

Short communications

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Low incidence of extra-pair paternity in the colonially nesting common swift

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The frequency of extra-pair paternity in a wild colony of swifts *Apus apus* was determined by multilocus DNA fingerprinting in two successive breeding seasons. The data were used to examine the expectation that extra-pair paternity is frequent in colonial-nesting species, either for proximal reasons such as the increased opportunity for extra-pair matings, or because extra-pair matings are important in the evolution and maintenance of coloniality. Forty-two broods containing 88 chicks were analysed. The genetic analysis revealed four cases of extra-pair paternity (4.5% of chicks) from four (9.5%) nests. Rapid mate-switching was considered unlikely to be the cause of extra-pair paternity since three of the cases were in the nests of previously established breeding pairs. Extra-pair copulations were not observed, but were assumed to be the cause of extra-pair paternity. The data show that high levels of extra-pair paternity are not an inevitable feature of high-density nesting.

In many socially monogamous bird species individuals pursue and obtain extra-pair fertilisations as an alternative reproductive strategy in addition to raising offspring within a monogamous pair (reviewed by Birkhead and Møller 1992). A variety of potential direct and indirect costs and benefits of extra-pair fertilisation could affect both sexes. The direct benefit to males is an increase in reproductive success; females may gain from accruing indirect genetic benefits in their offspring or by increasing the probability of fertilisation (reviewed by Westneat et al. 1990, Birkhead and Møller 1992). The incidence of extra-pair paternity will be influenced by ecological constraints limiting the opportunities for extra-pair copulations (Westneat et al. 1990) and the efficacy of anti-cuckoldry tactics by paired males (Trivers 1972), so the observed pattern of social association and actual mating relationships between the

sexes may be very different (Gowaty 1985). Nesting dispersion may be particularly important in determining the frequency of extra-pair copulations either because of the increased opportunity afforded by high nesting densities or because the males of colonial species may not be able to guard their mates because of having to forage well away from the colony for long periods (Birkhead and Møller 1992).

Colonial nesting occurs widely but unevenly across avian taxa (reviewed by Wittenberger and Hunt 1985, Siegel-Causey and Kharitonov 1991). Several advantages of high density nesting that may select for coloniality have been proposed, including reduction of predation risk (Hoogland and Sherman 1976) and increased foraging efficiency (Brown 1988). However, an understanding of the evolution and maintenance of coloniality in birds is not straightforward because of the potential costs involved, particularly resource competition and increased risk of parasite transmission (Alexander 1974). It has been suggested that extra-pair matings may be important in the evolution of coloniality (Wagner 1993). According to this argument, most females should benefit from seeking extra-pair copulations whereas most males should suffer net costs from them. A consequence of females of monogamous species seeking extra-pair copulations will be an aggregation of males and subsequent colony formation. Thus extra-pair copulations are seen as integral to the maintenance of coloniality rather than being a consequence of it.

The common swift *Apus apus* is a migratory aerial-feeding insectivore which pairs monogamously and frequently nests colonially. In this paper we use

multi-locus DNA fingerprinting to determine the incidence of extra-pair paternity in this species. In particular, we use these data to examine the expectation that a high incidence of extra-pair paternity occurs in colonial-nesting monogamous-pairing species, either as a consequence of high nesting density or because extra-pair matings are important for the maintenance of coloniality.

