Effects of parental age at conception on offspring life history trajectories in a long-lived bird

Héloïse Moullec[1], Vérane Berger[1], Christoph Meier[3], Sophie Reichert[1,2*], Pierre Bize[3*]

*shared senior-authorship

[1] Department of Biology, University of Turku, Finland

[2] Institut pluridisciplinaire Hubert Curien (IPHC), Strasbourg, France

[3] Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[1]Correspondence: heloise.moullec@utu.fi

ABSTRACT

Parental age at conception can have both short- and long-term consequences on the health, survival, and reproduction of their offspring. To date, most of our knowledge comes from laboratory studies, and considers the effects of maternal age and a "snapshot" of the life history trajectory of the offspring. Here, we use a multigenerational demographic dataset in a free-living, long-lived (median lifespan is 7 years old) bird, the Alpine swift (*Tachymarptis melba*), to investigate the effects of maternal and paternal age on offspring traits, from nestling to adulthood, and considering all major life history traits, from growth and age at first reproduction to reproductive success and lifespan. Parental age affected offspring phenotype before fledging and lifespan, but differently so for sons and daughters. Offspring from old-age mothers (≥ 11 years old) and fathers (≥ 9 years old) were bigger and less infested by ectoparasites before fledging, except sons from old-age fathers that show no reduction in ectoparasite load. We also report evidence of negative effects of paternal age on the lifespan of their offspring (i.e. Lansing

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

© The Author(s) 2025. Published by Oxford University Press on behalf of The Society for the Study of Evolution (SSE). This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

effect), with sons (but not daughters) from old-age fathers having shorter lifespans. Our findings highlight the importance of the transgenerational effects of parental age at conception on the reproductive performance, survival and phenotype of their offspring.

Keywords

Ageing, life-history, intergenerational effects, lifespan, parasite, maternal age, paternal age, senescence, Alpine swift.

TEASER TEXT

Does reproducing at an older age have an impact on offspring life-history trajectories and fitness? In this study, we investigate the effect of parental age on early-life condition and later-life fitness of offspring in a long-lived bird, the Alpine swift. More precisely, we describe the consequences of having older parents on offspring mass, size and ectoparasite load before fledging, as well as on offspring age at first reproduction, lifespan, and lifetime reproductive success.

1 | INTRODUCTION

Parents can influence the phenotype of their offspring through genetic and non-genetic factors (Mousseau & Fox, 1998; Smiseth, 2019; Wolf & Brodie, 1998). Insights on non-genetic factors are essential for an in-depth understanding of the evolutionary trajectory of phenotypes and how they are shaped. For instance, parental age has been found to be a key driver of offspring phenotype and was first studied in humans by Bell (1918) who found that children born from older parents are shorter lived. Later called the Lansing effect (Lansing, 1947), this negative effect of being born from older parents on offspring's lifespan, and more recently evidenced in other offspring traits, such as survival or reproduction, has been highlighted in

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

several human populations (Arslan et al., 2017; Gillespie et al., 2013; Wen et al., 2023) as well as in laboratory animals (Benton et al., 2008; Fox et al., 2003; Hercus & Hoffmann, 2000; Kern et al., 2001; Monaghan et al., 2020; Priest et al., 2002; Wang & vom Saal, 2000). Investigating the effects of parental age on fitness-related traits in offspring is important not only to understand the evolution of animal life histories, and in particular inter-individual variation in the rates of aging, but also to gain original insights on population dynamics via changes in offspring (demographic) traits such as survival and reproductive performance, which may have important implications for animal conservation (Benton et al., 2008; Monaghan et al., 2020; Priest et al., 2002).

Effects of parental age at conception are increasingly studied in natural populations (reviewed in Fay et al., 2016). However, no general pattern has emerged from the results. Some studies found a negative effect of having old parents on offspring survival or lifespan, such as in the Asian elephant (*Elephas maximus;* Reichert et al., 2020), Common tern (*Sterna hirundo*; Bouwhuis et al., 2015), Red-billed chough (*Pyrrhocorax pyrrhocorax*; Reid et al., 2010), Red deer (*Cervus elaphus*; Clutton-Brock et al., 1987; Nussey et al., 2009), Red squirrel (*Tamiasciurus hudsonicus*; Descamps et al., 2008), Rhesus macaque (*Macaca mulatta;* Hoffman et al., 2010), Wandering albatross (*Diomedea exulans;* Fay et al., 2016), and Yellow-bellied marmot (*Marmota flaviventer*; Kroeger et al., 2020); or a negative effect of parental age at conception on offspring reproductive success, such as in the Blue footed boobie (*Sula nebouxii*; Torres et al., 2011), Common tern (Bouwhuis et al., 2015), European rabbit (*Oryctolagus cuniculus L.*; Rödel et al., 2009), House sparrow (*Passer domesticus*; Schroeder et al., 2015), and Weddell seal (*Leptonychotes weddellii;* Hadley et al., 2007). Conversely, other studies found a positive effect of parental age at conception on offspring survival, such as in the European rabbit (Rödel et al., 2009), Herring Gull (*Larus argentatus*; Bogdanova et al., 2007), and Weddell seal (Hadley et al., 2007), as well as on offspring reproductive success,

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

such as in the Asian elephant (Reichert et al., 2020) and Yellow-bellied marmot (Kroeger et al., 2020). In a recent meta-analysis of the Lansing effect in 22 studies distributed across 15 species, including laboratory invertebrates (15 studies) and birds (1), mammals (5) and invertebrates (1) in natural environment, maternal age was found to account for 17–22% of the decrease in offspring lifespan (Ivimey-Cook et al., 2023). However, this negative effect of maternal age on offspring lifespan appears to be mainly driven by studies in rotifers and insects, whereas no significant negative effect was apparent in mammalian species (mostly humans) (Ivimey-Cook et al., 2023). A similar meta-analysis of maternal age effect on juvenile survival found negative effects in invertebrates and mammals, but a positive effect in birds (Ivimey-Cook & Moorad, 2020).

Furthermore, despite an increasing number of studies investigating parental age effects on wild populations, most studies, especially on mammals, are restricted to the effect of the age of the mother (Fay et al., 2016) due to the greater complexity of assessing male reproductive success in the wild. The effects of the age of the father can, however, differ from the effects of the age of the mother, especially when considering also the sex of their offspring (Fay et al., 2016). Sex-specific effects of parental age at conception on sons and daughters might arise from differences in male and female sensitivity and response to environmental conditions early in life (Jones et al., 2009; Lindström, 1999; Wilkin & Sheldon, 2009), or from sex-specifically inherited epigenetic alterations, as more recently highlighted (Monaghan & Metcalfe, 2019). Therefore, we need to look at both parents and their effects on sons and daughters to gain an exhaustive evaluation of parental effects on offspring.

Finally, most of the studies carried out to date are also cross-sectional (Monaghan et al., 2020) and focus on only a small part of their offspring's lives. Rare are the studies investigating the effects of parental age with longitudinal data (Bouwhuis et al., 2010, 2015; Kroeger et al., 2020; Reichert et al., 2020; Rödel et al., 2009; Schroeder et al., 2015; Sparks et al., 2022) among

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

which only three investigated the effects of both maternal and paternal age on male and female offspring (Bouwhuis et al., 2015; Schroeder et al., 2015; Sparks et al., 2022). Such longitudinal data requires long-term, individually based monitoring of a population to report the survival and reproduction of individuals throughout their lives and to know the identity of both their parents. The time and economic constraints associated with obtaining such long-term datasets make these studies rare but highly valuable (Clutton-Brock & Sheldon, 2010). As such, studies on long-lived species are also scarce, despite being essential for gaining a full understanding of parental age effects. According to the fast-slow continuum of life histories (Stearns, 1977; Stott et al., 2024), long-lived species would produce fewer offspring, which are more dependent on their parental investment early in life. Species' pace of life may therefore influence the intensity of parental age effects on offspring phenotype and life-history trajectories, hence the need for more studies exploring this question in long-lived species. In addition, the variation of the phenotypic composition of a population, for example, the selective appearance or disappearance of low-quality individuals in the population, can prevent the detection of parental age effects (Nussey et al., 2008; van de Pol et al., 2006). Indeed, if there is selective disappearance (van de Pol et al., 2006; Vaupel et al., 1979), parents of lower quality and producing shorter-living offspring would die at a younger age, and the remaining longer-surviving parents would be of better quality and produce many longer-living offspring. This demographic process may mask the probability of detecting a Lansing effect in the population. Therefore, we still need more studies on natural populations investigating the effect of parental age while controlling for selective disappearance (see Bouwhuis et al., 2015; Reichert et al., 2020; Sparks et al., 2022).

