Low levels of extrapair paternity in the long-lived colonial Alpine swift (*Tachymarptis melba*)

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Abstract

It has been suggested that a high aerial lifestyle makes it difficult for males to limit mating opportunities for their partners. This would explain the particularly high levels of extra-pair paternity (EPP) observed in swallows and martins (Hirundinidae, Passeriformes). Here, we investigated EPP in the Alpine swift (*Tachymarptis melba*), whose aerial lifestyle is similar to that of the Hirundinidae, but which is a phylogenetically distinct taxon (Apodiformes). We found 9 cases of EEP in 9 broods out of 216 (4.2%) nestlings and 87 (10.3%) broods analysed. This low incidence of extra-pair paternities is similar to the only estimate reported so far in Apodiformes (i.e. 4.5% of nestlings in the common swift; *Apus apus*). We discuss the fact that the ecology (incubation of the clutch by both sexes in swifts versus female-only in swallows and martins) and life history (swifts are long-lived and can switch mate from one year to another), rather than aerial lifestyle, may explain the differences in EPP between swifts and swallows or martins.

Keywords: polygamy, sexual selection, extra-pair copulation,

Introduction

Almost a century ago, David Lack, a British pioneering researcher who bridged the fields of evolutionary biology and ornithology, suggested that most birds live in monogamous relationships, and therefore that extra-pair paternity is irrelevant (Lack, 1940). Since then, a wide range of molecular methods have become available and permit a reliable assessment of paternity (Jones & Wang, 2010). By now, more than 500 studies in over 300 species have reported the rate of extra-pair paternity (EPP). This has unveiled a broad range from 0% to 80% of offspring being sired by a different father than the observed father (i.e. the social father) (Brouwer & Griffith, 2019).

Explaining this variation is of great interest to ecologists and evolutionary biologists as males can potentially increase their fitness by EPP, which has far-reaching consequences for sexual selection and conflict between sexes (Brouwer & Griffith, 2019; Webster et al., 1995). Indeed, males can increase their reproductive success by engaging in extra-pair activity without having to pay the full costs of brood care. The benefits for females are often less obvious, and it remains debated what rate of EPP might be adaptive to them (Boulton et al., 2018; Forstmeier et al., 2014; Lifjeld et al., 2019).

To date, research on EPP in birds remains strongly taxonomically biased, with most of the information coming from Passeriform birds. Given the importance that certain behaviours and ecology of a species may have on EPP incidence, more studies on less-represented bird orders with unusual ecology are welcome (Brouwer & Griffith, 2019). Swifts, from the order Apodiformes, are well known for their extraordinary flying habits, spending most of their lives in the air, often landing only to raise their offspring (Hedenström et al., 2016; Liechti et al., 2013), which has fascinated ornithologists such as David Lack (Lack, 1956). Swifts have a similar ecology and aerial lifestyle as the Hirundinidae (swallows and martins), which are songbirds with high levels of EPP (Hasegawa & Arai, 2020; Møller & Birkhead, 1994). The high aerial lifestyle of Hirundinidae has been hypothesised to explain the high occurrence of EPP by making it difficult for a male to continuously monitor their fertile partner and to constrain mating opportunities (Møller & Birkhead, 1994); but see (Hasegawa & Arai, 2020) for an alternative explanation based on incubation behaviour). However, the one study quantifying EPP rate in the family Apodiformes has reported low rates of EPP in the common swift (*Apus apus*; 4.5% of nestlings being sired by a non-social father; (Martins et al., 2002).

The aim of this study is to broaden our knowledge on EPP in Apodiformes by investigating the incidence of EPP in the Alpine swift (*Tachymarptis melba*). We used microsatellite loci suitable to study EPP in swifts (Cibois et al., 2022) to analyse the probability of finding EEP in 93 broods of Alpine swifts sampled in two different colonies over up to three years.

Methods

Study system and data collection

Alpine swifts breed in colonies of a couple to hundreds of breeding pairs in cliffs or buildings in the Palearctic, Africa and southern Asia (Chantler et al., 2023). The European populations of Alpine swifts are migratory across the Sahara (Meier et al., 2020). They are long-lived, frequently reaching over 15 years of age (Moullec et al., 2023), and are faithful to their breeding colony and nest (Dumas et al., 2025). Females lay a single clutch per year, consisting of 1 to 4 eggs. Both parents incubate the clutch for 18 days and then feed their nestlings until fledging (> 50 days after hatching) with insects caught exclusively in the air (Masoero et al., 2024). There is cryptic sexual dimorphism, the sexes being indistinguishable to human observers, but the males nevertheless having a fork that is slightly (7%) longer than the females (Dumas et al., 2024).

