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Breeding synchrony and paternity in the barn swallow (*Hirundo rustica*)

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Abstract The barn swallow (*Hirundo rustica*) is a socially monogamous passerine which usually breeds in colonies where extra-pair copulations are frequent. Males intensively guard their mates during the female fertile period. Since males are more likely to be available for extra-pair copulations when their mate is not fertile, synchrony in timing of breeding may affect paternity of individual males. In this study, we analysed the change in mate-guarding rate by males in relation to the fertility condition of the female, and the relationships between breeding synchrony and density with paternity in first broods of 52 male barn swallows. Paternity (proportion of nestlings fathered in own brood) was assessed by typing of three highly polymorphic microsatellite loci. Mate guarding by males peaked during the fertile period of their mates. Paternity increased as breeding synchrony in the colony increased. Paternity of barn swallows is positively associated with the degree of exaggeration of male tail ornaments. The relationship between male ornamentation and paternity was partly mediated by an effect of ornament size on breeding synchrony. We suggest that females might delay breeding with low-quality males to enhance their opportunities for being fertilised by high-quality extra-pair males.

Key words Breeding synchrony · Breeding density · *Hirundo rustica* · Paternity · Male ornaments · Mate guarding

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Introduction

Extra-pair copulations resulting in fertilisations are now recognised as a common phenomenon in bird species with socially monogamous mating systems. Extra-pair paternities have been detected in several passerines, and large variability exists in the frequency of extra-pair fertilizations at the interspecific level (Westneat et al. 1990; review in Birkhead and Møller 1992; Stutchbury and Morton 1995), at the inter-population level (e.g. Lifjeld et al. 1991; Gelter and Tegelström 1992), as well as at the inter-individual level (Birkhead and Møller 1992; Kempenaers et al. 1992; Stutchbury et al. 1994; Saino et al. 1997).

In species in which females have at least partial control over which extra-pair males will obtain copulations, female choice is expected to play an important role in determining the frequency of cuckoldry experienced by their mates. However, other factors are also predicted to determine the frequency of extra-pair paternity. Although the potential role played by these factors has been repeatedly acknowledged (Westneat et al. 1990; Birkhead and Møller, 1992; Dunn et al. 1994; Møller 1994), little is known about the effect of ecological, demographic and social variables (Gibbs et al. 1990; Gowaty and Bridges 1991a; Dunn et al. 1994; Kempenaers 1997; Yezerinac and Weatherhead 1997). Density of breeding pairs, for example, may affect the frequency of extra-pair paternity because it influences the time males or females have to spend in finding extra-pair copulation partners (but see Westneat and Sherman 1997). The operational sex ratio, being variable through space and time, may also influence the frequency of extra-pair paternity. Moreover, it has been suggested that, at the intraspecific level, breeding synchrony lowers the frequency of extra-pair fertilizations (Birkhead and Biggins 1987; Westneat et al. 1990), while others argue that synchrony should result in a higher frequency of extra-pair paternity (Stutchbury and Morton 1995; Stutchbury 1998a, 1998b).

The fitness loss imposed on males by being cuckolded should have selected for behavioural and/or physiological adaptations to reduce the frequency of extra-pair copulations of their mates (Trivers 1972). One of the most common tactics adopted by male birds to ensure parentage is mate guarding (Birkhead 1979, 1982; Davies 1983; Møller 1985; Morton 1987; Gowaty et al. 1989; Birkhead and Møller 1992). Some studies have indicated that the presence of the male closely following his partner prevents the female from engaging in extra-pair copulations (e.g. Björklund and Westman 1983; Davies 1985; Møller 1985; Alatalo et al. 1987; Birkhead et al. 1989; but see Gowaty and Bridges 1991b; Kempenaers et al. 1995). In the barn swallow, experimental short-term removal of males during a single morning in the fertile period of their mates revealed that the presence of the male mate indeed prevented neighbouring males from getting copulation access to a female (Møller 1987). Since mate guarding competes with other mutually exclusive activities, males are expected to engage less frequently in extra-pair copulations while their mates are fertile, as shown in many different species (e.g. Møller 1985; review in Birkhead and Møller 1992). Synchronously breeding males will thus experience a comparatively low competition for paternity in their own broods because most of the competing males will be engaged in mate guarding.