In this study, we examined the effects of both maternal and paternal age at conception on the age at first reproduction (AFR), lifespan, and lifetime reproductive success (LRS) of their offspring in a long-lived bird, the Alpine swift (*Tachymarptis melba).* We also investigated

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

the influence of the age of the parents on the phenotype of their offspring early in life, as the long-term effects of parental age at conception may be mediated by changes in early growth conditions (Hamel et al., 2009; Lindström, 1999). Accordingly, there is accumulating evidence of negative effects of parental age on offspring phenotype early in life, such as body mass and size just before independence (Bowen et al., 2006; Hamel et al., 2012; Hoffman et al., 2010; Nussey et al., 2009; Saino et al., 2002; Weladji et al., 2002), which can have long-lasting consequences on offspring's future survival and reproductive success (Douhard et al., 2014; Festa-Bianchet et al., 2000; Martínez-Padilla et al., 2017; Vasilieva & Tchabovsky, 2020). We tested for effects of parental age at conception on offspring body mass, body size (wing, tail, and sternum length) and ectoparasite load at 50 days after hatching, which is close to fledging (Masoero et al., 2024). Alpine swifts are infested by blood-sucking hippoboscid louse-flies that impact their growth and survival (Bize et al., 2003). The resistance of Alpine swift nestlings to this ectoparasitic fly depends, at least in part, on their cutaneous immune response (Bize et al., 2008). We therefore used the ectoparasite load of the offspring as a proxy of their immune response, which has been shown in previous studies to be influenced by maternal age (Beamonte-Barrientos et al., 2010; Saino et al., 2002). By taking advantage of long-term monitoring of three Alpine swift colonies, we investigated the effects of parental age at conception on a total of 366 to 420 individuals for life history traits in adulthood (AFR, lifespan, LRS), and from 185 to 201 individuals for phenotypic traits before fledging. It has previously been reported that the Alpine swift shows senescence in several phenotypic and fitness traits, with stronger reproductive senescence for females (Moullec et al., 2023). We therefore hypothesized a negative impact of parental age on offspring fitness, with a particularly pronounced negative effect of maternal age. In the Alpine swift, selection favors birds that start reproducing early and can reproduce until old age, with an increase in LRS as the number of reproductive years and, therefore, lifespan, increases (Tettamanti et al., 2012). Hence, we

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

predicted that the negative impact of older parents on their offspring could manifest itself in an older age at first reproduction, shorter lifespan, and reduced reproductive success throughout life. We also predicted that the negative effects of parental age at conception would already be noticeable on their offspring phenotype before fledging, shown by a lighter mass, smaller size, and higher ectoparasite load in offspring from older parents.

2 | MATERIAL AND METHODS

Study system

The Alpine swift is a long-lived bird, with a median lifespan of 7 years, and with the oldest individual recorded being 26 years old. Individuals start breeding at 2 to 4 years of age (Tettamanti et al., 2012), and morphological and fitness traits were shown to vary with age, with an improvement in the first years after the start of breeding, followed by a plateau and then senescence after 9 to 15 years of age (Moullec et al., 2023). In Switzerland, this migratory bird returns from migration in April and reproduces between May and August in colonies located in cliffs or tall buildings before migrating back in September to the western part of Africa for the winter (Meier et al., 2020). Assortative mating concerning age is moderate in this population (Pearson r = 0.24), and although Alpine swifts are considered socially monogamous, the rate of divorce is high (16.6% of pairs; Dumas et al., 2025). Females produce one clutch per year of 1 to 4 eggs (modal clutch size is 3). Both parents incubate the eggs for around 18 days and feed their nestlings for at least 50 days, until they fledge. In this population, more than half of the fledglings are recruited locally (i.e., low natal dispersal), and no breeding dispersal is observed (Bize et al., 2017). Thus, detailed individual information can be collected from the nestling stage to the full adult life history trajectory (e.g. Dumas, St. Lawrence, et al., 2024; Moullec et al., 2023).

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

For the present study, we used data from 4 urban colonies of Alpine swifts located under the roof of four buildings in 3 different Swiss cities: Baden (Stadturm: ST, Landvogteischloss: LVS), Biel (Stadtkirche: SK), and Solothurn (Bieltor: BT). Although nestlings have been ringed each year since 1932 in Solothurn, 1968 in Biel, and 1991 in Baden, data used in the analyses are from intensive individual-based monitoring of adults and their reproductive success initiated in 1991 in Baden, 1999 in Solothurn, and 2000 in Biel, and still ongoing in 2025. Hence, every bird is identified with a unique ring fitted at the nestling stage, or when first captured as an adult if the bird has not been ringed yet (ca. 30% of the individuals in the population). Over the past 2 decades, there were ca 15 breeding pairs per year in Baden ST, 35 in Baden LVS, 65 in Biel SK, and 50 in Solothurn BT. Each year, nests are regularly controlled during the breeding season to record reproductive parameters from laying date to brood size at fledging. Parents are assigned to a nest by capturing them by hand during incubation or while brooding nestlings. As adult Alpine swifts appear sexually monomorphic to human observers (Dumas, Bize, et al., 2024), parents were molecularly sexed using DNA extracted from blood or feather samples (Griffiths et al., 1998).

Bird handling and ringing were conducted under licenses delivered by the Swiss Federal Agency of Environment, Forests, and Landscapes, and all animal manipulations were performed under licenses delivered by the Swiss Veterinary Services.

Data collection

Offspring life history traits at adulthood

We investigated the effects of parental age at conception on the life history trajectory of their offspring into adulthood, by looking at age at first reproduction (AFR), lifespan, and lifetime reproductive success (LRS). AFR is estimated as the age at which an individual was seen reproducing for the first time in the study population; AFR varied from 1 to 6 years of age, with

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

a mean ± SE of 3.0 ± 0.04 years. Lifespan is estimated as the age at which an individual was found dead in the colony, or the age at which it was last seen alive before not being captured anymore in the colony for at least 2 consecutive years (Bize et al., 2009). The annual probability to capture recruits present in the colonies after they start breeding is virtually 1 (SE = 0.003) (Bize, Gasparini, et al., 2006), thus offering exceptional repeated reproductive information throughout adults' life until they died or disappeared (i.e., assumed dead since there is no breeding dispersal; Bize et al., 2017). Offspring lifespan varied between 1 and 20 years of age, with a mean ± SE lifespan of 6.3 ± 0.17 years. Finally, LRS is computed as the total number of fledglings produced by an individual throughout its reproductive life. The reproductive life is defined as the period from when an individual was first seen breeding in the population (i.e., AFR) until it died or disappeared from the population (i.e., lifespan). LRS varied from 0 to 28 fledglings, with a mean ± SE LRS of 6.7 ± 0.33 fledglings. An LRS of 0 comes from individuals that laid eggs but failed to produce fledglings (N=41 individuals, i.e. 11% of the dataset, see Figure S6). Eight individuals were observed prospecting at a young age (1 to 2 years) in the colonies, but most likely dispersed to an unmonitored colony to breed, and were therefore excluded from the AFR, LRS, and lifespan analyses (8 out of 374 recruits: 2.1%). As most of the offspring were not sexed before being recruited as adults, which has to be done by molecular methods as this species shows no apparent sexual dimorphism to the human eye (Dumas, Bize, et al., 2024; Dumas, St. Lawrence, et al., 2024), it was not possible to study the effects of parental age on the rate of recruitment of sons and daughters into the population. Sample sizes vary between traits at adulthood (Table 1) as, for example, some individuals started reproducing (information on AFR) but were still alive (no information on lifespan or LRS) when the data were analyzed (i.e., 2023).

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Offspring phenotype at the fledging stage

We investigated the effects of parental age at conception on offspring phenotype at 50 days of age, which is just before they fledge. We conducted this second set of analyses to better understand some of the processes behind the long-term effects of parental age at conception, since environmental conditions encountered early in life, for example in relation to the ability of parents to raise their young, can have long-lasting consequences on the life history trajectory of their offspring into adulthood. Every year in Biel and Solothurn, but not in Baden, nestlings are measured at 50 days of age: their body mass is measured with a digital scale (± 0.1 g), their wing, and tail length with a ruler (± 0.1 cm), and their sternum length with a caliper (± 0.01 cm). Nestling Alpine swifts are highly infested by the louse-fly *Crataerina melbae* (Diptera, Hippoboscidae), a hematophagous parasite that was shown to impact growth (Bize et al., 2003; Bize, Roulin, & Richner, 2004) and reproductive success (Bize, Roulin, Tella, et al., 2004). Thus, we also counted the number of louse-flies in the plumage of offspring at 50 days after hatching. The sample sizes for the effects of parental age are smaller for traits measured at the nestling stage than adulthood (Tables 1, 2), as nestling traits were only measured in two of the four colonies, namely Stadtkirche in Biel and Bieltor in Solothurn.

Statistical analyses

Analyses were performed on parents and offspring that reproduced at least once in their lives. Parental age was calculated from their year of birth, which is exact if individuals were ringed at the nestling stage, or approximated based on plumage traits (one year old versus older) and behaviors (roosting at night versus breeding) when they were first ringed as adults. We investigated the effects of parental age using models with the age of the mother and father divided into two age categories, namely “prime-age” versus “old-age” parents (for a similar approach, see Colominas-Ciuró et al., 2024). The threshold between the two age categories

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

corresponds to the onset of senescence, determined as 11 years of age for the mothers and 9 years of age for the fathers, based on previous results on aging trajectories of male and female Alpine swifts in the same population (see Figures 3 and A3 in the appendix from Moullec et al., 2023). In this study, the onset of senescence (i.e., second breakpoint) varied between 11 and 15 years of age for the females and between 9 and 12 years of age for the males, depending on the trait studied. To be inclusive in determining the “old-age” parents, we thus chose to set the limit between the two age categories at the earliest onset of senescence found in both sexes, i.e., 11 years of age for the females and 9 years of age for the males. The use of models with parental age divided into two categories (prime-age versus old-age) has the advantage over ‘classic’ quadratic models of allowing the effects of age to be asymmetrical on either side of the threshold, as frequently reported in the literature on animal aging (Berman et al., 2008; Froy et al., 2013; Moullec et al., 2023). To show how the choice of threshold affected the results, we conducted sensitivity analyses by increasing and decreasing the mother or father age threshold by 1 year (Supplementary Figures S1, S2). We also performed additional analyses to investigate the effects of parental age when modeled as a continuous (smooth) variable by using generalized additive mixed models (GAMM) from the mgcv package (Simon, 2023). As the use of conditional Akaike Information Criterion (AIC) to compare and select the best models shows that models with age categories outperform GAMM models (Table S3), we therefore report in the present study the results from models with parental age modeled as a 2-level factor, and we present the results of the GAMM models in the supplementary material (Supplementary Figures S3, S4; Supplementary Tables S1, S2).