Data were collected in two urban colonies in the Swiss town of Baden. These two colonies are located under the roofs of two historic buildings, Landvogteischloss (LVS; 47.47286°N, 8.31096°E) and Stadtturm (ST; 47.47322°N, 8.-30788°E), and have been monitored since 1991. Each year, nests were regularly visited to record the breeding parameters (e.g. clutch size, hatching date) and to ring nestlings 11 to 32 days after hatching. Social pedigrees were collected by capturing adults by hand while sitting on their nest during incubation or brooding young nestlings. Adults were ringed at their first capture if they had not already been ringed as nestlings.

To establish the genetic pedigree, we collected a drop of blood by puncturing a vein with a sterile hollow needle, sponged the blood with cellulose paper prepared in 0.5 M EDTA, and then air-dried the paper with blood before storing it at -40°C. In order to limit the possible consequences of haematoma following blood sampling, the blood was taken from a wing vein in the nestlings and from a foot vein in the adults, as the nestlings rely mainly on their feet to move around when they remain in the nest, whereas the adults rely heavily on their wings to forage. Adults were sampled independently of their breeding status when captured either before or after breeding during bi-annual night captures in early May and mid-August (Robinson et al., 2020). For this study, nestlings were blood sampled at the same time as they were ringed (11 to 32 days of age) in the years 2015, 2016, and 2017 at the colony LVS and in 2016 in the colony ST.

In total we sampled 229 nestlings in 93 nests, which accounted for 82% of all broods and 76% of all nestlings raised at the colonies in those years (Table 1). We sampled 190 adults present in these breeding colonies during the study period. We had genetic information on offspring and both parents for 207 nestlings from 83 broods, on offspring and their social mothers only for 13 nestlings from 6 nests, and on offspring and their social fathers only for 9 nestlings from 4 nests.

DNA extraction and genotyping

We extracted DNA from dry blood on the cellulose paper by punching three 2-mm diameter disks from the papers using 2 mm Harris Uni-Core hole punches (Sigma-Aldrich) into a 1.5 mL tube containing 220 µL PBS buffer (50 mM potassium phosphate, 150 mM NaCl, pH 7.2), 20 µL proteinase K and 200 µL AL buffer (Qiagen). Tubes were incubated for 1 h at 56°C before proceeding with DNA extraction (96-well plate) following the manufacturers recommendations (DNeasy Blood and Tissue Kit, Qiagen). DNA extractions were stored for 1–3 days at 4°C prior to PCR amplification.

All the samples were genotyped at nine microsatellite loci (Table 2) developed for swift species *(A. apus*, *A. pallidus*, *T. melba*) as described in (Cibois et al., 2022). We also used a CHDgene fragment to determine the sex of the individuals (Cayuela et al., 2019). PCR were set up in 10 µL reaction containing 1x Type-it Master Mix (Qiagen), 0.3–0.7 µM of each primer (Table 2) and 2 µL DNA, and with the following PCR conditions: 5 min at 95°C, 37 cycles of [30 s at 94°C, 2 min at 58°C and 45 s at 72°C], 15 min at 72°C. Samples were amplified in two independent PCR reactions to quantify the risk of genotyping errors (Miquel et al., 2006; Taberlet et al., 1996). PCR fragments were then mixed with an internal size standard (Orange Size Standard, MC Lab) and analysed by electrophoresis on a semi-automated DNA sequencer (ABI 3130, ThermoFisher). We used the program GENEMARKER (SoftGenetics) to determine the size of the PCR fragments and record the allele combination at each locus. Despite of high-quality and quantity DNA templates, we failed to amplify 76 alleles Interestingly, 74 of the amplification failures involved nestlings, indicating that factors other than DNA quality and quantity can lead to allelic dropout and non-amplification of the target fragment (Soulsbury et al., 2007).

Paternity analyses

Parentage assignment were performed with Cervus Version 3.0.7 using maximum likelihood methods (Kalinowski et al., 2007). All nine microsatellite loci were polymorphic, with number of alleles ranging from 4 (T06) to 18 (T14) (mean = 11.1 alleles) (Table 2). Observed heterozygosity ranged from Ho = 0.057 (T06) to Ho = 0.905 (T14), which suggests that inbreeding is uncommon in the species (Table 2). The combined probability of exclusion for their genetic parents of all loci was > 99.999%.

