Low levels of extra-pair 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 several species of swallows and martins (Hirundinidae, Passeriformes), but EPP in the other bird lineages with a high aerial lifestyle, such as swifts (Apodiformes), is largely unknown. Here, we investigated EPP in the Alpine swift (*Tachymarptis melba*). We found 9 cases of EPP in 9 broods out of 214 (4.2%) nestlings and 87 (10.3%) broods analysed with information on fathers. 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 suggest that life-history traits (biparental incubation, long lifespan, and frequent mate retention across years), rather than their aerial lifestyle, may explain the low incidence of EPP in swifts.

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

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 or songbirds. 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 in several species (Hasegawa & Arai, 2020; Møller & Birkhead, 1994). For example, rates of EPP were found to range from 7 to 56% of offspring produced as the result of extra-pair behaviour among 5 species of New World *Tachycineta* swallows (Ferretti et al. 2019). It has been suggested that the high aerial lifestyle and the breeding asynchrony of Hirundinidae may favour 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; Morton et al., 1990; but see Hasegawa & Arai, 2020 for an alternative explanation based on incubation behaviour). However, the only study quantifying EPP rate in the family Apodiformes reported low EPP in the common swift (*Apus apus*; 4.5% of nestlings sired

by a non-social father (Martins et al., 2002)), which is inconsistent with the idea that an aerial life history may favour high EPP rates.

The aim of this study is to broaden our knowledge of EPP in Apodiformes by investigating the incidence of EPP in the Alpine swift (*Tachymarptis melba*). We used a set of nine microsatellite loci to reconstruct parent–offspring trios (Cibois et al., 2022) and quantify EPP in 93 broods of Alpine swifts sampled over up to three years in two different urban colonies. While both Alpine and common swifts exhibit very similar breeding ecologies (colonial nesting with biparental incubation and nestling care), Alpine swifts often live in denser colonies, where they share the same cavity entrances and thus nest close to each other (up to less than 50 cm apart). In contrast, common swifts defend their cavity entrances and do not nest next to each other. Hence, whether Alpine and common swifts show similarly low levels of EPP remains to be tested.

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., 2025a). 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 have a fork that is slightly (7%) longer than the females (Dumas et al., 2025b).

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, both colonies were visited at least once a week 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. 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. In some broods, only one parent was identified: for 9 nestlings from 4 nests we had genetic data for offspring and their social fathers only, and for 13 nestlings from 6 nests we had genetic data for offspring and their social mothers only.

DNA extraction and genotyping

We extracted DNA from dry blood on the cellulose paper by punching three 2-mm diameter disks from the paper 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 manufacturer's recommendations (DNeasy Blood and Tissue Kit, Qiagen). DNA extractions were stored for 1–3 days at 4°C prior to PCR amplification.

All samples were genotyped at nine microsatellite loci (Table 1) developed for swift species *(A. apus*, *A. pallidus*, *T. melba*) as described by 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 1) 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 the high quality and quantity of DNA templates, we were unable to amplify 76 alleles. 74 of the amplification failures involved nestlings, indicating that factors other than DNA quality and quantity may lead to allelic dropout and prevent 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 1). 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%.

Preliminary analyses identified two cases from two different broods in which nestlings did not genetically match both social parents. In both cases, parentage analysis assigned the nestlings to the parents of a neighbouring brood, indicating that they had most likely switched nests before being uniquely identified with a ring and blood sampled. Alpine swifts can build their nests in close proximity (< 50 cm), and up to 27% of nestlings have been reported to switch nests from 15 days after hatching onward and seek adoption in neighbouring nests (Bize & Roulin, 2006; Bize et al., 2003). Accordingly, these two individuals were aged 22 and 27 days at ringing, and there was unambiguous evidence for at least one of them that it had switched nests before ringing, as shown by an increase in brood size after hatching. We discarded these two nestlings from our paternity analyses.

Statistical analyses

We tested for differences in EPP rates among years and colonies using Fisher's exact tests in R v.4.4.2 (R Core Team, 2024).

Results

When focusing on the 214 nestlings and 87 broods with information of social fathers, we found that 9 nestlings from 9 different broods were not genetically related to their social fathers and were therefore classified as extra-pair offspring resulting from extra-pair copulations (Table 2). In contrast, among the 218 nestlings and 89 broods with social-mother data, all nestlings were

genetic offspring of their social mothers. All the 9 EPP nestlings were from 9 different mothers mating with 9 different social fathers. There were no differences in EPP rates among years at colony LVS (2015: 3.95%; 2016: 2.90%; 2017: 5.56%; fisher exact test: $p = 0.785$) or between colonies LVS and ST in 2016 (LVS: 2.90%; ST: 6.06%; fisher exact test: $p = 0.467$).