When testing for effects of maternal or paternal age at conception on offspring life history trajectories (AFR, lifespan, LRS), we included as fixed factors in the models: the mother or father age category (2-level factor: prime-age versus old-age), the sex of the offspring (2-level factor: son versus daughter), the lifespan of the mother or father (continuous variable), the

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

annual mean nestling survival (continuous variable); and as random factors: the year of birth of the offspring, the colony (4-level factors: Baden-ST, Baden-LVS, Biel-SK, Solothurn-BT), and the parent identity (i.e. ring). We included in the models the lifespan of the mother or father (which in our population also corresponds to the age at last reproduction) to control for selective disappearance (Berman et al., 2008; Froy et al., 2013; van de Pol et al., 2006), and the annual mean nestling survival in the year of birth of a focal offspring to control for possible effects of inter-annual variation in environmental harshness, which can also induce long-term consequences on offspring phenotype (Hamel et al., 2009; Lindström, 1999). Annual mean nestling survival is computed, per colony, as the mean proportion of offspring who survived from hatching up to fledging. During the study period, it varied from 55% in 2007 to 96% in 2011, with a mean ± SE of 86% ± 0.5%. Alpine swifts are insectivorous birds that forage exclusively on prey caught while flying, thus, offspring can face food shortages during prolonged periods of rain and cold weather (Bize, Metcalfe, et al., 2006), which can lead to low nestling survival, as in 2007. To control for potential selective effects towards individuals with a short lifespan and low AFR in the last cohorts, we restricted the analyses to offspring born before 2015.

When testing for effects of maternal or paternal age at conception on offspring phenotype before fledging (body mass, wing, tail, sternum, ectoparasite load), we included as fixed factors in the models: the mother or father age category (2-level factor: prime-age versus old-age), the sex of the offspring (2 level factor: son versus daughter), the lifespan of the mother or father (continuous variable), the exact age of the offspring (which was not always exactly 50 days old; continuous variable), the brood size at 50 days (continuous variable), the hatching date (continuous variable), the annual mean nestling survival (continuous variable), the colony identity (2-level factors; nestling phenotype before fledging was collected only in the colonies

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Biel-SK and Solothurn-BT), and the time of measurement for the body mass only; and as random factors: the year of birth of the offspring, and the parents identity (i.e. ring).

All the analyses were performed using the R software version 4.2.1 (R Core Team, 2022). Effects of parental age on offspring life-history trajectories and phenotype at 50 days were tested using linear or generalized linear mixed-effect models (LMM or GLMM) in the package *lme4* (Bates et al., 2015). GLMM with a Poisson distribution were run when analyzing effects on offspring, LRS, and ectoparasite load; LMM were run otherwise with a log-transformation for offspring lifespan and AFR. The significance of fixed effects was computed using the F-tests and P-values obtained in the package *lmerTest* (Kuznetsova et al., 2017) for LMM and using Wald chi-square tests and P values in the package *car* (J. Fox & Weisberg, 2019) for GLMM. To investigate whether parental age at conception had different consequences on sons and daughters, for all models we tested the interaction between the age category of the parent and the sex of the offspring. Non-significant interactions were removed from the final models. When an interaction was significant, we conducted a post-hoc test using pairwise comparisons with the *emmeans* package (Lenth et al., 2023) to identify which factors of the interaction were significant. Figures were built using the package *ggplot2* (Wickham, 2016).

3 | RESULTS

Offspring life history traits at adulthood

Results show that offspring lifespan was significantly explained by the interaction between paternal age category and offspring sex (Table 1, Figure 1). Post-hoc tests indicate that the age category of the father had a significant effect on their sons' lifespan (β=0.262±0.099, P=0.009) but not on their daughters' lifespan (β=0.032±0.088, P=0.719), with old-age fathers producing

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

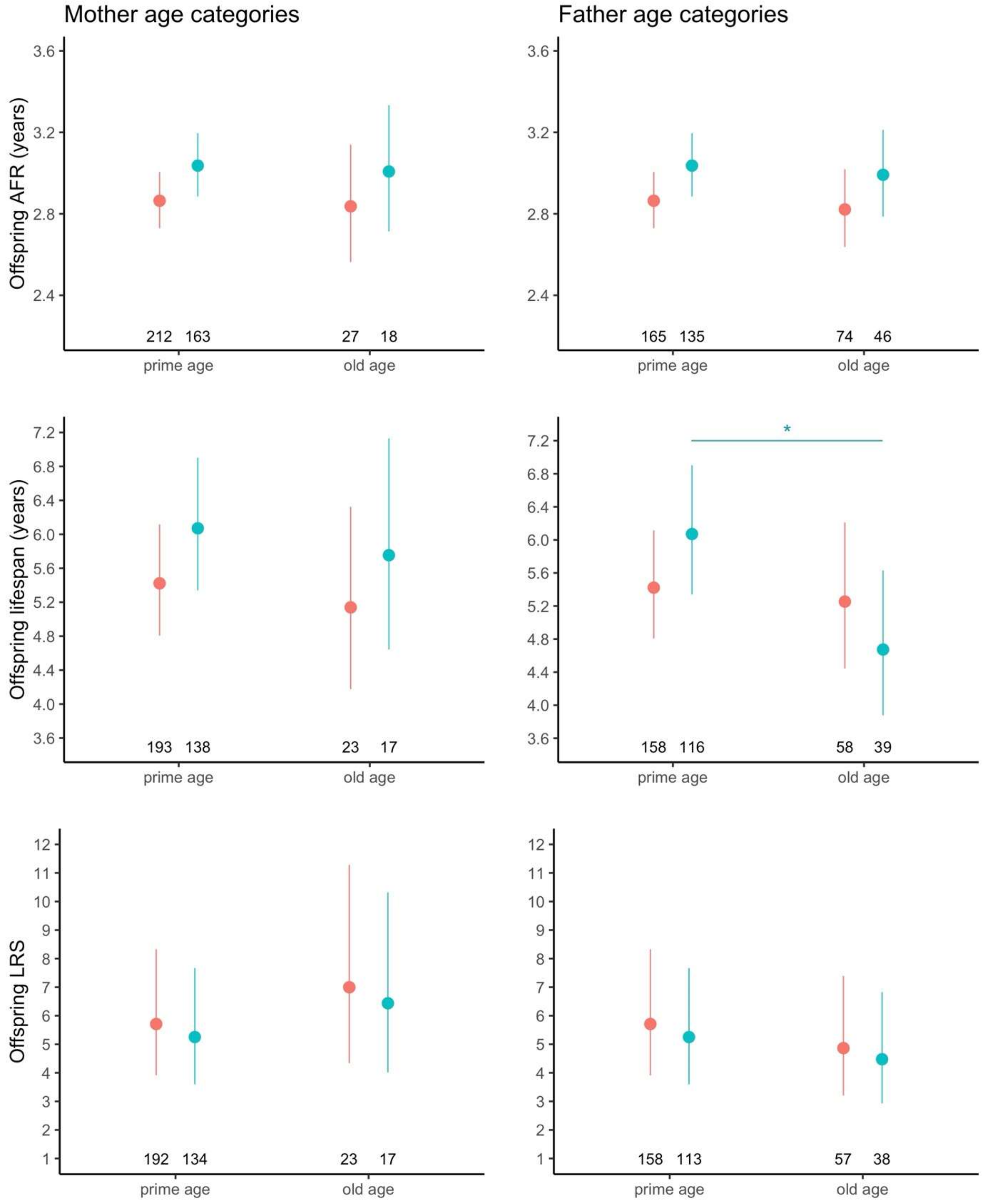
sons with a shorter lifespan. We also found a tendency (P=0.060) for an effect of the annual nestling survival on offspring lifespan (Table 1), with offspring born in harsher years tending to have a longer lifespan. Note that this negative effect of annual nestling survival is significant in GAMM models (Table S1; P=0.037). Maternal age had no significant effect on their offspring lifespan (Table 1, Figure 1). There was no evidence that the mother or father age category at conception affected their offspring AFR or LRS (Table 1, Figure1). We detected no evidence of selective disappearance of lower quality parents in these life-history traits models (i.e., no significant effect of the mother and father lifespan, Table 1).

Sensitivity analyses (Figure S1), where the parental age threshold is modified by one year, and GAMM models (Table S1, Figure S3), show that the effects of father age at conception on their sons' lifespan are robust. Interestingly, these complementary analyses suggest also that father age at conception has a negative effect on their sons' LRS, with such effects being apparent when father age-threshold is decreased by 1 year (Figure S1; P=0.001), or using GAMM models with father age as a continuous variable (Table S1; s(Father age in interaction with offspring sex): F=4.28, P=0.039).