Methods

The study was carried out in 1991 and 1992 as part of a long term study (Martins and Wright 1993a, b, 1994, Martins 1997) using the established nest-box colony of swifts in the tower of the University Museum, Oxford, U.K. (Lack 1956). Birds arrive back at the breeding colony from wintering in Africa in early May; eggs (two or three) are laid two to three weeks later. Incubation lasts for three weeks and nestlings fledge approximately 40 days after hatching. Both incubation and feeding of nestlings is undertaken by both sexes. As adult swifts are very sensitive to disturbance and prone to deserting, parents were caught at night in their nest boxes whilst roosting but only when they had near-fledging chicks or after their chicks had just fledged. Alternatively they were caught during the day whilst feeding near-fledging chicks. Breeding females had been previously marked on the head with hydrogen peroxide using a long fine brush after being identified while laying the eggs (Malacarne and Griffa 1987). Both parents were subsequently given sex-specific colour rings. The identity of breeding birds was checked against records for the previous years. Blood samples were taken from nestlings and adults by brachial vein puncture. 50–300 μ l blood was removed and mixed with an equal volume of BLB buffer (250 mM EDTA, 5% SDS, 50 mM Tris pH 8.0) and stored at -20°C .

Parentage analysis was performed on a sample of 16 families of swifts from 1991 and 26 from 1992. This represented approximately from a third to half the pairs that attempted breeding in the tower in each year. The rest of the pairs were not sampled because nesting attempts were abandoned before sampling (27% of nesting attempts), or fingerprinting was not performed because both parents were not trapped, or the nests were used in an experimental manipulation. Protocol for blood storage and multilocus DNA profiling was based upon established methodology (Burke and Bruford 1987, Burke 1989, Birkhead et al. 1990, Bruford et al. 1992). Band sharing was scored for each individual using acetate overlays superimposed on the autoradiographs, bands were scored as homologous or not using Birkhead et al. (1990). The proportion of bands shared within a dyad was calculated as the band-sharing coefficient D according to Wetton et al. (1987). To detect

excluded parentage, offspring were first examined for the presence of novel bands, i.e. not present in either putative parent. Offspring with few novel bands consistent with being mutations were considered to be the putative parents' provided the band-sharing values were consistent with that expected for parents and offspring.

Parentage analysis from fingerprints was carried out by comparing the distributions of empirical band-sharing values between groups of assumed relatives and assumed non-relatives (Westneat 1990). For these statistical comparisons, each fingerprint was only compared to one other to avoid pseudo-replication. Therefore, when pairs of dyads from unrelated adults are compared with mated pair members those included in the first group are removed from the second and parent-offspring dyad comparisons have been done only when there was no overlap, i.e. within a pair, male would be paired with one chick and the female with another. So, in families of three chicks the last dyad was not included in the statistical analyses.

Results and discussion

The minisatellite probe 33.15 generated an average (\pm SD) of 19.4 ± 4.7 ($N = 176$; range 10–32) scoreable bands per individual in the size-range 3–15 kb in swift fingerprints. The average number of bands scored in adults and offspring were virtually identical (19.1 ± 4.9 and 19.6 ± 4.6 respectively), so there was no systematic tendency to score more bands of either age class. Band-sharing statistics (D) for different dyad comparisons are summarised in Table 1. The background level of band-sharing (i.e. that due to chance, not relatedness) was determined from dyads of assumed unrelated breeding adults ($n = 18$) run less than five lanes apart on gels. This was not significantly different from that of male-female mate-pairs ($n = 23$) ($t = 0.58$, $df = 39$, $P = 0.57$).

Table 1. Summary band-sharing statistics for independent pairwise comparisons (dyads) of swift fingerprints (one fingerprint compared with just one other). Values of band sharing coefficient D are shown as mean \pm SD of N comparisons.

Dyad comparison	D \pm S.D.	Range	N
Adult-Adult (non-mates) ¹	0.160 \pm 0.061	0.061–0.276	18
Male-Female (mate-pairs) ²	0.185 \pm 0.054	0.054–0.276	42
Adult-Adult (independent dyads) ³	0.166 \pm 0.057	0.054–0.276	41
Male-Offspring	0.552 \pm 0.084	0.400–0.686	31
Female-Offspring	0.563 \pm 0.064	0.400–0.667	31
Parent-offspring (no novel fragments)	0.557 \pm 0.075	0.400–0.686	62
Parent-Offspring (≤ 2 novel fragments)	0.577 \pm 0.101	0.410–0.764	18

¹ Unrelated breeding adults run less than five lanes apart on gels.

