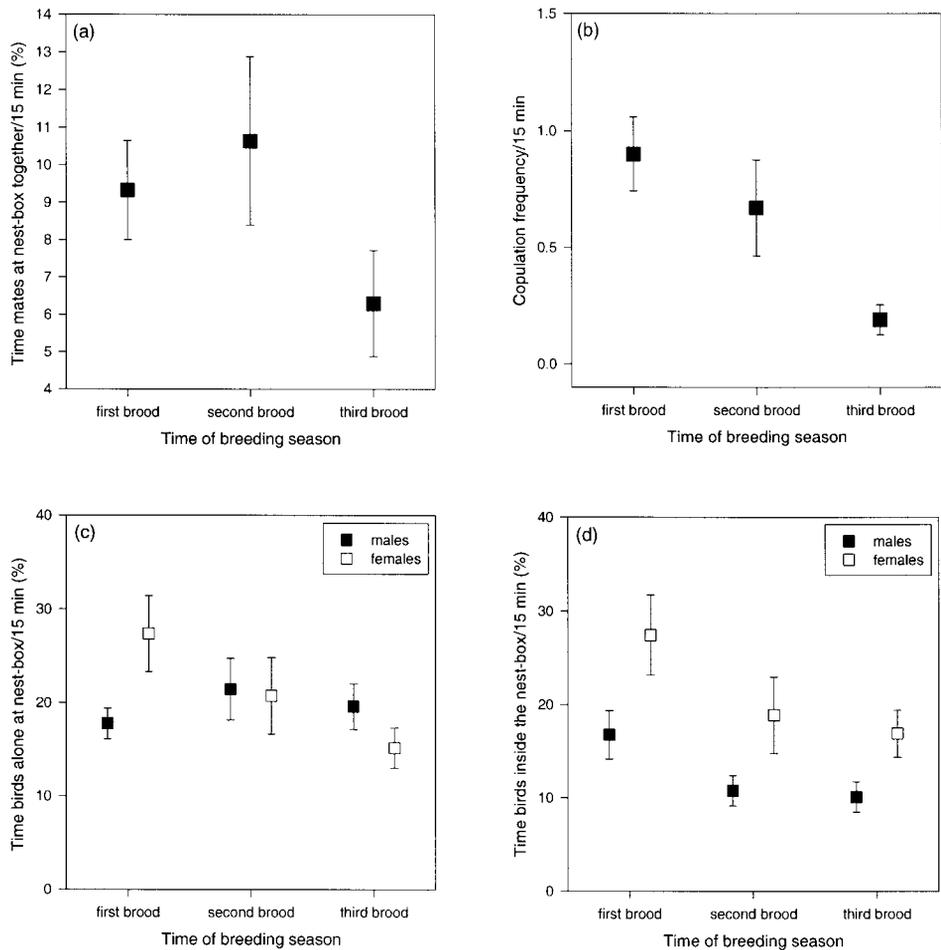
appeared to decline towards the end of season (Fig. 4a). Copulation frequency, however, significantly declined with the breeding season (Fig. 4b). In contrast to males, the time females stayed during egg laying at the nest alone decreased with the time of season (Fig. 4c). Moreover, males and females seemed to reduce the time they stayed inside the nest-boxes during egg laying after the first breeding attempt (Fig. 4d).

Paternity losses (proportion of extra-pair chicks/brood) did not significantly differ between breeding attempts (first attempt: 6.7%; second attempt: 28.8%; third attempt: 24%; Kruskal-Wallis  $H_{2,25} = 3.78$ ,  $p = 0.15$ ).

### The role of colony size for reproductive success, behaviour during egg laying and paternity losses

After controlling for the effect of season, multiple regression analyses revealed a relationship only between clutch size and the number of breeding pairs. Specifically, clutch size increased with colony size (Fig. 5) (including the 5 and 10 nest-boxes set-up only). In addition, the partial regression coefficient suggests that clutch size was larger in five than in ten nest-box plots (see Table 1).

We found a relationship between nest guarding behaviour and colony size (Table 2). Nevertheless, birds of both sexes breeding in the plots with five nest-boxes stayed in their nests during egg laying significantly longer than birds in the plots with ten nest-boxes (see Fig. 6, Table 2). The time males and females stayed at the nest alone was not related to colony size or the type of set-up (see Table 2). Similarly, paternity assurance behaviours do not seem to be largely related to colony size (Table 2). There is, however, indication of a link between copulation frequency and colony size (see Table 2). Finally, the relationship between colony size and paternity losses seemed to be positive but not significantly ( $r = 0.18$ ,  $p > 0.4$ ,  $n = 24$ ).