The barn swallow (*Hirundo rustica*) is a good model organism for a study of the effects of breeding synchrony and density on paternity because it is a socially monogamous passerine which usually breeds in dense colonies, males intensely guard their mates during the fertile period of the female, and the frequency of extra-pair copulations and fertilisations is high (Smith et al. 1991; Møller 1994; Møller and Tegelström 1997; Saino et al. 1997). After arrival from migration to the breeding sites, males establish a small nesting territory and start singing and displaying their tail ornaments to prospecting females which can visit several males before making their choice of a mate. Males are often seen intruding on territories of mated males and seeking extra-pair copulations, which are particularly frequent during the fertile period of the female (Møller 1994). Females apparently cannot be forced to copulate and, thus, they have control over the identity of copulation partners (Møller 1994). However, males are able to thwart extra-pair copulation attempts if they are in close proximity to their mates (Møller 1994). Hence, intense mate guarding might be an efficient way to ensure genetic parentage. There is strong directional sexual selection in this species for long tail ornaments in males (Møller 1988, 1994). As a result of female preference, males with large tail ornaments experience a lower level of cuckoldry and realise a larger reproductive success compared to those with small ornaments (Møller and Tegelström 1997; Saino et al. 1997).

The main aims of this study were to analyse (1) the change of intensity of mate guarding by individual males in relation to the fertility condition of their mates, and (2) the relationships between paternity, expressed as the proportion of biological offspring in own first broods, and breeding synchrony and density, of colonial barn swallows. In previous studies (Møller 1994; Saino and Møller 1995), mate guarding of individual males was found to peak during the fertile period of their mate. To check for the consistency of this pattern between populations, we analysed variation of mate-guarding rate during female fertile and non-fertile periods, with the prediction that there would be more intense mate guarding during the female fertile period. We also predicted a positive correlation between breeding synchrony and paternity and a negative correlation between density of breeding pairs and paternity.

In the present paper, we will not deal specifically with the effect of male ornament size on paternity because this is the subject of companion studies (Møller and Tegelström 1997; Saino et al. 1997).

Methods

Study area and methods

This field study was carried out during spring 1994 on 52 pairs of barn swallows with unmanipulated tail length (546 of 96 breeding pairs) in seven distinct colonies, each located in a different stable range of colony sizes in our study area east of Milan (northern Italy), while the study of mate guarding included six additional colonies. The distance between nearest neighbouring colonies considered in this study was always more than 500 m. The modal distance between nearest neighbouring nests was 2 m. Barn swallows were caught by mist nets during the day. Swallows were marked with a metal ring on one leg and a plastic colour ring on the other, and by unique combinations of colour markings on breast and belly feathers. Individuals were sexed according to the shape of the cloacal protuberance (Svensson 1984). Assignment to sex was later confirmed by inspection for presence (female) or absence (male) of an incubation patch and by observation of sexual and breeding behaviour. Blood samples (ca 180 μl in heparinised haematocrit capillary tubes) were also taken for parentage analysis. At the time of first capture, we measured a number of morphological variables including the length of the left and right outermost tail feathers. Tail length was then expressed as the mean of the two measures.

Adults were assigned to nests and broods by observation of colour rings and markings. For each brood we considered as putative father the male that defended the territory in which the nest was located and fed the nestlings. These criteria allowed us to unequivocally identify a putative father for each brood considered in this study.

Nests were inspected every 2nd day until laying had been completed, 2 days before the estimated hatching date and every 2nd day during the nestling period. When nestlings were 7 or 8 days old, they were ringed and a blood sample of ca 50 μl was taken.

The intensity of mate guarding was measured by daily observation sessions lasting 1 h between 6.00 and 10.00 a.m. from pair formation until 15 days after laying of the first egg, and was expressed as the percentage of instantaneous observations every second minute in which a male was observed inside the space he actively defended from other males (hereafter 'mate-guarding rate'). These data were recorded for 19 males with unmanipulated tail length.

Breeding asynchrony of each pair with respect to the other pairs in the same colony was expressed using the following procedure. For each pair, we assigned a value of 0 to each day in the fertile period of the female, and a value 1 to each day after territory establishment outside the fertile period of the female. The value 0 indicated days in which males were very active in guarding their mates (Møller 1994; Saino and Møller 1995; see also Results) and, hence, had little time to devote to seek extra-pair copulations, while a value of 1 indicated that males were available for extra-pair copulations. An index of breeding asynchrony for a given male was obtained as the sum of the scores assigned to the other males in the same colony during the fertility period of his mate divided by the number of males in the same colony.