² Male-female mate-pairs.

³ Independent adult-adult dyads after combining ¹ and ², i.e. each adult appears in only one pair.

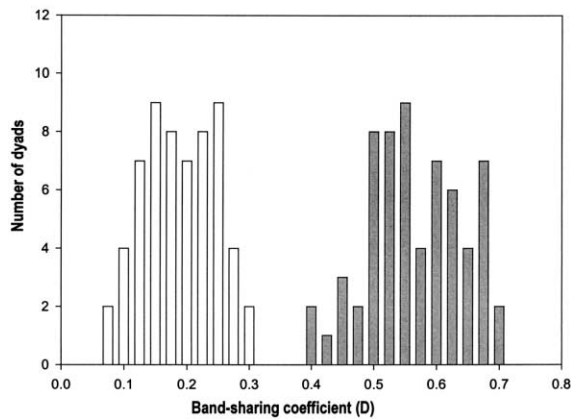


Fig. 1. Frequency distribution of the proportion of bands shared (D) between unrelated adults dyads (open bars) and parent-offspring dyads for offspring with no novel bands (solid bars).

This is not surprising given the very low return rate of fledglings to the natal colony (Perrins 1971), so breeding individuals in the colony are unlikely to be closely related. Values of D for mate-pairs and other unrelated adult dyads were therefore combined to give a background frequency distribution of D due to chance (Table 1).

The distribution of D for parent-offspring dyads was determined using offspring which had no novel bands. Male-offspring and female-offspring values of D were combined since they were not significantly different from each other and were independent (male-one chick (n = 31); female-another chick (n = 31)) ($t = -0.54$, $df = 60$, $P = 0.59$). The mean parent-offspring proportion of bands shared ($D = 0.557$) is slightly higher than 0.5; this is internally consistent with a background $D = 0.177$ since the parent-offspring band-sharing is expected to be $0.177 + [(1 - 0.177)/2] = 0.585$ (Pember-ton et al. 1992). Alternatively, assuming all bands are unlinked and are alleles of equal frequency, the mean allele frequency $q = 0.091$ ($D = 2q - q^2$; Jeffreys et al. 1985). The proportion of bands expected to be shared between parents and offspring is thus $(1 + q - q^2)/(2 - q) = 0.567$ (Burke et al. 1989), again agreeing closely with the empirical value from parent-offspring comparisons.

The mean values of background (unrelated adults, $n = 41$) and parent-offspring values of D ($n = 62$) are highly significantly different (Table 1; $t = -28.61$, $df = 101$, $P < 0.001$), and there is no overlap between their ranges or the 99% confidence limits of the distributions (background: 0.019–0.312; parent-offspring: 0.365–0.749, calculated as $\text{mean} \pm t^*SD$; Hartley et al. 1993). Hence empirical band-sharing values separate parent-offspring dyads from unrelated dyads (Fig. 1).

The frequency distribution of novel bands (i.e. bands present in offspring but not scored in either parent) in

offspring is shown in Fig. 2. Most offspring (62; 74%) did not have any novel bands, and these all had band-sharing values consistent with that expected for parent-offspring dyads (see above). A further 18 offspring (21.4%) had only one or two novel bands. The frequency of offspring with 0, 1, 2 novel bands does not differ significantly from a Poisson distribution (with $\mu = 0.262$; i.e. number of novel bands/number of offspring; $\chi^2 = 1.97$, $d.f. = 2$, $P > 0.25$) expected as a result of mutation events (Westneat 1990). This corresponds to a mutation rate of 0.013 mutations/band/generation, which is comparable with minisatellites of other avian species (e.g. 0.011 for indigo bunting *Passerina cyanea*, Westneat 1990; 0.004 for dunnocks *Prunella modularis*, Burke et al. 1989). Despite the presence of the novel bands, these offspring ($n = 18$) had a mean value of parent-offspring D with both putative parents (Table 1) which is not significantly different from parent-offspring D for offspring with no novel bands ($n = 62$) ($t = 0.91$, $df = 78$, $P = 0.37$), but very different from the unrelated band-sharing distribution ($n = 41$) ($t = 19.94$, $df = 57$, $P < 0.001$). We therefore conclude that the 84 offspring with no or few novel bands (one or two) were all descendent from their putative parents.