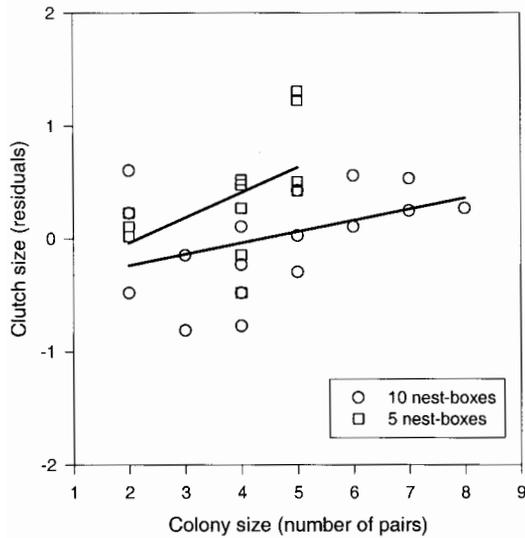


**Fig. 4.** Seasonal variation of mate guarding behaviour (means  $\pm$  s.e.) in terms of (a) time mates stayed at nests together (1-way repeated measures ANOVA:  $F_{2,14} = 2.34$ ,  $p = 0.13$ ) and, (b) copulation frequency ( $F_{2,14} = 5.02$ ,  $p = 0.02$ ; 1-3\* and 2-3\*), and nest guarding behaviour (means  $\pm$  s.e.) in terms of (c) time males stayed at nests alone ( $F_{2,14} = 0.90$ ,  $p = 0.43$ ; time females alone ( $F_{2,14} = 4.09$ ,  $p = 0.04$ ; 1-3\*), (d) time males inside the nest ( $F_{2,14} = 6.32$ ,  $p = 0.01$ ; 1-2\* and 1-3\*) and time females inside the nest ( $F_{2,14} = 2.81$ ,  $p = 0.09$ ). After tests are showed post hoc comparisons (\*  $p < 0.05$ ).

## The role of breeding synchrony for reproductive success, behaviour during laying and paternity losses

After controlling for the effect of season, a multiple regression analysis revealed a relationship only between hatching success and breeding synchrony (Fig. 6a). Specifically, the number of hatched chicks increased when egg laying was more synchronous at a colony. However, the influence of breeding synchrony on brood size at fledging (Fig. 6b) and fledging success was not significant (see Table 1).

Experimental manipulation of the laying synchrony in 2000 supported our result from the natural condition about the existence of a relationship between hatching size and laying synchrony. Although we found no significant difference in clutch size between synchronous



**Fig. 5.** The relationship between clutch size and the number of pairs at nest site. Values of clutch size were standardised for the time of season. Lines are linear regressions for each types of nest site.

**Table 1.** Partial regression coefficients ( $\beta$ ) from stepwise multiple regression models between socio-ecological factors and parameters of reproductive success. Whole model values are  $r^2$ , (n) and corresponding p. Variables of reproductive success were controlled for the time of season (we used residual values).

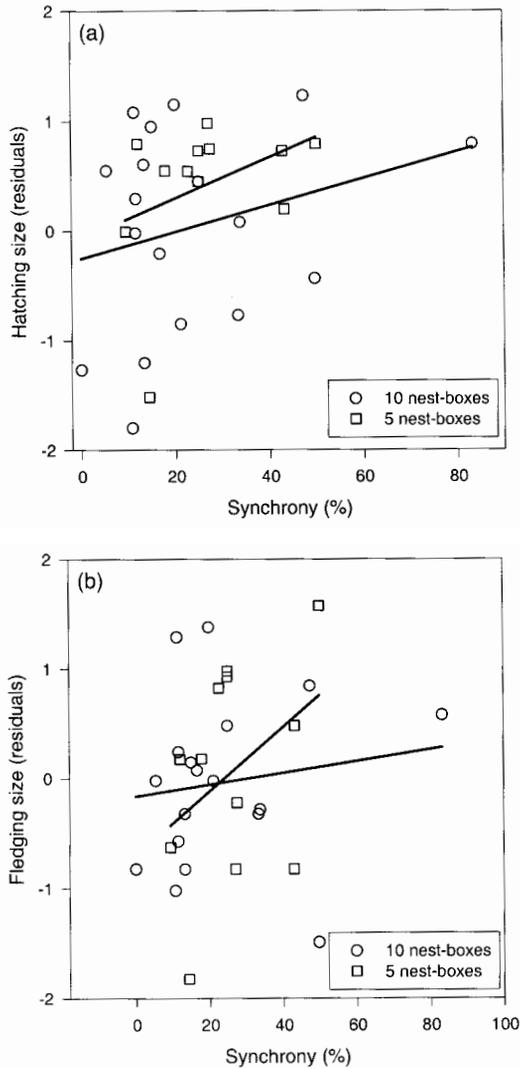
Parameters of reproductive success	Socio-ecological variables			
	colony size	breeding synchrony	type of set-up	whole model
clutch size	0.50 (0.013)	0.20 (0.28)	-0.45 (0.01)	0.32 (30)*
hatching size	0.38 (0.07)	0.44 (0.03)	0.27 (0.13)	0.24 (30) (0.07)
hatching failure	-	-0.36 (0.05)	-	0.13 (30)*
brood size at fledging	-	0.22 (0.25)	-	0.05 (30) (n.s.)
fledging success	-	0.21 (0.27)	-	0.04 (30) (n.s.)