Figure 1| Effects of maternal and paternal age at conception on age at first reproduction (AFR), lifespan, and lifetime reproductive success (LRS) of sons (blue closed points) and daughters (red closed points) in the Alpine swift. Parents are divided into prime-age (2 to 10 years of age for the mothers and 2 to 8 for the fathers) or old-age (>10 years for the mothers and >8 years for the fathers). Means ± SE of the predictions of the statistical models in Table 1 are shown on each panel. Horizontal segments above the panels with an asterisk indicate a significant effect of parental age on sons (blue) or daughters (red), with the latter results derived from post-hoc tests when the interaction between parental age category and offspring sex was significant. Sample sizes are reported at the bottom of the panels.

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025



Offspring phenotype at fledging

The mass of the offspring at 50 days old did not vary with the age category of the parents at conception (Table 2, Figure 2). However, we found a significant effect of the age category of

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

the parents on the length of the wings and tail of the offspring before fledging (Table 2, Figure 2). Offspring from old-age mothers and fathers had longer wings and tail at 50 days old (Table 2, Figure 2). Offspring sternum length at 50 days old was significantly explained by the interaction between maternal age categories and offspring sex (Table 2, Figure 2). The post-hoc test shows that sons from old-age mothers have a shorter sternum than sons from prime-age mothers (β=0.95±0.47, P=0.043), but this interaction is mainly driven by the sternum length difference between sons and daughters from prime-age mothers (β=-0.80±0.17, P<0.0001), which is not observed between sons and daughters from old-age mothers (β=0.57±0.50, P=0.257). We also found a highly significant interaction between the age category of the father and the sex of the offspring on their parasite load (Table 2, Figure 2). Daughters from old-age fathers had a lower parasite load at 50 days old than daughters from prime-age fathers (β=0.77±0.22, P<0.001), whereas the parasite load of sons from old-age fathers was not significantly different than sons from prime-age fathers (β=-0.36±0.23, P=0.120). We also detected a trend (P=0.08) for an effect of maternal age category on offspring parasite load, with offspring (sons and daughters) from old-age mothers tending to be less parasitized at 50 days old than offspring from younger mothers (Table 2, Figure 2).

Sensitivity analyses and GAMM models show that positive effects of mother and father age categories on offspring tail and wing length, and negative effects of father age on daughters' parasite load were the most robust. In contrast, the effect of mother age on offspring sternum length needs to be interpreted with caution (Table S2; Figures S2, S4). Moreover, the trend toward lower parasite loads in sons and daughters from older mothers becomes statistically significant (P < 0.001) when the maternal age threshold is reduced by one year (Figure S2). A negative effect of paternal age category on offspring mass is also observed when the paternal age threshold is increased by one year. However, as these effects emerge in only a single model, they should also be interpreted cautiously (see Table 3).

ORIGINAL UNEDITED MANUSCRIPT

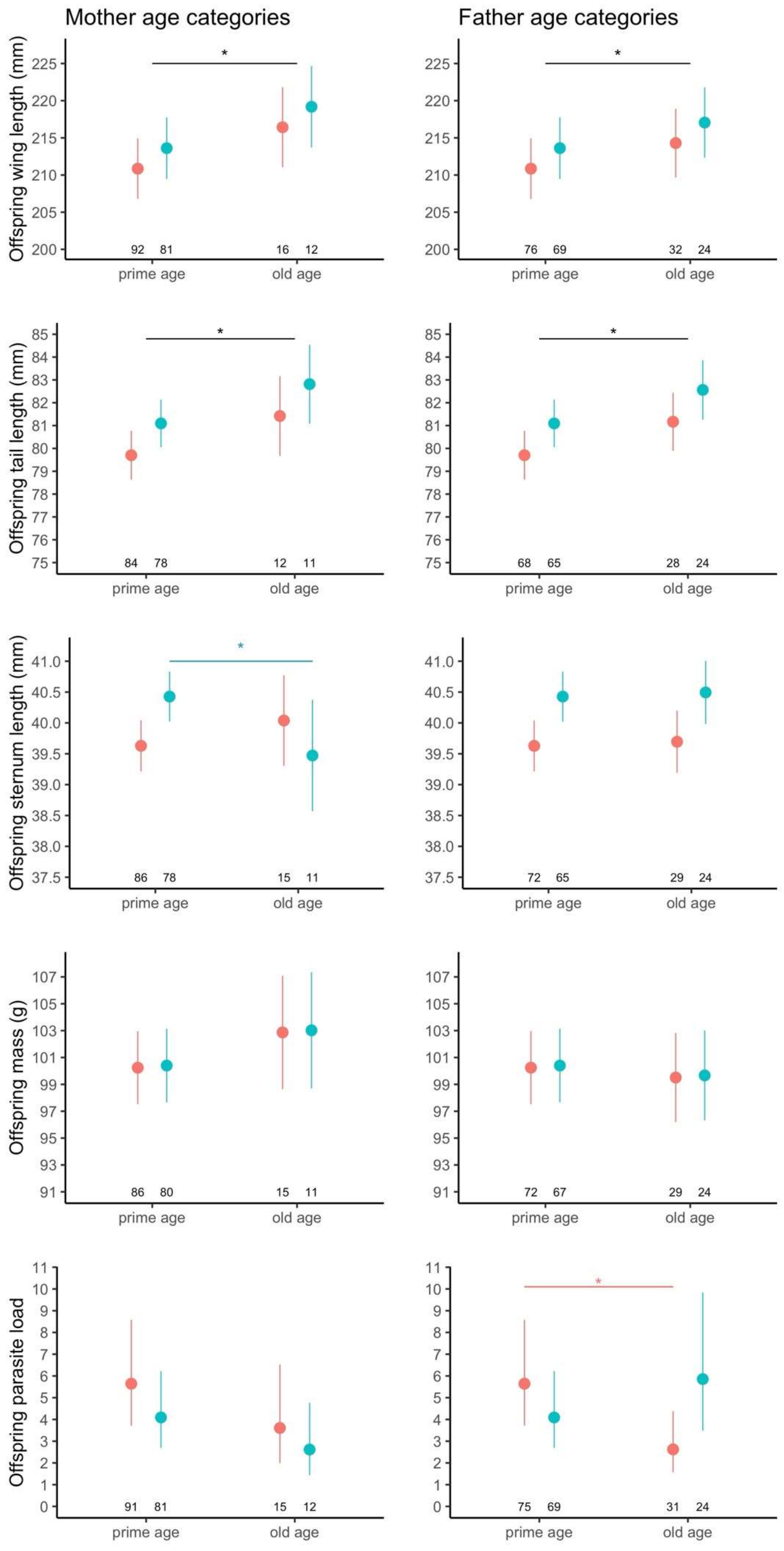
Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Results also show similar biological (i.e., negative) effects of brood size at 50 days and annual nestling survival on the wing, tail, sternum length, and offspring mass (Table 2). Offspring in bigger broods (i.e., more siblings and thus less food per capita: harsher environment) at 50 days of age had shorter wings, tail, and sternum and had a lower mass (Table 2), and offspring born in harsher years with lower nestling survival were significantly smaller (shorter wings, tail, and sternum; Table 2). These early-life environment variables were not significant for the offspring's parasite load (Table 2). We detected no evidence of selective disappearance of lower quality parents in any of the offspring phenotype models, with the exception of the negative effect of mother lifespan on offspring wing length (Table 2): mothers with a longer lifespan produced offspring with shorter wings.

Figure 2| Effects of maternal and paternal age at conception on wing, tail, sternum length, mass, and parasite load at 50 days old of sons (blue closed points) and daughters (red closed points) in the Alpine swift. Parents are divided into prime-age (2 to 10 years of age for the mothers and 2 to 8 for the fathers) or old-age (>10 years for the mothers and >8 years for the fathers). Means ± SE of the predictions of the statistical models in Table 2 are shown on each panel. Horizontal segments above the panels with an asterisk indicate a significant effect of parental age on offspring (black) or more specifically on sons (blue) or daughters (red), with the latter results derived from post-hoc tests when the interaction between parental age category and offspring sex was significant. Sample sizes are reported at the bottom of the panels.

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025



OR NUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

4 | DISCUSSION

Our results from a long-lived wild bird, the Alpine swift, show both short- and long-term effects of parental age at conception on their offspring's life history trajectory, from fledging up to adult lifespan and reproductive success (summarized in Table 3), which is in line with a growing number of studies on this topic in wild animals (Fay et al., 2016; Ivimey-Cook et al., 2023; Ivimey-Cook & Moorad, 2020). However, it is interesting to note that many of the effects observed in our study depended on the sex of the parents and/or of their offspring. By studying the effects of parental age at conception on both the phenotype of the offspring at fledging and later in life, we hypothesize that the negative effects of parental age on offspring lifespan (i.e. the Lansing effect; Lansing, 1947) could be explained by early life changes in offspring's exposure to parasites and, by extension, in their immune capacity.