Results

A total of 207 nestlings from 83 broods had complete information for both of their social parents. Nine of these nestlings, from 9 different broods, were not genetically related to their social fathers, and therefore considered to be the result of extra-pair copulations (EPC). We also found 2 cases where nestlings did not genetically match either their social father or their social mother. The parentage analysis indicates that, in both cases, the nestling came from a neighbouring brood, thus suggesting that it had most likely switched nest before being uniquely identified with a ring and blood sampled (Bize & Roulin, 2006; Bize et al., 2003). All the other 205 nestlings were genetic offspring of their social mothers. Furthermore, none of the 9 nestlings from 4 broods with only information on their social father were considered the result of EPC; all the 13 nestlings from 6 broods with only information on their social mother were genetically associated with their mothers. Hence, altogether it indicates that extra-pair paternities (EPP) occur in 4.2% of the nestlings and 10.3% of the broods (i.e. 9 of 216 nestlings, and 9 of 87 broods, with information on social father identity). Those 9 EPP nestlings were from 9 different mothers mating with 9 different social fathers.

Discussion

Although swifts (Apodiformes) have an aerial lifestyle similar to that of swallows and martins (Passeriformes, Hirundinidae; both taxa are migratory, breed in colonies and feed on aerial insects), and this lifestyle has been hypothesised to explain the high levels of extra-pair paternity (EPP) observed in Hirundinidae (Brouwer & Griffith, 2019; Lifjeld et al., 2019; Møller & Birkhead, 1994), we found no support for this hypothesis in swifts. Indeed, our results show an EPP rate of 4.2% in 216 nestling Alpine swifts (10.3% of 87 broods). This is very similar to the only estimate of EEP reported to date in Apodiformes by (Martins et al., 2002), with a rate of 4.5% of EEP found in 88 nestling common swifts (9.5% of 42 broods).

In a recent phylogenetic comparative analysis on sexual selection in swallows and martins, (Hasegawa & Arai, 2022) highlighted that incubation behaviour is likely an important driver of the evolution of sexual dimorphism and extra-pair copulation in Hirundinidae, as species with biparental incubation are more likely to be sexually monomorphic and to have lower rates of EPP compared to species with female-only incubation. Indeed, in species with biparental incubation, time constraints may limit the opportunities for males to seek extra-pair copulations (Lifjeld et al., 2019; Magrath & Komdeur, 2003). Selection may also act on females if soliciting extra-pair copulations may favour the evolutionary loss of male participation in incubation (Kokko & Jennions, 2008). Alpine and common swifts show biparental incubation, which supports the alternative hypothesis that incubation behaviour rather than aerial lifestyle could, at least in part, explain the lower rates of EPP observed in these species. An additional factor to explain the lower incidence of EPP in Alpine and common swifts when compared to Hirundinidae is that swifts live longer. A long lifespan may allow individuals to divorce and mate with different partners during their lives, which can provide an alternative to EPP (Lifjeld et al., 2019; Warrington et al., 2015). For example, Alpine swifts have a median lifespan of approximately 7 years, around 16.6% of pairs divorce each year, and individuals who divorce do so between 1 and 5 times throughout their lives (Dumas et al., 2025).

Alpine swifts often build their nests in proximity (< 50 cm), and up to 27% of the nestlings were reported to switch nests from 15 days after hatching onward and seek adoption in neighbouring nests (Bize & Roulin, 2006; Bize et al., 2003). Nestling Alpine swifts have a long development period (> 50 days) for their body size (about 100 grams), and they rely entirely on parental care for their development (Masoero et al., 2024). The frequent occurrence of adoption in colonial bird species (Riedman, 1982), like seen in the Alpine swift, has been hypothesized to evolve as an offspring strategy to obtain more resources or find better rearing conditions in foster nests when compared to their natal nest (Bize et al., 2003; Pierotti, 1991). In our study, we found two nestlings that were unrelated to their observed social parents and paternity analyses assigned them to a neighbouring brood. These nestlings were 22 and 27 days of age at ringing, and there was unambiguous evidence for at least one nestling that it had switched nests before ringing (i.e. increase in brood size after hatching). An alternative hypothesis for nestlings being unrelated to their observed social parents is the occurrence of egg parasitism (Lyon & Eadie, 2008). Although there is no evidence of such behaviour in our colonies on the basis of the record of egg-laying sequences over the last 25 years (PB, pers. obs.), paternity analyses using blood taken at the time of hatching are still necessary to formally exclude this hypothesis. We recommend that, in order to assign nestlings appropriately to their social parents in colonial birds where nests are close together, nestlings should ideally be ringed before they are old enough to change nests, i.e. no later than 20 days in the Alpine swift (Bize & Roulin, 2006).