\*  $p < 0.05$

**Table 2.** Partial regression coefficients ( $\beta$ ) from stepwise multiple regression models between socio-ecological factors and behaviours related to mate and nest guarding. Whole model values are  $r^2$ , (n) and corresponding p. All variables referring to behaviour were controlled for the time of season (we used residual values).

Mate and nest guarding behaviours	Socio-ecological variables			
	colony size	breeding synchrony	type of set-up	whole model
copulation frequency	-0.21 (0.32)	-	-	0.04 (26) (n.s.)
time mates together <sup>a</sup>	0.11 (0.63)	0.07 (0.77)	0.04 (0.87)	0.01 (26) (n.s.)
time males in the nest	-0.28 (0.12)	-0.45 (0.02)	-0.46 (0.01)	0.41 (26)**
time females in the nest	-	-0.33 (0.08)	-0.38 (0.04)	0.30 (26)*
time males at the nest alone	-0.35 (0.10)	-0.27 (0.20)	-0.30 (0.14)	0.20 (26) (n.s.)
time females at the nest alone	-	-0.29 (0.13)	-0.33 (0.09)	0.23 (26)*

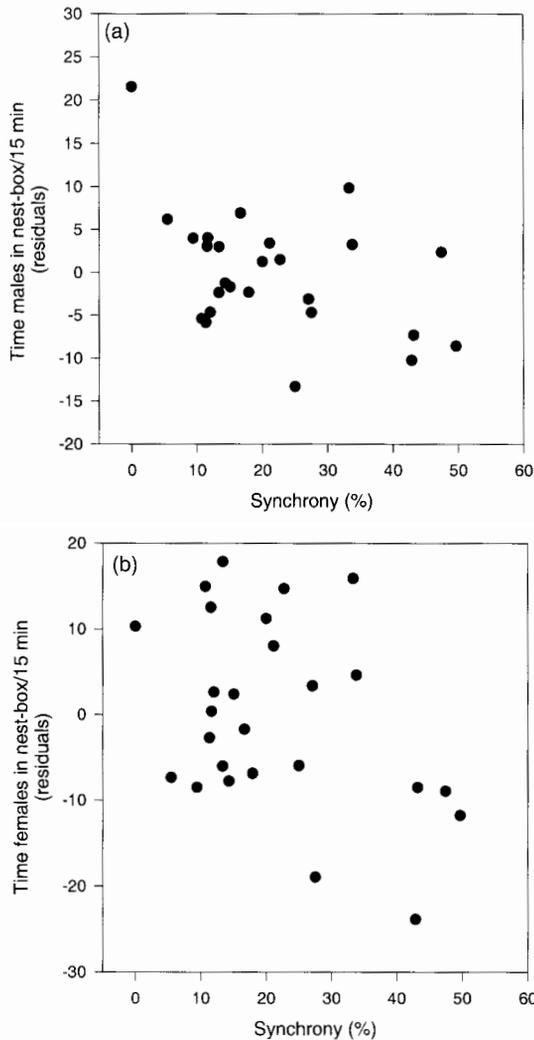
<sup>a</sup> none of the factors was significant and therefore we performed standard multiple regression  
 $p < 0.05$ , \*\*  $p < 0.01$



**Fig. 6.** Hatching size (a) and brood size at fledging (b) in relation to breeding synchrony. Values of hatching size and brood size at fledging were standardised for the time of season. Lines are linear regressions for each types of nest site.

and asynchronous pairs ( $t = 1.09$ ,  $p = 0.28$ ,  $n = 28, 20$ ), pairs nesting synchronously hatched significantly more chicks ( $t = 2.37$ ,  $p = 0.022$ ,  $n = 28, 20$ ). Moreover, differences in brood size at fledging and fledging success between synchronously and asynchronously laying pairs were marginally significant (brood size at fledging:  $t = 1.97$ ,  $p = 0.054$ ,  $n = 28, 20$ ; fledging success:  $t = 1.86$ ,  $p = 0.069$ ,  $n = 28, 20$ ).