Parental age effect on offspring life history traits at adulthood

Our study in the Alpine swift shows that paternal age had a negative influence on the lifespan of their sons and, to some extent, on their LRS. Parental age at conception in the Alpine swift, however, had no influence on age at first reproduction. Our results showing a Lansing effect in the Alpine swift are consistent with observations on other long-lived bird species. In the common tern, older fathers produce shorter-lived sons (Bouwhuis et al., 2015), similarly to our observations, and in the Seychelles warbler (*Acrocephalus sechellensis*), older mothers produce shorter-lived daughters (Sparks et al., 2022). Furthermore, older fathers were found to produce sons with a lower LRS in the Common tern and House sparrow (Bouwhuis et al., 2015; Schroeder et al., 2015), and older mothers to produce daughters with a lower LRS in the Common tern, House sparrow, and Seychelles warbler (Bouwhuis et al., 2015; Schroeder et al., 2015; Sparks et al., 2022). Effects of parental age at conception on the LRS of their offspring can be driven by effects on the productivity (as suggested in Kroeger et al., 2020; Schroeder et

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

al., 2015) and/or breeding lifespan of their offspring (Bouwhuis et al., 2015; Sparks et al., 2022). Accordingly, in the Alpine swift, variation in LRS is largely explained by variation in lifespan (Figure S5, see also Mourocq et al., 2016; Tettamanti et al., 2012). It suggests that the negative effects of father age at conception on the LRS of their sons (detected when decreasing the father age threshold by 1 year and in GAMM models) are primarily driven by the reduction of their sons' lifespan.

We also tested whether the selective disappearance of a particular parental phenotype could explain some of our results by including the lifespan of the parents in our models (see also Berman et al., 2008; Froy et al., 2013). As we found no evidence of selective disappearance in this Alpine swift population when analyzing the different offspring fitness traits, it suggests that the sex-specific effects of parental age on offspring lifespan were unlikely to be explained by sex-specific demographic changes within the population. However, we did find evidence for a relationship between early-life environment, approximated by brood size at fledging or annual nestling mortality, and offspring size close to fledging, as well as adult lifespan. Offspring recruited from a year with high nestling mortality, as well as from larger broods (more competitive, harsher environment; Bize & Roulin, 2006) were significantly smaller at 50 days old, and offspring recruited from a year with high nestling mortality tended to live longer. Hence, one explanation is that in years or broods with harsh early life environments, offspring are growing at slower rates (due to higher stress and/or lower access to nutrients), they are smaller in size at 50 days, close to fledging (Masoero et al., 2024), but they live longer, as predicted by the 'growth rate-lifespan trade-off hypothesis' (Lee et al., 2013; Metcalfe & Monaghan, 2003). It is worth noting that in harsh years, when the mortality rate of fledglings is high, selection may also eliminate lower quality fledglings, leaving only higher quality fledglings to fledge, which have a longer life expectancy, as predicted by the 'viability selection hypothesis' (Hadfield, 2008; Mojica & Kelly, 2010). The trade-off between growth rate and

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

lifespan (Lee et al., 2013; Metcalfe & Monaghan, 2003), as well as the selective disappearance of lower-quality offspring at the nestling stage in response to harsh early environments (Hadfield, 2008; Mojica & Kelly, 2010) remain to be studied in detail in the Alpine swift.

Parental age effect on offspring at fledging

Changes in life history trajectories at adulthood are often rooted in changes in early-life condition (Douhard et al., 2014; Festa-Bianchet et al., 2000; Hamel et al., 2009; Vasilieva & Tchabovsky, 2020). Hence, examining the effects of parental age on offspring phenotype early in life may give us indications as to the mechanisms leading to parental age effects on offspring life history traits at adulthood observed previously. One hypothesis is that, as a result of senescence, older parents show a decline in parental care and performance (Catry et al., 2006; Hammers et al., 2021; Lecomte et al., 2010; Zimmer et al., 2011). Consequently, in the Alpine swift, we predicted that senescing parents would produce offspring of lower condition, size, and immunity, as previously reported in the Barn swallow (Saino et al., 2002). However, contrary to our prediction, we found positive effects of parental age at conception on offspring phenotype before fledging. Old-age parents produced offspring that, 50 days after hatching, had longer wings and tail and were less infested by ectoparasites, with the exception of the sons from old-age fathers, which showed no reduction in parasite load. Sons from old-age mothers, however, had shorter sternum, although this result should be interpreted with caution as it is not consistent when using alternative statistical approaches. We found no effect of parental age at conception on offspring mass at 50 days after hatching. Positive effects on offspring wing and tail length are in line with previous results in the Alpine swift, showing that wing length (and presumably feather growth) best integrates environmental conditions encountered throughout development (Masoero et al., 2024). These positive effects of parental age on offspring wing and tail length early in life suggest that parental care is unlikely to be the cause of the observed

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

long-term negative effect of paternal age on offspring (sons) lifespan (Lansing effect). This is in line with an experimental cross-fostering study on wild house sparrows showing that offspring fitness was not influenced by the age of their foster parents (Schroeder et al., 2015).

The positive effects of parental age at conception on offspring wing and tail length early in life suggest that, in the Alpine swift, parental care efficiency might increase with age, possibly due to increased rearing experience and foraging efficiency (Cameron et al., 2000; Forslund & Pärt, 1995; Weladji et al., 2006). As the reproductive senescence of female Alpine swifts was characterized by a decline in brood size at hatching and fledging (Moullec et al., 2023), it is also possible that the offspring from older mothers, belonging to a small brood, would benefit from lower competition and higher parental care. Research on foraging effort and success is now needed in the Alpine swift to test if parents change their parental care strategy with age, as observed in the Wandering albatross (Lecomte et al., 2010). Finally, a meta-analysis of maternal age effect on juvenile survival found a positive effect of maternal age in birds, most of which exhibit biparental care, as opposed to a negative maternal age effect in mammals and invertebrates for which biparental care is relatively rare (Ivimey-Cook & Moorad, 2020). This study suggests that biparental care might reduce the effect of maternal age and could explain the positive effect observed in birds as opposed to other taxa. This would also be supported by our results, considering the positive parental age effect on offspring condition, and because Alpine swifts also exhibit biparental care.

Our results show a tendency for lower parasite load in offspring from older mothers, and a clear sex-dependent effect of paternal age at conception, with daughters, but not sons, being significantly less parasitized. Hosts can use various strategies to reduce their parasite load, with parasite removal behavior and immunity being the most common strategies. Parasite removal behavior, however, seems inefficient in swifts against louse-flies, and it is not frequently observed. Thus, it is unlikely that the lower parasite load in daughters from old-age

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

fathers and in sons and daughters of old-age mothers would only be explained by a more efficient parasite removal behavior from older parents. This scenario would also imply that fathers can distinguish the sex of their offspring, which remains to be demonstrated in this species with cryptic sexual dimorphism (Dumas, Bize, et al., 2024; Dumas, St. Lawrence, et al., 2024). Hence, rather than behavioral, these results could be driven by physiological mechanisms. The swifts and other birds defend themselves from these ectoparasites with a cutaneous immune response that makes the biting site unfavorable for the parasite, damages their tissue (Owen et al., 2010; Wikel, 1996, 1999), and affects their blood meal size and survival (Bize et al., 2008). Hence, one first hypothesis could be that older parents, who therefore live longer, would have better immunity against these parasites, and that they would be able to transmit this better immunity to their offspring. However, our results provide little support for this hypothesis, as we found no effect of parental lifespan on offspring parasite load. Another hypothesis is that offspring of older parents develop a stronger immune response to ectoparasites due to the better resources and care provided by older parents. In line with this hypothesis, our results show a positive effect of parental age on the size of their offspring before fledging. This effect of parental age on offspring parasite load, however, differed between daughters and sons, with sons of older fathers being as heavily or more infested than sons of fathers in prime age. It suggests that sons of older fathers might have a lower immune response against this louse fly when compared to daughters. Although a previous study found no sex differences in parasite load in nestling Alpine swifts, nor a sex difference in their cell-mediated immunity (Bize et al., 2005), our study over a longer period and with larger sample sizes suggests that male and female immunity might be influenced by parental age. This is in agreement with studies on the Barn swallow and Blue-footed booby which report that the immune response of their offspring depends on parental care (Saino et al., 1997) and maternal age (Beamonte-Barrientos et al., 2010; Saino et al., 2002). Given early-life effects of parental

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

age on offspring ectoparasite load close to fledging and adult lifespan, future studies should investigate whether the negative effect of paternal age on the lifespan of sons in the Alpine swift could be a consequence of reduced immunity from early life, which in turn reduces the survival and lifespan of offspring.

Conclusion

Our study contributes to the growing body of evidence showing parental age effects in the wild. It would now be important to investigate the mechanisms underlying these effects, such as epigenetic transmission mechanisms, in the Alpine swift and wild species in general. Moreover, we still need to disentangle whether the lower lifespan of individuals from older parents is a result of lower survival throughout their life or to higher rate of senescence later in their life. Because offspring were not sexed before they were recruited into the population as adults, we have no information on the proportion of daughters and sons that fledged and were subsequently recruited into the population. Hence, the effects of parental age on this 'invisible fraction' (Grafen, 1988; Mittell & Morrissey, 2024) remain to be studied in detail. Understanding the mechanisms is even more crucial as parental age effects might have important implications in demography and life-history evolution. In particular, it might have significant implications for sexual selection (Radwan, 2003). For example, in the context of this study, it might be beneficial for female Alpine swifts to mate with younger males to increase their fitness. A current study on this population is investigating mating choice. The results will thus be particularly interesting in the light of these findings.

Table 1| Results from generalized linear mixed effect models testing the effect of parental age at conception on offspring age at first reproduction (AFR), lifetime reproductive success (LRS), and lifespan in the long-lived Alpine swift. Parental age at conception is modeled as a 2-level

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

factor where parents are classified as either prime-age (2 to 10 years of age for the mothers and 2 to 8 for the fathers) or old-age (>10 years for the mothers and >8 years for the fathers), and the consequences are investigated on sons and daughters (offspring sex). Models also account for the effects of early growth environment (estimated by annual nestling survival) and of parental selective disappearance (estimated via mother and father lifespan). Models were run with both the age of the mother and the age of the father.