Discussion

In the present study, we report a low level of EPP in Alpine swift (4.2% of 214 nestlings; 10.3% of 87 broods), very similar to the only estimate of EPP reported to date in another Apodiformes species (i.e. common swift, 4.5% of nestlings (Martins et al., 2002)). Swifts (Apodiformes) and swallows and martins (Passeriformes: Hirundinidae) share a similar ecology: they are aerial insectivores that often breed colonially and are long-distance migrants in temperate-zone populations. However, Apodiformes (Martins et al., 2002, this study) and Hirundinidae (Brouwer & Griffith, 2019; Ferretti et al., 2019; Lifjeld et al., 2019; Møller & Birkhead, 1994) largely differ in their level of extra-pair paternity (EPP), with up to 87% of nests with EPP nestlings in some species of Hirundinidae. This undermines the hypothesis that aerial lifestyle alone drives levels of EPP in these taxa.

In a recent phylogenetic comparative analysis on sexual selection in swallows and martins (Hasegawa & Arai, 2022) highlighted that incubation behaviour is a potential 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. Mean rate of EPP was 41.3% of nestlings in five species with female-only incubation and decreased to 11.7% in five species with biparental incubation (Hasegawa & Arai, 2022). 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 swifts and species of the Hirundinidae with biparental incubation.

However, an additional factor to explain the lower incidence of EPP in Alpine and common swifts (4.4% of nestlings) when compared to species of Hirundinidae with biparental incubation

(11.7% of nestlings (Hasegawa & Arai, 2022)) is that swifts live longer. Maximum lifespan of Alpine swifts is 26 years and of common swifts is 21.1 years (de Magalhães et al., 2024), whereas maximum lifespan of Hirundinidae species with biparental incubation included in Hasegawa & Arai (2022) range from 5.3 years for the fairy martin (*Hirundo ariel*) to 15 years for the western house martin (*Delichon urbicum*) (de Magalhães et al., 2024). As pointed out by Martins et al. (2002), this high longevity in swifts often also comes with long-term stability in pair bonds, and females may favour the retention of their mate, if maintaining a long-term pair-bond has a higher fitness benefit than obtaining extra-pair fertilisations in one season and risking a divorce. In the Alpine swift, 16.6% of Alpine swift pairs divorce each year, and individuals with a low reproductive success and of young age are more likely to divorce (Dumas et al., 2025a). Because repeatabililty of divorce in the Alpine swift was found to be moderate in females (10.8%) and low in males (2.3%), it was suggested that females may be more likely than males to switch mates (divorce) to potentially improve their fitness (Dumas et al., 2025a). The role of adaptive or non-adaptive selection pressures on females and/or males in explaining EPP in Alpine swifts remains an open question (Boulton et al., 2018; Forstmeier et al., 2014), which will require larger sample sizes to adequately address the importance, for example, of male and female age in shaping EPP and the links between EPP, divorce and reproductive success.

As Martins et al. (2002) noted, the high longevity of swifts is often associated with stable pair bonds, and females may therefore favour retaining a mate if maintaining a long-term pair bond yields greater fitness benefits than obtaining extra-pair fertilizations in a single season and risking divorce. In Alpine swifts, 16.6% of pairs divorce each year, and individuals with low reproductive success and younger age are more likely to divorce (Dumas et al., 2025a). Because the repeatability of divorce in Alpine swifts is moderate in females (10.8%) and low in males (2.3%), it has been suggested that females may be more likely than males to switch mates to potentially improve fitness (Dumas et al., 2025a). The role of adaptive or non-adaptive selection pressures on females and/or males in explaining extra-pair paternity (Boulton et al., 2018; Forstmeier et al., 2014) remains, however, to be addressed in detail in the Alpine swift. Larger sample sizes (i.e. more than 9 EPP cases) will be needed to assess, for example, the importance of male and female age in shaping extra-pair paternity and its links with divorce and reproductive success.

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).

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Table 1. 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		

Table 2. Overview of the number (%) of nests and nestlings sampled for each colony and year for an analysis of male parentage and extrapair paternity (EPP) in the Alpine swift. Data were collected in two urban colonies in Baden, Switzerland: (Landvogteischloss (LVS; 47.47286°N, 8.31096°E) and Stadtturm (ST; 47.47322°N, 8.30788°E).

Colony	Year	N active nests	N nestlings	N (%) sampled families with father ID		N (%) genotyped nestlings with father ID		N (%) EPP nestlings	
LVS	2015	33	94	30	(91%)	76	(81%)	3	(3.95%)
LVS	2016	31	76	30	(97%)	69	(90%)	2	(2.90%)
LVS	2017	37	98	15	(41%)	36	(37%)	2	(5.56%)
ST	2016	12	33	12	(100%)	33	(100%)	2	(6.06%)
Total		113	301	87	(77%)	214	(72%)	9	(4.17%)