However, since the duration of sperm storage, i.e. the interval between the last insemination and the laying of the last fertile egg (Birkhead and Møller 1992) in the barn swallow is not known, we could not precisely decide when the females had entered their fertile period, i.e. the period when an insemination can potentially result in fertilisation of one or more eggs. In passerines, sperm can be stored for some 8–10 days (see Birkhead and Møller 1992). We therefore repeated all the analyses implying a definition of the fertile period of the females (i.e. those on mate-guarding rates in relation to the stage in the breeding cycle and those on number of males whose mate was reproductively synchronous with the mate of the focal male) by setting, in turn, the start of the fertile period at 12, 9, 6 or 3 days before laying of the first egg, thus likely including the actual start of the fertile period. The end of the fertile period was set on the day before laying of the last egg.

In the remainder of this paper we adopt the following definitions: 'pre-fertile period' is the period between pair formation and the start of a female's fertile period, 'fertile pre-laying period' is the period between the start of the fertile period and the day preceding the start of egg laying, 'egg-laying period' is the female fertile period from laying of the first egg until the day the penultimate egg is laid, while 'incubation' period is the period after laying of the penultimate egg.

Paternity analyses

Paternity of individual nestlings was determined by microsatellite typing. DNA was extracted from 2 µl of packed red blood cells using a chelex extraction procedure. The biological parents of offspring were determined by tracing the inheritance of alleles segregating at three highly polymorphic swallow microsatellite loci (*HrU5*, *HrU6* and *HrU9*) as previously described (Primmer et al. 1995). The only exception was that the 72 °C extension step was increased in time to 80 s to allow amplification of long alleles. *HrU9* consists of an $(AAAG)_n$ repeat for which the primer sequencies are A-AACAATCAAGCCTCCCCAGG and B-ATATAGCAGGCACTCTCACA. PCR and electrophoresis were as for *HrU6*. We included a size ladder on every gel which consisted of around ten evenly spaced alleles. If at least two of the three markers excluded a male as being the putative father, we assumed this to represent an extra-pair fertilisation. The three-locus microsatellite system used in this study was very efficient for determining biological parents. There were an average of 18, 45 and 55 alleles per colony observed for *HrU5*, *HrU6* and *HrU9*, respectively. The total number of allelic variants observed in a sample of 355 adult birds was 24 for *HrU5* and over 100 for both *HrU6* and *HrU9*, making the latter two markers two of the most polymorphic ever isolated for any species. A null allele was observed at one of the loci, *HrU9*, with a frequency of less than 0.08 and should therefore not affect paternity analyses greatly (see also Primmer et al. 1996a). Using the allele frequency data, the average exclusion probability (Jamieson 1994) obtained by these three loci was calculated to be $>99.9\%$. All cases which we interpreted as extra-pair fertilisation events were such that the putative male was excluded by at least two of the three markers.

It is reasonable that the most polymorphic microsatellites are associated with the highest mutation rates (Weber and Wong 1993; Talbot et al. 1995) and it was therefore not surprising that during the genotyping process, occasional cases of mutations to new-length variants were observed at both *HrU6* and *HrU9* (Primmer et al. 1996b). This was suspected whenever the genotypes at two microsatellite loci of a putative father matched with an offspring's genotypes whilst the third differed by a small number of repeat units (most often one, but occasionally more). Using data obtained from about 1000 meioses analysed at each of the three loci used in this study, the observed mutation rates at *HrU5*, *HrU6* and *HrU9* are $<0.1\%$, 0.5% and 3.6%, respectively. To confirm that we had actually observed mutation events, we typed these individuals with our seven remaining swallow markers (Primmer et al. 1995, 1996a). In all cases, the markers matched with our original suspicion of a mutation as opposed to an incorrect parentage assignment. The average probability of false inclusion (the probability of a male matching as the father of an offspring purely by chance) was 1.7×10^{-3}.

Paternity of individual males was expressed as the ratio between the number of his biological offspring and the total number of nestlings in the brood of which he was the putative father.