	AFR (Gaussian distribution)			
Random effects	Variance			
mother ID	0.007			
father ID	0.000			
year of birth	0.003			
colony	0.000			
Fixed effects	Estimate	Std. Error	t value	P.value
mother age category (old-age)	-0.010	0.050	-0.193	0.847
father age category (old-age)	-0.015	0.036	-0.414	0.679
offspring sex (male)	0.058	0.026	2.260	**0.024***
lifespan mother	0.002	0.004	0.509	0.611
lifespan father	-0.003	0.004	-0.748	0.455
annual nestling survival	-0.020	0.200	-0.102	0.920
mother age category * sex	_	_	_	_
father age category * sex	_	_	_	_
Sample size				
Number of obs = 420, Nb mother.ID = 240, Nb father.ID = 238, Nb year of birth = 21, Nb colony = 4				

	LRS (Poisson distribution)			
Random effects	Variance			
mother ID	0.340			
father ID	0.312			
year of birth	0.102			
colony	0.096			
Fixed effects	Estimate	Std. Error	z value	P.value
mother age category (old-age)	0.203	0.161	1.261	0.207
father age category (old-age)	-0.160	0.125	-1.280	0.201
offspring sex (male)	-0.083	0.067	-1.250	0.211
lifespan mother	0.002	0.017	0.116	0.908
lifespan father	-0.003	0.016	-0.223	0.824
annual nestling survival	-0.911	0.928	-0.981	0.327
mother age category * sex	_	_	_	_
father age category * sex	_	_	_	_
Sample size				
Number of obs = 366, Nb mother.ID = 218, Nb father.ID = 217, Nb year of birth = 21, Nb colony = 4				

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

	Lifespan (Gaussian distribution)			
Random effects	Variance			
mother ID	0.000			
father ID	0.000			
year of birth	0.035			
colony	0.000			
Fixed effects	Estimate	Std. Error	t value	P.value
mother age category (old-age)	-0.054	0.095	-0.567	0.571
father age category (old-age)	-0.032	0.086	-0.367	0.714
offspring sex (male)	0.113	0.059	1.915	0.056
lifespan mother	0.005	0.008	0.615	0.539
lifespan father	0.010	0.007	1.462	0.145
annual nestling survival	-1.126	0.547	-2.060	0.060
mother age category * sex	_	_	_	_
father age category * sex	-0.230	0.117	-1.971	**0.050***
Sample size				
Number of obs = 371, Nb mother.ID = 219, Nb father.ID = 218, Nb year of birth = 21, Nb colony = 4				

*: P<0.05
**: P<0.01
***: P<0.001

Table 2| Results from the generalized linear mixed effect models testing the effect of the age of the parents on offspring phenotype at 50 days old in the long-lived Alpine swift. Parental age at conception is modeled as a 2-level factor where parents are classified as either prime-age (2 to 10 years of age for the mothers and 2 to 8 for the fathers) or old-age (>10 years for the mothers and >8 years for the fathers), and the consequences are investigated on sons and daughters (offspring sex). Models also account for the effects of early growth environment (estimated by annual nestling survival, brood size at 50 days), offspring exact age (in days), hatching date, colony (Biel or Solothurn), and parental selective disappearance (estimated via mother and father lifespan). Models were run with both the age of the mother and the age of the father.

	Wing length (Gaussian distribution)
Random effects	Variance
mother ID	6.108
father ID	0.818

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

year	47.640			
Fixed effects	Estimate	Std. Error	t value	P.value
mother age category (old-age)	5.568	2.183	2.551	**0.012 ***
father age category (old-age)	3.439	1.736	1.981	**0.050 ***
offspring sex (male)	2.755	1.170	2.354	**0.020 ***
offspring age	1.380	0.409	3.374	**<0.001 *****
brood size day 50	-2.227	0.910	-2.447	**0.015 ***
hatching date	-0.348	0.132	-2.645	**0.009 ****
mother lifespan	-0.401	0.189	-2.124	**0.036 ***
father lifespan	-0.140	0.176	-0.794	0.429
colony (Solothurn)	-0.820	1.420	-0.578	0.565
annual nestling survival	57.923	19.171	3.021	**0.009***
mother age category * sex	_	_	_	_
father age category * sex	_	_	_	_
Sample sizes				
Nb obs = 201, Nb mother.ID = 126, Nb father.ID = 125, Nb year = 19				
	Tail length (Gaussian distribution)			
Random effects	Variance			
mother ID	1.922			
father ID	0.000			
year	0.780			
Fixed effects	Estimate	Std. Error	t value	P.value
mother age category (old age)	1.718	0.795	2.162	**0.032***
father age category (old-age)	1.467	0.607	2.418	**0.017***
offspring sex (male)	1.392	0.391	3.561	**<0.001*****
offspring age	0.030	0.158	0.189	0.850
brood size day 50	-0.726	0.316	-2.298	**0.023 ***
hatching date	-0.034	0.036	-0.935	0.356
mother lifespan	-0.064	0.069	-0.928	0.356
father lifespan	-0.057	0.064	-0.901	0.369
colony (Solothurn)	-0.231	0.499	-0.462	0.645
annual nestling survival	9.161	3.615	2.534	**0.022 ***
mother age category * sex	_	_	_	_
father age category * sex	_	_	_	_
Sample size				
Number of obs = 185, Nb mother.ID = 115, Nb father.ID = 115, Nb year = 15				
	Sternum length (Gaussian distribution)			
Random effects	Variance			
mother ID	0.168			
father ID	0.424			
year	0.000			
Fixed effects	Estimate	Std. Error	t value	P.value
mother age category (old-age)	0.411	0.385	1.066	0.288
father age category (old-age)	0.067	0.245	0.274	0.784

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

offspring sex (male)	0.799	0.169	4.724	**<0.001** ***
offspring age	-0.051	0.052	-0.973	0.332
brood size day 50	-0.513	0.131	-3.911	**<0.001** ***
hatching date	-0.006	0.012	-0.490	0.625
mother lifespan	0.018	0.029	0.614	0.540
father lifespan	-0.002	0.028	-0.070	0.944
colony (Solothurn)	-0.138	0.210	-0.657	0.513
annual nestling survival	4.185	1.146	3.653	**<0.001** ***
mother age category * sex	-1.365	0.515	-2.652	**0.009** **
father age category * sex	_	_	_	_
Sample size				
Number of obs = 190, Nb mother.ID = 120, Nb father.ID = 121, Nb year = 17				
	Body mass (Gaussian distribution)			
Random effects	Variance	Std.Dev.		
mother ID	0.000	0.000		
father ID	9.093	3.016		
year	6.187	2.487		
Fixed effects	Estimate	Std. Error	t value	P.value
mother age category (old-age)	2.623	2.017	1.301	0.195
father age category (old-age)	-0.734	1.570	-0.467	0.641
offspring sex (male)	0.157	1.040	0.151	0.880
offspring age	0.043	0.344	0.124	0.902
brood size day 50	-2.780	0.836	-3.325	**0.001** **
hour measurement	0.545	0.200	2.729	**0.007** **
hatching date	-0.025	0.096	-0.259	0.797
mother lifespan	-0.168	0.171	-0.986	0.326
father lifespan	0.180	0.167	1.075	0.285
colony (Solothurn)	-4.584	1.272	-3.603	**<0.001** ***
annual nestling survival	-17.584	9.894	-1.777	0.089
mother age category * sex	_	_	_	_
father age category * sex	_	_	_	_
Sample size				
Number of obs = 192, Nb mother.ID = 120, Nb father.ID = 121, Nb year = 17				
	Parasites load (Poisson distribution)			
Random effects	Variance	Std.Dev.		
mother ID	0.327	0.572		
father ID	0.243	0.493		
year	0.383	0.619		
Fixed effects	Estimate	Std. Error	z value	P.value
mother age category (old-age)	-0.447	0.259	-1.730	0.084
father age category (old-age)	-0.766	0.221	-3.464	**<0.001*** **
offspring sex (male)	-0.322	0.111	-2.888	**0.004****
offspring age	-0.037	0.040	-0.937	0.349

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

brood size day 50	-0.033	0.081	-0.407	0.684
hatching date	-0.012	0.013	-0.910	0.363
mother lifespan	0.020	0.023	0.892	0.372
father lifespan	0.020	0.021	0.963	0.336
colony (Solothurn)	0.091	0.181	0.501	0.616
annual nestling survival	-0.502	1.723	-0.291	0.771
mother age category * sex	_	_	_	_
father age category * sex	1.125	0.240	4.682	**<0.001*****
Sample size				
Number of obs = 199, Nb mother.ID = 126, Nb father.ID = 125, Nb year = 19				

*: P<0.05
**: P<0.01
***: P<0.001

Table 3| Summary table of the direction of the effects ("0": no effect, "−": negative effects; "+": positive effects) of the age of the mother and father on male and female offspring phenotype and life-history trajectories in the Alpine swift. The summary is based on results given in Tables 1, 2, S1, S2, and Figures S1, S2. Effects deemed "robust" are in bold (found in at least 2 models with ± 1 year thresholds and in GAMM), those "plausible" are in normal font (effects found in at least 1 model with ± 1 year thresholds and in GAMM), and those considered "weak" are in brackets (found in only one threshold model). AFR: age at first reproduction. LRS: lifetime reproductive success.