Based on the above analyses, we used a combination of two criteria to exclude parentage: (i) offspring have > 3 novel bands and (ii) a value of $D < 0.330$ with one of its putative parents. On this basis the four offspring with seven or eight novel bands all excluded their putative male parent (mean $D = 0.117$; range 0.059–0.222) but not their female parent (mean $D = 0.617$; range 0.593–0.650) from being their true genetic parents. A minimum of five non-maternal bands (m) were scored in each offspring, so the probability of false inclusion of an unrelated male as the genetic father is no greater than 1.5×10^{-4} (since the probability of an unrelated individual containing these bands by chance is Dm ; Burke et al. 1989). We conclude therefore that these four offspring were the result extra-pair fertilisa-

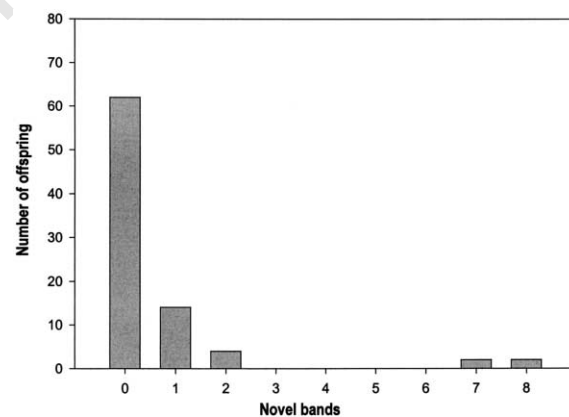


Fig. 2. Distribution of the number of novel bands present in multilocus DNA fingerprints of individual swift offspring.

tions and that no cases of egg-dumping were present. Thus, of a total of 88 offspring analysed, four (4.5%; 95% C.I. 1.3–11.2%) were sired by an extra-pair male. These four extra-pair offspring were distributed in four of 42 nests, one in 1991 and three in 1992, so 9.5% (95% C.I. 2.7–22.6%) of male swifts in the sample were cuckolded.

Our results show that the four extra-pair offspring detected by DNA fingerprinting were the result of extra-pair fertilisation (only male excluded) and not intra-specific brood parasitism (egg-dumping) where both parents are excluded, or quasi-parasitism (Wrege and Emlen 1987), where the putative female parent only is excluded. The data show that extra-pair paternity occurs in colonially-nesting swifts, but that its frequency is relatively low compared to many other monogamously-pairing species (reviewed by Birkhead and Møller 1992), both in terms of the number of males that are cuckolded and the proportion of chicks sired by extra-pair males.

Extra-pair paternity can arise by two means; either as the result of extra-pair copulations outside of the pair-bond, or by rapid mate-switching (Birkhead and Møller 1992). Rapid mate-switching has received rather little attention in birds, although the few species where it has been quantified are monogamous colonial nesters (Birkhead and Møller 1992) and it may lead to apparent extra-pair paternity (e.g. Pinxten et al. 1993). Apparent mate-switching has been recorded in swifts (Cutcliffe 1955). However, in the nests with extra-pair paternity, we have no indication of mate-switching having occurred as in three of the nests with extra-pair offspring the parents were paired in at least one previous breeding season, in the case of one pair for at least two breeding seasons. Given the long-term pair bonds in swifts (Weitnauer 1975), this suggests mate-switching has not occurred in these pairs. However, mate-switching cannot be completely excluded as the cause of extra-pair paternity in our study. If it did occur, then this would mean that extra-pair copulations are at an even lower frequency than that detected by DNA fingerprinting.