Results

To analyse the pattern of variation in mate-guarding rate among the four reproductive periods we defined (i.e. pre-fertile, fertile pre-laying, egg laying and incubation periods, see Methods) we first computed the mean within-period mate-guarding rates of each male. Mean mate-guarding rates were found to vary markedly during the breeding cycle. The percentage of observations every 2 min in which a male was observed inside his territory together with his mate was lower during the pre-fertile and incubation periods than during the fertile period (Fig. 1). In a two-way analysis of variance in which period and individual were entered as factors, we consistently found a highly significant effect of period in the breeding cycle on mate-guarding rate when setting the start of the fertile period 12, 9, 6 or 3 days before laying of the first egg (Table 1). This pattern closely resembles that found in a Danish population of barn swallows (Møller 1985; Saino and Møller 1995).

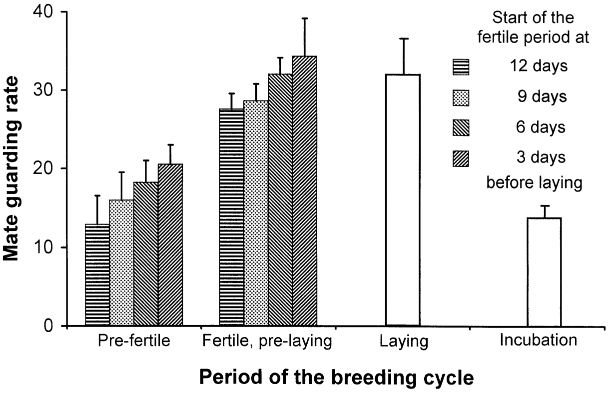

Fig. 1 Mean (+SE) mate-guarding rate, expressed as percentage of observations every 2nd minute during 1-h daily observation sessions in which a male was inside his territory together with his mate, in relation to fertility condition of the female. Since the duration of the fertile period before egg laying in barn swallows is unknown, we assumed, in turn, that the fertile period started 12, 9, 6 or 3 days before the day on which the first egg was laid

Table 1 Results of two-way analyses of variance of male mate-guarding rate in which period in the breeding cycle (pre-fertile, fertile pre-laying, egg laying and incubation, see Methods) and individual were entered as factors. For each male, mate-guarding rates entered in the analysis are means computed within periods in which the female breeding cycle was subdivided. The analyses were repeated for start of the fertile period set at 12, 9, 6 or 3 days before laying of the first egg

Fertile period start (days before egg laying)		Mean square	*df*	*F*	*P*
12 days	Period	1800	3	9.73	< 0.001
	Individual	223.5	18	1.21	NS
9 days	Period	1604.1	3	8.25	< 0.001
	Individual	212.4	18	1.09	NS
6 days	Period	1736.4	3	10.52	< 0.001
	Individual	204.3	18	1.24	NS
3 days	Period	1834.0	3	7.48	< 0.001
	Individual	294.3	18	1.20	NS

Mate guarding was unrelated to male tail length ($r = -0.15$, $n = 19$, NS), as in a previous study in Denmark (Møller 1994).

In the 52 first broods considered for paternity analysis, 61 of the 214 nestlings (29%) were not sired by their putative father, and 52% of the 52 broods had some extra-pair offspring. Forty of these nestlings, belonging to 14 broods, were fathered by males of known identity from the same colony which were mated and had at least one own brood during the breeding season. The remaining 21 nestlings were either fathered by unmated males or by unidentified males.

Cuckolders were not synchronous in breeding with cuckolded males. In all cases of cuckoldry in which the identity of the cuckolder was known ($n = 14$), the mate of the cuckolder laid her first egg either more than 8 days before or 6 days after the extra-pair female (Fig. 2). In most cases (9 out of 14; 64%), males were cuckolded by one of the two nearest neighbours. The cuckolder was one of the two nearest neighbours more frequently than expected under the hypothesis that the cuckolder was a random male in the colony ($\chi^2 = 4.46$, $df = 1$, $P < 0.05$).