		Maternal age		**Paternal age**	
		Sons	Daughters	Sons	Daughters
Offspring traits at adulthood					
	AFR	0	0	0	0
	LRS	(−)	0	−	0
	Lifespan	0	0	**−**	0
Offspring traits at 50 days of age					
	Wing length	+	**+**	+	+
	Tail length	+	+	**+**	+
	Sternum length	(−)	0	0	0
	Mass	0	0	(−)	(−)

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

	Parasite load	(−)	(−)	0	–

DATA AVAILABILITY

The data used in this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.1c59zw48k

AUTHOR CONTRIBUTIONS

HM, SR, and PB designed the study. PB and CM organized data collection and managed the database. HM, VB, and PB carried out the statistical analyses. HM drafted the manuscript, and all authors revised it.

FUNDING

HM was supported by the Ella and Georg Ehrnrooth Foundation (Ella ja Georg Ehrnroothin Säätiö), the Turku University Foundation (Turun Yliopistosäätiö), and the University of Turku Graduate School UTUGS (Turun yliopiston tutkijakoulu). SR was supported by the Academy of Finland [324257] and the MCSA [101110339]. The long-term monitoring of this Alpine swift population was supported over the years via funding from the Swiss National Science Foundation to PB and the Swiss Ornithological Institute.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ACKNOWLEDGMENTS

We are grateful to all the people who participated in the fieldwork over the years in Biel, Solothurn, and Baden, with particular thanks to Willem Witvliet, who monitored the colonies in Baden between 1991 and 2015.

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

REFERENCES

Arslan, R. C., Willführ, K. P., Frans, E. M., Verweij, K. J. H., Bürkner, P.-C., Myrskylä, M., Voland, E., Almqvist, C., Zietsch, B. P., & Penke, L. (2017). Older fathers' children have lower evolutionary fitness across four centuries and in four populations. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1862), 20171562. https://doi.org/10.1098/rspb.2017.1562

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Beamonte-Barrientos, R., Velando, A., Drummond, H., & Torres, R. (2010). Senescence of Maternal Effects: Aging Influences Egg Quality and Rearing Capacities of a Long-Lived Bird. *The American Naturalist*, *175*(4), 469–480. https://doi.org/10.1086/650726

Bell, A. G. (1918). *The Duration of Life and Conditions Associated with Longevity: A Study of the Hyde Genealogy*. Genealogical Record Office.

Benton, T. G., St Clair, J. J. H., & Plaistow, S. J. (2008). Maternal effects mediated by maternal age: From life histories to population dynamics. *Journal of Animal Ecology*, *77*(5), 1038–1046. https://doi.org/10.1111/j.1365-2656.2008.01434.x

Berman, M., Gaillard, J.-M., & Weimerskirch, H. (2008). Contrasted patterns of age-specific reproduction in long-lived seabirds. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1655), 375–382. https://doi.org/10.1098/rspb.2008.0925

Bize, P., Criscuolo, F., Metcalfe, N. B., Nasir, L., & Monaghan, P. (2009). Telomere dynamics rather than age predict life expectancy in the wild. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1662), 1679–1683. https://doi.org/10.1098/rspb.2008.1817

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Bize, P., Daniel, G., Viblanc, V. A., Martin, J. G. A., & Doligez, B. (2017). Negative phenotypic and genetic correlation between natal dispersal propensity and nest-defence behaviour in a wild bird. *Biology Letters*, *13*(7), 20170236. https://doi.org/10.1098/rsbl.2017.0236

Bize, P., Gasparini, J., Klopfenstein, A., Altwegg, R., & Roulin, A. (2006). Melanin-based coloration is a nondirectionally selected sex-specific signal of offspring development in the alpine swift. *Evolution; International Journal of Organic Evolution*, *60*(11), 2370–2380. https://doi.org/10.1111/j.0014-3820.2006.tb01871.x

Bize, P., Jeanneret, C., Klopfenstein, A., & Roulin, A. (2008). What makes a host profitable? Parasites balance host nutritive resources against immunity. *The American Naturalist*, *171*(1), 107–118. https://doi.org/10.1086/523943

Bize, P., Metcalfe, N. B., & Roulin, A. (2006). Catch-up growth strategies differ between body structures: Interactions between age and structure-specific growth in wild nestling Alpine Swifts. *Functional Ecology*, *20*(5), 857–864. https://doi.org/10.1111/j.1365-2435.2006.01157.x

Bize, P., & Roulin, A. (2006). Sibling competition and the risk of falling out of the nest. *Animal Behaviour*, *72*(3), 539–544. https://doi.org/10.1016/j.anbehav.2005.10.021

Bize, P., Roulin, A., Bersier, L.-F., Pfluger, D., & Richner, H. (2003). Parasitism and developmental plasticity in Alpine swift nestlings. *Journal of Animal Ecology*, *72*(4), 633–639. https://doi.org/10.1046/j.1365-2656.2003.00734.x

Bize, P., Roulin, A., & Richner, H. (2004). Parasitism, Developmental Plasticity and Bilateral Asymmetry of Wing Feathers in Alpine Swift, Apus melba, Nestlings. *Oikos*, *106*(2), 317–323. https://doi.org/10.1111/j.0030-1299.2004.13019.x

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Bize, P., Roulin, A., Tella, J. L., Bersier, L.-F., & Richner, H. (2004). Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift. *Journal of Animal Ecology*, *73*(6), 1080–1088. https://doi.org/10.1111/j.0021-8790.2004.00880.x

Bize, P., Roulin, A., Tella, J. L., & Richner, H. (2005). Female-biased mortality in experimentally parasitized Alpine Swift Apus melba nestlings. *Functional Ecology*, *19*(3), 405–413. https://doi.org/10.1111/j.1365-2435.2005.00995.x

Bogdanova, M. I., Nager, R. G., & Monaghan, P. (2007). Age of the Incubating Parents Affects Nestling Survival: An Experimental Study of the Herring Gull Larus argentatus. *Journal of Avian Biology*, *38*(1), 83–93. https://doi.org/10.1111/j.2007.0908-8857.03701.x

Bouwhuis, S., Charmantier, A., Verhulst, S., & Sheldon, B. C. (2010). Trans-generational effects on ageing in a wild bird population. *Journal of Evolutionary Biology*, *23*(3), 636–642. https://doi.org/10.1111/j.1420-9101.2009.01929.x

Bouwhuis, S., Vedder, O., & Becker, P. H. (2015). Sex-specific pathways of parental age effects on offspring lifetime reproductive success in a long-lived seabird. *Evolution*, *69*(7), 1760–1771. https://doi.org/10.1111/evo.12692

Bowen, W. D., Iverson, S. J., Mcmillan, J. I., & Boness, D. J. (2006). Reproductive performance in grey seals: Age-related improvement and senescence in a capital breeder. *Journal of Animal Ecology*, *75*(6), 1340–1351. https://doi.org/10.1111/j.1365-2656.2006.01157.x

Cameron, E. Z., Linklater, W. L., Stafford, K. J., & Minot, E. O. (2000). Aging and Improving Reproductive Success in Horses: Declining Residual Reproductive Value or Just Older and Wiser? *Behavioral Ecology and Sociobiology*, *47*(4), 243–249. https://doi.org/10.1007/s002650050661

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Catry, P., Phillips, R. A., Phalan, B., & Croxall, J. P. (2006). Senescence effects in an extremely long-lived bird: The grey-headed albatross Thalassarche chrysostoma. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1594), 1625–1630. https://doi.org/10.1098/rspb.2006.3482

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1987). Interactions Between Population Density and Maternal Characteristics Affecting Fecundity and Juvenile Survival in Red Deer. *Journal of Animal Ecology*, *56*(3), 857–871. https://doi.org/10.2307/4953

Clutton-Brock, T., & Sheldon, B. C. (2010). Individuals and populations: The role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, *25*(10), 562–573. https://doi.org/10.1016/j.tree.2010.08.002

Colominas-Ciuró, R., Gray, F. E., Arikan, K., Zahn, S., Meier, C., Criscuolo, F., & Bize, P. (2024). Effects of persistent organic pollutants on telomere dynamics are sex and age-specific in a wild long-lived bird. *Science of The Total Environment*, *943*, 173785. https://doi.org/10.1016/j.scitotenv.2024.173785

Descamps, S., Boutin, S., Berteaux, D., & Gaillard, J.-M. (2008). Age-specific variation in survival, reproductive success and offspring quality in red squirrels: Evidence of senescence. *Oikos*, *117*(9), 1406–1416. https://doi.org/10.1111/j.0030-1299.2008.16545.x

Douhard, M., Plard, F., Gaillard, J.-M., Capron, G., Delorme, D., Klein, F., Duncan, P., Loe, L. E., & Bonenfant, C. (2014). Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1785), 20140276. https://doi.org/10.1098/rspb.2014.0276

Dumas, M. N., Bize, P., & Martin, J. G. A. (2024). *Temporal changes in sex-specific cryptic sexual dimorphism and allometric scaling in the long-lived Alpine swift Tachymarptis melba.* OSF Preprints. https://doi.org/10.31219/osf.io/7gc5b

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Dumas, M. N., Meier, C. M., Bize, P., & Martin, J. G. A. (2025). Who Keeps the House after Divorcing? Partner and Nest Fidelity in the Long-Lived Alpine Swift. *The American Naturalist*, *205*(2), 224–239. https://doi.org/10.1086/733307