Extra-pair copulations should be a feature of high nesting density as opportunities are higher and mate-guarding too costly (Birkhead et al. 1987). High levels of extra-pair paternity have been detected in colonial breeders (e.g. 34.6% of offspring in purple martins *Progne subis*, Morton et al. 1990), however, it is not an inevitable feature of high-density nesting, and in some cases it may even occur at extremely low frequency (e.g. 0.0% in fulmar *Fulmarus glacialis*, Hunter et al. 1992; 1.0% in European bee-eater *Merops apiaster*; Jones et al. 1991).

There are several possible explanations as to why the frequency of extra-pair paternity is also low in colonial swifts. In swifts, copulation occurs primarily on the wing or in the nest cavity, since they are unable to

perch easily elsewhere. Both sexes are known to defend the nest site against conspecifics and the costs of entering an occupied nest site could be high as swifts can fight for a nest site until one or the other dies. However, recently it has been shown that male and female swifts have very distinctive calls (Kaiser 1997). This has very interesting behavioural implications as it means that when non-breeding birds fly past, “bang” outside nest sites and vocalise (Lack 1956), they are allowing the occupants not only to indicate their presence but also their sex. This means that this banging behaviour which happens just before egg-laying (Lack 1956) might offer females the opportunity to accept extra-pair copulations. Also, as copulations in swifts can take place on the wing (in this case only with female cooperation) opportunities for females to accept EPCs are available both in the colony and away from it. If there are opportunities for extra-pair copulations in swifts (Lack 1956), then why are extra-pair fertilisations not frequent?

Methods of paternity assurance other than mate-guarding behaviour may be effective in preventing extra-pair paternity. Males of colonial species can increase their certainty of paternity by copulating frequently (Birkhead et al. 1987), by inseminating last before fertilisation (Birkhead 1988) or by having high quality ejaculates (Møller 1994). The relative frequency of copulation in the nest cavity and on the wing in swifts is not known for certain. In the nest cavity copulation typically occurs 3 or 4 times in quick succession in the evening just prior to roosting and early in the morning before emergence (Lack 1956). This behaviour is consistent with males timing copulations to maximise their probability of fertilisation. Also, swifts have relatively large testes with respect to their body size (A. Møller pers. comm.), suggesting that copulation frequency and ejaculate quality may be used by males to increase their certainty of paternity (Møller 1994).

However, the relatively low frequency of extra-pair fertilisations in swifts could be simply because females have little to gain from them. For females, the most likely benefits of obtaining extra-pair copulations are indirect fitness benefits in their offspring (Kempnaers et al. 1992, Møller 1994, Hasselquist et al. 1996). In swifts, pair-bonds apparently have long-term stability, up to 12 yr (Weitnauer 1975) and both sexes share in incubation and provisioning the young (Lack and Lack 1951). If maintaining a long-term pair-bond has a higher fitness benefit to females than obtaining extra-pair fertilisations in one season (i.e. if seeking extra-pair copulations carries a risk of divorce) and the variance in male quality is low then females should rarely seek extra-pair copulations. The age of first breeding in swifts is usually 4 yr, although younger birds may be present in the museum colony and sometimes attempt to breed, but usually not successfully (Perrins 1971).

The fact that males rarely succeed in breeding before 4 yr of age suggests low variance in genetic quality in the colony's adult male breeding population. The museum colony could thus be a high quality breeding site where a non-random sample of high quality males nest, with low quality males breeding in smaller colonies or even solitarily. Hence females from solitary nests might seek extra-pair copulations from males in the colony, but not vice versa. This explanation requires a clear fitness benefit for breeding colonially, that high quality males preferentially nest colonially, and predicts that we should find a much higher incidence of extra-pair fertilisation in singly nesting birds. At present we have no data to test this hypothesis.

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