The change of mate-guarding rate during the breeding cycle and the breeding asynchrony between cuckolder and cuckolded males indicated that males that were busy guarding their mate did not actually obtain extra-pair fertilisations. Moreover, cuckolders were frequently the neighbouring males. For these reasons, as an index of density of asynchronous breeding pairs experienced by each pair, we used the mean distance of the two nearest neighbours whose mates laid their first egg more than 8 days before or 6 days after the mate of the focal male. Of course, increasing values of this index indicate decreasing breeding densities. The distance to the two nearest neighbouring asynchronous males was only weakly and non-significantly correlated with paternity ($\tau = 0.07$, $n = 52$, NS).

Paternity was negatively correlated with the breeding asynchrony index (Table 2), indicating that males whose mate was fertile when most of the other females in the colony were not suffered the largest loss of paternity (Fig. 3). Male tail length was strongly and negatively correlated with breeding asynchrony (Table 2). Hence, the females of sexually attractive, long-tailed males were fertile when most of the other females were also fertile. Paternity was positively correlated with tail length ($\tau = 0.29$, $n = 52$, $P = 0.005$; Saino et al. 1997).

Hence, the effect of tail length on paternity might have been direct and/or might have been mediated by breeding synchrony. We tried to ascertain the direct and

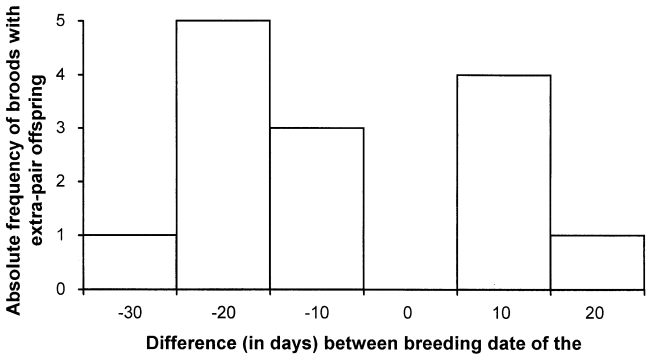

Fig. 2 Frequency of extra-pair paternity in relation to the difference, in days between date of laying of the first egg by the mate of the cuckolded male and the mate of the extra-pair male. Differences between laying dates are grouped in 10-day classes (for example −35 to −26)

Table 2 Kendall τ simple correlation coefficients between breeding asynchrony index and paternity or male tail length when the start of the fertile period of the females was set at different dates before laying of the first egg. Values of the asynchrony index increased with the number of females that were outside their fertile period when the mate of the focal male was fertile

Start of fertile period (days before egg laying)	Correlation of asynchrony index with	
	Paternity	Male tail length
12 days	−0.22 ($P = 0.04$)	−0.45 ($P < 0.001$)
9 days	−0.27 ($P = 0.01$)	−0.50 ($P < 0.001$)
6 days	−0.29 ($P = 0.006$)	−0.52 ($P < 0.001$)
3 days	−0.29 ($P = 0.006$)	−0.51 ($P < 0.001$)

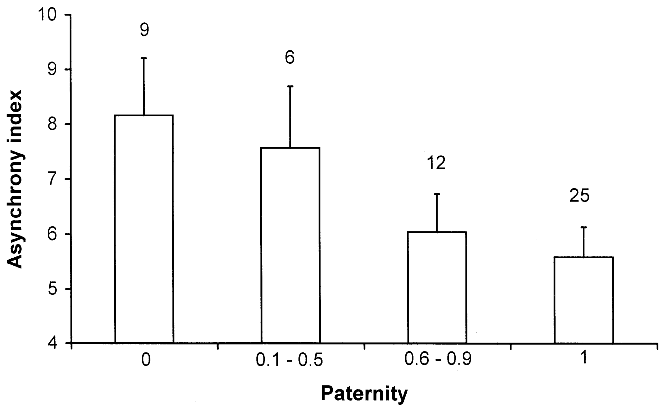

Fig. 3 Mean (+SE) asynchrony index for males that experienced different levels of paternity (expressed as the proportion of biological offspring in their first brood). The fertile period of females is assumed to start on day 9 before laying of the first egg. Qualitatively similar results were obtained when the start of the fertile period was set at 12, 6 or 3 days before laying of the first egg

indirect effects of tail length on paternity in a path analysis (Sokal and Rohlf 1995) according to the causal relationships envisaged in Fig. 4. The assumption of a causal influence of tail length on paternity is supported by the observation that experimental manipulation of tail length alters paternity (Smith et al. 1991; Saino et al. 1997). Male tail length might also influence breeding synchrony because it may affect female decisions about timing of breeding to ensure an increased chance of being fertilised by high-quality males. The reason for assuming causation between breeding synchrony and paternity has been discussed previously: the chances of being cuckolded are likely to increase as the number of males available for extra-pair copulations increases. Path analysis implies the use of standardised multiple regression coefficients and parametric correlation analyses. However, no statistical inferences from path analysis can be drawn, so violation of the assumptions about the nature and statistical distribution of the data did not constitute a problem.