With respect to behaviour, synchrony seems to have a large influence only on nest guarding behaviour. Both males and females spent a longer time in the nest with decreasing synchrony (Fig. 7a and b, Table 2). We did not find any stronger relationship between synchrony and paternity assurance behaviours (see Table 2). Similarly, there was no significant relationship between breeding synchrony and paternity losses (Fig. 8). However,

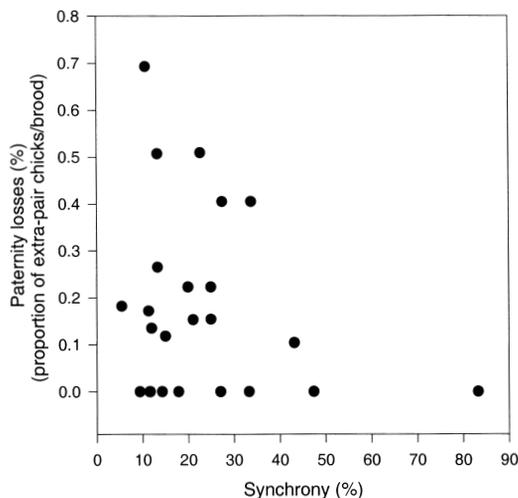


**Fig. 7.** Nest guarding behaviours in relation to breeding synchrony. (a) Time males stayed in the nest. (b) Time females stayed in the nest. Duration of nest guarding was standardised for the time of season.

the shape of the relationship between synchrony and paternity losses indicates that males suffered a loss of their paternity less often with increasing synchrony.

## Discussion

Our results suggest that colony size does not have a strong effect on reproductive success, behaviour and paternity losses. Clutch size seemed to increase with colony size but finally there was no difference in the reproductive success in relation to colony size. Surprisingly, we did not find a substantial effect of colony size on investment in paternity guards or nest guarding behaviours and consequently only a weak effect on paternity losses. This is in contrast to some other studies, which found a density dependent effect on paternity losses (Gowaty & Bridges 1991, Hill et al. 1994, Hoi & Hoi-Leitner 1997)



**Fig. 8.** The relationship between paternity losses and breeding synchrony ( $r = -0.21$ ,  $p = 0.31$ ,  $n = 24$ ). Paternity losses were log transformed to achieve normality.

as well as on investment in paternity assurance tactics (Birkhead et al. 1987, Hatchwell 1988, for house sparrows see Tost 1994). Hence, although sperm competition occurred in our study population, it did not seem to be directly linked to colony size. An explanation could be that extra-pair copulations occurred at the foraging sites and colony size would hence not reflect the level of sperm competition. This is, however, unlikely since Wotton et al. (1995) showed specifically for house sparrows and Birkhead & Møller (1992) for other colonially breeding species that extra-pair males are often neighbours. There is still a possibility that density may be important for extra-pair fertilisations since we manipulated only colony size but not density and the distance between nest-boxes remained similar in all colonies. In contrast to Tost (1994), who found that house sparrows adjust their paternity guards in relation to colony size, we may not have found such a relationship for another reason. Tost's (1994) population nested under natural conditions, whereas our study provides an example of an unnatural nest-box population. There are several important differences between natural and nest-box populations that need to be stressed. Firstly, in nest-box populations, quality of nesting sites does not necessarily reflect territory quality, such as food abundance. Secondly, if females seek extra-pair fertilisations (EPF) according to the male territorial quality, equal quality of nest-boxes disables females to judge the quality of males because male dominance is no longer reflected in nest site quality. Thirdly, the cost of searching extra-pair males may be too high in uniform and high quality nesting habitats (Slagsvold & Dale 1991, Westneat 1992). Our results are, in respect of the latter two points, similar to the study by Veiga & Boto (2000), who did not find in their nest-box colony higher levels of EPP than those reported from lower density nest-box colonies of house sparrows. Nonetheless, other factors like breeding synchrony (see later, Stutchbury & Morton 1995), territory quality (Hoi et al. 1995) or intense intraspecific competition (Veiga 1992) might have outweighed the role of breeding density in our study. Also, it is important to mention that the phenotype of birds was not considered in our study due to a small sample size and hence we might lose an important component of variation in our analyses.