In conclusion, our study shows that the incidence of EPP is low in Alpine swifts. We suggest that biparental incubation behaviour and their long lifespan are the most likely evolutionary factors explaining these low rates of EPP, in line with a recent meta-analysis on this topic in birds (Lifjeld et al., 2019). The role of adaptive or non-adaptive selection pressures on males and/or females in explaining EPP in Alpine swifts remains an open question (Boulton et al., 2018; Forstmeier et al., 2014), which will require larger sample sizes (i.e. more than 9 EPP cases) to be adequately addressed.

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Permits. All work was conducted in accordance with international standards on animal welfare and in compliance with national regulations: ringing permit were delivered by the Swiss Federal Office for the Environment and blood sampling authorised by the Swiss Veterinary Services.

Author contributions

CMM, GJ and PB designed the study, CMM, MB CS and AS collected the data, GJ performed the laboratory work, CMM, GM, PB and GJ analyzed the data, CMM and PB wrote the first draft and all authors commented on the manuscript.

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Table 1. Overview of the number (%) of nests and nestlings sampled for each colony and year for an analysis of parentage and extrapair paternity (EPP) in the Alpine swift.

Colony	Year	N active nests	N (%) sampled families	N nestlings	N (%) genotyped nestlings	N nests with ID of both parents	N nests with only father ID	N nests with only mother ID	EPP nestlings
LVS	2015	33	32 (97%)	94	79 (84%)	28	2	2	3
LVS	2016	31	31 (100%)	77	73 (95%)	29	1	1	2
LVS	2017	37	18 (49%)	99	44 (47%)	14	1	3	2
ST	2016	12	12 (100%)	33	33 (100%)	12	0	0	2
Total		113	93 (82%)	303	229 (76%)	83	4	6	9

Table 2. List of amplified markers and estimates of genetic diversity based on nine microsatellites loci in the Alpine swift. For each locus, we indicate F- and R- sequences and the final concentration of each primer (*µM*); N_{indiv}, number of individuals analysed; allele size range in base pairs (bp); N_A, number of alleles; H_0, observed heterozygosity; H_e, expected heterozygosity; PIC, polymorphic information content; Excl 1, probabilities of exclusion based either on the genotype of no parent known; Excl 2, genotype of one parent known; *F* (Null), frequency of null alleles. None of these loci significantly deviated from Hardy-Weinberg expectation (HWE; NS: non-significant, ND: not done). Mean diversity figures and total exclusionary probabilities over the 9 loci are given in the last row. All calculations were performed using the program CERVUS 3.0.7

Locus	*Sequences (5'–3')*	*µM*	N_{indiv}	*Size range (bp)*	N_A	H_o	H_e	*PIC*	*Excl 1*	*Excl 2*	*F (Null)*	*HWE*
T05	F: NED-GCAGAAGGTGTGGATGGAGT R: GGTGCTTCCCAACCCTAACA	0.6	419	141-169	10	0.811	0.828	0.808	0.494	0.846	0.0105	NS
T06	F: VIC-GGCTTTTATCCTTTGCTACTCGT R: CATGGTGATGTGCGTGCTC	0.4	419	121-129	4	0.057	0.058	0.057	0.002	0.057	0.0246	ND
T08	F: NED-CACATCTTAAGTGAGTGCTCTGA R: TCACTGTCCAAAGGCTCTCA	0.5	419	191-223	12	0.826	0.826	0.804	0.486	0.836	0.0010	NS
T10	F: FAM-ACTGATTTTGGGCTTTTCTCTCA R: TGAAGTGCTCAAAATCTACCTGT	0.7	412	235-267	13	0.796	0.843	0.823	0.520	0.859	0.0291	NS
T12	F: VIC-CTGCAGAAGTGGCAGTTGTT R: GCAACACCATCAAACCTCAGT	0.4	419	213-241	12	0.802	0.815	0.789	0.459	0.813	0.0077	NS
T14	F: PET-ACATCCCACAGGTAGGTCTT R: AGGCTCTGATTCCCGAATGA	0.5	419	240-296	18	0.905	0.909	0.901	0.689	0.946	0.0014	NS
T15	F: FAM-AGTGCCCTGATCTGATACTTGT R: TCAGCCAATAGTTGTCAAATCCT	0.6	419	184-204	8	0.561	0.599	0.564	0.208	0.580	0.0215	NS
T16	F: PET-ACAGAGGTGGTAGGATGTTAGA R: TCACCTGATTTGGCTGAATTTTC	0.5	388	124-152	7	0.701	0.695	0.643	0.280	0.631	-0.0072	NS
T17	F: FAM-AGGGTACTGTGGACATAGAGAT R: TGAGCATGGAAACTGAGTTGAG	0.6	419	99-139	16	0.864	0.883	0.871	0.617	0.915	0.0093	NS
Mean						0.703	0.717	0.696	0.417	0.720		
Total									0.9954	0.9998		