Values of the path coefficient from length of tail ornaments, reflecting the direct effect of tail length on paternity, ranged from 0.19 to 0.21 whereas the path coefficients from breeding asynchrony index and paternity ranged from −0.23 to −0.25 depending on the number of days before egg laying on which the female fertile period was assumed to start. The compound path coefficient reflecting the contribution to paternity from tail length mediated by the effect of tail length on breeding asynchrony was lower than the direct path coefficient but non-negligible (values ranging from 0.14 to 0.17 according to the limit set for the start of the fertile period). The overall coefficient of determination of paternity ranged from 0.15 to 0.16. Summarising, path analysis indicated that the effect of tail length on paternity was partly a direct one. However, tail length also affected paternity via an effect on breeding synchrony.

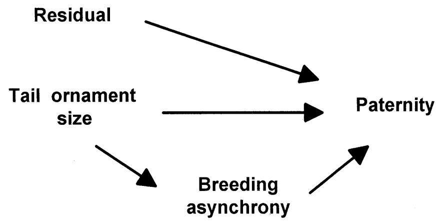

Fig. 4 Causal relationships between male tail ornament size, breeding asynchrony and paternity, as assumed in a path analysis (Sokal and Rohlf 1995) of the direct and indirect effect of tail size on paternity. See text for justification of the assumptions on direction of causal relationships and values of path and compound path coefficients

Discussion

The intensity of mate guarding by male barn swallows was related to the fertility condition of their mates and this relationship was in the predicted direction. When females were in their fertile period, their mates spent approximately 30% of their time guarding them inside the territory, while the proportion of time spent together by partners in their territory was much lower outside the female fertile period. It should be emphasised that our estimate of the proportion of time spent by males guarding their mates is a conservative one because it does not take into account mate guarding that occurs when both mates are outside their territory. Indeed, during the female fertile period, both members of breeding pairs are simultaneously away from the territory for more than half of the time (57%, on average, of the observations every 2nd minute; N. Saino, unpublished data) and, hence, the value of 30% accounts for more than two-thirds of the time spent by either or both of the members of each breeding pair inside their territory. In addition, it seems likely that mate guarding is also intense outside the territory because, for example, males often follow their mates when they leave the territory (Møller 1994). The observation of this type of relationship between mate guarding and female fertility condition is not a novel one for the barn swallow and is qualitatively consistent with previous studies on a Danish population of this species (Møller 1985, 1987; Saino and Møller 1995).

Extra-pair fathers tended to be males that were breeding asynchronously with respect to the extra-pair females they fertilised. This result and the observation that mate guarding was particularly intense during the fertile period of their mates served as a basis to calculate a breeding asynchrony index which reflected the number of males actually available for extra-pair copulations. Implicit in our procedure was the assumption that all males produced sperm soon after arrival, and that all were still fertile when the penultimate egg in the last first clutch had been laid. The validity of this assumption is supported by the following considerations: (1) in this study, we show that some males could fertilise females that laid their first egg as long as 22 days before or 32 days after the males' own mates laid their first egg, (2) we could collect sperm from males whose mates had completed egg laying at least 31 days earlier (unpublished data) and (3) extra-pair copulations also involve males whose mates are still far from entering their fertile period (Møller 1985; N. Saino and A.P Møller, unpublished data). Finally, it might be speculated that in a species in which extra-pair fertilisations are frequent, males should have been selected to expand their fertile period in order to increase their chances of fertilising females mated with other males. There is empirical evidence for this prediction in other bird species (Murton and Westwood 1977; Hegner and Wingfield 1990; Birkhead and Møller 1992).