The missing relationship between colony size, behaviour, reproductive success and achieved paternity may also be due to a nonlinear relationship between them. *Tost* (1994) found a considerable variation of breeding sociality, ranging from rare cases of solitary breeding pairs up to colonies of 200 breeding pairs. Yet, even within these huge colonies, he could usually distinguish clusters with two to seven pairs. This suggests that birds avoided to nest solitary as well as in large groups and the observed aggregations reflected the preferred colony size. In line with this, we found that, regardless of the nest-box availability, there was no significant difference in the colony size between plots with 5 and 10 nest-boxes. Pairs nested most frequently in groups of four to five pairs in both plots with 5 or 10 nest-boxes, whereas in the plots with 3 nest-boxes, naturally, in smaller groups of two to three pairs. Although our results about the role of nesting site type need to be treated with caution because plot size was confounded to the year of study, it seems that breeding in groups of four to five pairs at the nest site may have been beneficial. We have two indications for this assumption. First, pairs in the plots with 3 nest-boxes started breeding at approximately same time as the pairs in the plots with 5 and 10 nest-boxes, but it took them longer to fledge their chicks (Fig.1). This may be disadvantageous since it is known that offspring produced late in the season have a shorter time to build up their energetic reserves for the winter, reach a lower hierarchical status and suffer higher mortality (*Lack* 1954, *Klomp* 1970, see *Daan & Tinbergen* 1997). Second, despite the positive relationship between clutch size and colony size, pairs in 5 nest-box plots had significantly larger clutches than pairs in 10 nest-box plots (Table 1). Therefore, it seems that availability of nest-boxes could serve as a habitat cue reflecting future colony size. Consequently, birds may try to avoid nesting sites that deviate from the preferred colony size.

In contrast to colony size, we found that breeding synchrony influenced hatching success. Namely, more chicks hatched under both natural and experimental conditions in situations when pairs laid eggs at the nest site more synchronously. Again, breeding synchrony did not seem to largely influence paternity assurance behaviour but paternity losses appeared to decrease with higher breeding synchrony (Fig. 8). Hence, this finding supports *Birkhead & Biggin's* (1987) hypothesis that EPP decreases with breeding synchrony due to the incompatibility of males to guard their mates and seek extra-pair copulations simultaneously. This is in contrast to the hypothesis of *Stutchbury & Morton* (1995), which implies an increase in extra-pair paternity with breeding synchrony because females should have better possibilities to compare the quality of possible copulation partners that all breed at the same time. In contrast to paternity assurance behaviour, we found that breeding synchrony significantly influenced investment in nest guarding behaviour. Synchrony is usually thought to be advantageous because it decreases the risk of nest depredation (e.g. *Wittenberger & Hunt* 1985, *Imms* 1990) but may also reflect the time when the environmental conditions for breeding are at best (*Brown & Brown* 1996). However, in our population house sparrows had three breeding attempts with fluctuating reproductive success, but without obvious fluctuations of breeding synchrony. Synchrony may, however, mediate different levels of intraspecific competition. Indeed we found that nest guarding behaviour apparently increased with decreasing synchrony. *Veiga* (1990, 1992) showed that competition between females over the superior males, eventually leading to egg destruction, decreases with breeding synchrony. Since we have shown that egg losses are in general very high in house sparrows and substantially influence reproductive success also in our population, nest guarding seems to be very important in this species. Moreover, our previous works (*Václav & Hojín*

press, V á c l a v et al. in press) show that egg losses were highest in the nests of males that were cuckolded most often, possibly reflecting male harassment upon females. Hence, since males are cuckolded less often and females suffer lower clutch losses when breeding synchronously, intra-sexual competition in both sexes may favour breeding synchrony and consequently genetic monogamy. The reason why house sparrows do not prefer to breed in large colonies and prefer to stay in loose groups might therefore be rooted in avoidance of breeding asynchronously.

To summarise, our study showed that colony size does not seem to be a factor substantially explaining reproductive success, extra-pair behaviour and paternity losses in house sparrows. Although clutch size increased with colony size, birds preferred nesting in rather small groups. Higher hatching success and possibly also higher fledging success and lower risk of paternity losses increased when birds nested more synchronously. Since synchrony decreased with colony size in our study population, this might be a reason why house sparrows of both sexes prefer to breed in small groups.

#### A c k n o w l e d g e m e n t s

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