Extra-pair paternity has been claimed to be either positively or negatively related to breeding synchrony (positive relationship: Stutchbury and Morton 1995; Stutchbury 1998a; negative relationship: Birkhead and Biggins 1987; Westneat et al. 1990). If males risk losing paternity by engaging in extra-pair copulations, extra-pair activity should peak outside the fertile period of the mate, as observed in most solitarily breeding species of birds (Birkhead and Møller 1992, Table 10.2). Extra-pair paternity should therefore be less frequent when breeding is synchronous. The alternative point of view is based on the assumption that synchronous breeding provides more opportunities for extra-pair paternity (Stutchbury and Morton 1995). This hypothesis thus predicts a positive correlation between extra-pair paternity and breeding synchrony across species. Although comparative evidence has been presented to support this hypothesis (Stutchbury and Morton 1995), the conclusion was based on the use of statistically dependent observations (see Harvey and Pagel 1991). More recently, Stutchbury (1998a) has presented evidence from inter-specific comparisons while controlling for phylogenetic effects showing a positive relationship between synchrony and frequency of extra-pair paternity. However, this evidence has not been considered as a conclusive by other authors (Weatherhead and Yezerinac 1998) based on intra-specific analysis of paternity in relation to reproductive synchrony. Hence, there is no compelling intraspecific or interspecific support for the hypothesis that synchrony promotes extra-pair paternity.

We showed that paternity was higher for males that bred when most of the other males in the same colony were intensely guarding their mates after controlling for the effect of colony size. Asynchronous nearest neighbouring males whose females were not fertile were most likely to fertilise an extra-pair female. The distance to the two nearest neighbours apparently did not predict the probability of individual males being cuckolded.

There are some important implications of our findings with respect to decision making by males and females about time of reproduction. Breeding times for individual barn swallows can be envisaged as an optimisation process of costs and benefits of early breeding under the constraints imposed by ecological, social, and demographic conditions in the breeding areas. The individual's time of breeding can also be influenced or constrained by its partner's decision. Females, of course, may have full control or, at least, substantial ability to influence the time of breeding. However, males might still be able to influence, for example, the timing of ovulation by their partners. One possible mechanism involves singing behaviour. Indeed, male song is known to stimulate ovulation and low singing rates thus might delay the onset of ovulation (e.g. King and West 1977). Theoretically, males might also reduce their contribution to nest building, thus delaying reproduction. The costs of delayed reproduction include a reduced probability of recruitment by offspring (Møller 1994; N. Saino and A.P. Møller, unpublished data).

Differential benefits and costs for males or females from breeding synchrony are under some circumstances likely to give rise to sexual conflict over the time of breeding. In species with strong mate preferences, such as sexually dichromatic species, one relevant factor which can influence a male's decision about timing of reproduction is his relative sexual attractiveness which, in turn, will affect his mate's fidelity and the number of extra-pair fertilisations that he obtains. If nest predation and male sterility are rare, females mated to sexually attractive males should not have marked preferences with respect to breeding synchrony and availability of extra-pair copulation partners. Their own partners will provide high-quality genes for offspring, for example, genes for sexual attractiveness of their sons (Weatherhead and Robertson 1979) or resistance to parasites (Hamilton and Zuk 1982). The advantages of early reproduction for successful recruitment of offspring should select for relatively early breeding. In pairs with less attractive males, however, the conflict of interests between mates is likely to be more intense. Males of low attractiveness may tend to reduce the risk of being cuckolded by breeding simultaneously with males that, being attractive to females, are more likely to obtain extra-pair copulations. By definition, interests of females mated to low-quality males with respect to paternity of their offspring should differ from those of their mates. These females should tend to tune their breeding time so that their chances of being fertilised by high-quality extra-pair males are maximised. The positive correlation observed between degree of sexual ornamentation of males and breeding synchrony is consistent with the idea that females mated to low-quality males bred when most males were available for extra-pair copulations, but is also consistent with unattractive, short-tailed males becoming paired late. However, given that very attractive males are rare, we might expect males with short tails to breed relatively more synchronously than long-tailed ones. This was clearly not the case.

We conclude that the seeking of extra-pair fertilisations by a male barn swallow competes with guarding his own mate during her fertile period. Breeding synchrony enhances paternity possibly because synchrony reduces the number of males available for extra-pair copulations. The negative correlation between male tail ornament size and number of males available for extra-pair copulations may result from females mated to low-quality males breeding when their chances of being fertilised by high-quality extra-pair males are comparatively high.

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