Dumas, M. N., St. Lawrence, S., Masoero, G., Bize, P., & Martin, J. G. A. (2024). Adult body mass is heritable, positively genetically correlated and under selection of differing shapes between the sexes in a bird with little apparent sexual dimorphism. *Journal of Animal Ecology*, *93*(5), 567–582. https://doi.org/10.1111/1365-2656.14064

Fay, R., Barbraud, C., Delord, K., & Weimerskirch, H. (2016). Paternal but not maternal age influences early-life performance of offspring in a long-lived seabird. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1828), 20152318. https://doi.org/10.1098/rspb.2015.2318

Festa-Bianchet, M., Jorgenson, J. T., & Réale, D. (2000). Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology*, *11*(6), 633–639. https://doi.org/10.1093/beheco/11.6.633

Forslund, P., & Pärt, T. (1995). Age and reproduction in birds—Hypotheses and tests. *Trends in Ecology & Evolution*, *10*(9), 374–378. https://doi.org/10.1016/S0169-5347(00)89141-7

Fox, C. W., Bush, M. L., & Wallin, W. G. (2003). Maternal age affects offspring lifespan of the seed beetle, Callosobruchus maculatus. *Functional Ecology*, *17*(6), 811–820. https://doi.org/10.1111/j.1365-2435.2003.00799.x

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression, Third edition.* Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Froy, H., Phillips, R. A., Wood, A. G., Nussey, D. H., & Lewis, S. (2013). Age-related variation in reproductive traits in the wandering albatross: Evidence for terminal improvement following

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

senescence. *Ecology Letters*, *16*(5), 642–649. https://doi.org/10.1111/ele.12092

Gillespie, D. O. S., Russell, A. F., & Lummaa, V. (2013). The effect of maternal age and reproductive history on offspring survival and lifetime reproduction in preindustrial humans. *Evolution*, *67*(7), 1964–1974. https://doi.org/10.1111/evo.12078

Grafen, A. (1988). On the uses of data on lifetime reproductive success. In T. H. Clutton-Brock (Ed.), *Reproductive success: Studies of individual variation in contrasting breeding systems* (pp. 454–471). University of Chicago press.

Griffiths, R., Double, M. C., Orr, K., & Dawson, R. J. G. (1998). A DNA test to sex most birds. *Molecular Ecology*, *7*(8), 1071–1075. https://doi.org/10.1046/j.1365-294x.1998.00389.x

Hadfield, J. D. (2008). Estimating evolutionary parameters when viability selection is operating. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 723–734. https://doi.org/10.1098/rspb.2007.1013

Hadley, G. L., Rotella, J. J., & Garrott, R. A. (2007). Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. *Oikos*, *116*(4), 601–613. https://doi.org/10.1111/j.0030-1299.2007.15528.x

Hamel, S., Craine, J. M., & Towne, E. G. (2012). Maternal allocation in bison: Co-occurrence of senescence, cost of reproduction, and individual quality. *Ecological Applications*, *22*(5), 1628–1639. https://doi.org/10.1890/11-2181.1

Hamel, S., Gaillard, J.-M., Festa-Bianchet, M., & Côté, S. D. (2009). Individual quality, early-life conditions, and reproductive success in contrasted populations of large herbivores. *Ecology*, *90*(7), 1981–1995. https://doi.org/10.1890/08-0596.1

Hammers, M., Kingma, S. A., van Boheemen, L. A., Sparks, A. M., Burke, T., Dugdale, H. L.,

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Richardson, D. S., & Komdeur, J. (2021). Helpers compensate for age-related declines in parental care and offspring survival in a cooperatively breeding bird. *Evolution Letters*, *5*(2), 143–153. https://doi.org/10.1002/evl3.213

Hercus, M. J., & Hoffmann, A. A. (2000). Maternal and grandmaternal age influence offspring fitness in Drosophila. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1457), 2105–2110. https://doi.org/10.1098/rspb.2000.1256

Hoffman, C. L., Higham, J. P., Mas-Rivera, A., Ayala, J. E., & Maestripieri, D. (2010). Terminal investment and senescence in rhesus macaques (Macaca mulatta) on Cayo Santiago. *Behavioral Ecology*, *21*(5), 972–978. https://doi.org/10.1093/beheco/arq098

Ivimey-Cook, E. R., & Moorad, J. (2020). The diversity of maternal-age effects upon pre-adult survival across animal species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1932), 20200972. https://doi.org/10.1098/rspb.2020.0972

Ivimey-Cook, E. R., Shorr, S., & Moorad, J. A. (2023). The distribution of the Lansing Effect across animal species. *Evolution*, *77*(2), 608–615. https://doi.org/10.1093/evolut/qpac045

Jones, K. S., Nakagawa, S., & Sheldon, B. C. (2009). Environmental Sensitivity in Relation to Size and Sex in Birds: Meta-Regression Analysis. *The American Naturalist*, *174*(1), 122–133. https://doi.org/10.1086/599299

Kern, S., Ackermann, M., Stearns, S. C., & Kawecki, T. J. (2001). Decline in offspring viability as a manifestation of aging in Drosophila melianogaster. *Evolution; International Journal of Organic Evolution*, *55*(9), 1822–1831. https://doi.org/10.1111/j.0014-3820.2001.tb00831.x

Kroeger, S. B., Blumstein, D. T., Armitage, K. B., Reid, J. M., & Martin, J. G. A. (2020). Older mothers produce more successful daughters. *Proceedings of the National Academy of Sciences*,

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

117(9), 4809–4814. https://doi.org/10.1073/pnas.1908551117

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Lansing, A. I. (1947). A Transmissible, Cumulative, and Reversible Factor in Aging. *Journal of Gerontology*, *2*(3), 228–239. https://doi.org/10.1093/geronj/2.3.228

Lecomte, V. J., Sorci, G., Cornet, S., Jaeger, A., Faivre, B., Arnoux, E., Gaillard, M., Trouvé, C., Besson, D., Chastel, O., & Weimerskirch, H. (2010). Patterns of aging in the long-lived wandering albatross. *Proceedings of the National Academy of Sciences*, *107*(14), 6370–6375. https://doi.org/10.1073/pnas.0911181107

Lee, W.-S., Monaghan, P., & Metcalfe, N. B. (2013). Experimental demonstration of the growth rate–lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1752), 20122370. https://doi.org/10.1098/rspb.2012.2370

Lenth, R. V., Bolker, B., Buerkner, P., Giné-Vázquez, I., Herve, M., Jung, M., Love, J., Miguez, F., Riebl, H., & Singmann, H. (2023). *emmeans: Estimated Marginal Means, aka Least-Squares Means* (Version 1.10.0) [Computer software]. https://cran.r-project.org/web/packages/emmeans/index.html

Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, *14*(9), 343–348. https://doi.org/10.1016/S0169-5347(99)01639-0

Martínez-Padilla, J., Vergara, P., & Fargallo, J. A. (2017). Increased lifetime reproductive success of first-hatched siblings in Common Kestrels Falco tinnunculus. *Ibis*, *159*(4), 803–811. https://doi.org/10.1111/ibi.12494

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

Masoero, G., Dumas, M. N., Martin, J. G. A., & Bize, P. (2024). Trait-specific sensitive developmental windows: Wing growth best integrates weather conditions encountered throughout the development of nestling Alpine swifts. *Ecology and Evolution*, *14*(6), e11491. https://doi.org/10.1002/ece3.11491

Meier, C. M., Karaardıç, H., Aymí, R., Peev, S. G., Witvliet, W., & Liechti, F. (2020). Population-specific adjustment of the annual cycle in a super-swift trans-Saharan migrant. *Journal of Avian Biology*, *51*(11). https://doi.org/10.1111/jav.02515

Metcalfe, N. B., & Monaghan, P. (2003). Growth versus lifespan: Perspectives from evolutionary ecology. *Experimental Gerontology*, *38*(9), 935–940. https://doi.org/10.1016/S0531-5565(03)00159-1

Mittell, E. A., & Morrissey, M. B. (2024). The missing fraction problem as an episodes of selection problem. *Evolution*, *78*(4), 601–611. https://doi.org/10.1093/evolut/qpae022

Mojica, J. P., & Kelly, J. K. (2010). Viability selection prior to trait expression is an essential component of natural selection. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1696), 2945–2950. https://doi.org/10.1098/rspb.2010.0568

Monaghan, P., Maklakov, A. A., & Metcalfe, N. B. (2020). Intergenerational Transfer of Ageing: Parental Age and Offspring Lifespan. *Trends in Ecology & Evolution*, *35*(10), 927–937. https://doi.org/10.1016/j.tree.2020.07.005

Monaghan, P., & Metcalfe, N. B. (2019). The deteriorating soma and the indispensable germline: Gamete senescence and offspring fitness. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1917), 20192187. https://doi.org/10.1098/rspb.2019.2187

Moullec, H., Reichert, S., & Bize, P. (2023). Aging trajectories are trait- and sex-specific in the

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

long-lived Alpine swift. *Frontiers in Ecology and Evolution*, *11*, 983266. https://doi.org/10.3389/fevo.2023.983266

Mourocq, E., Bize, P., Bouwhuis, S., Bradley, R., Charmantier, A., de la Cruz, C., Drobniak, S. M., Espie, R. H. M., Herényi, M., Hötker, H., Krüger, O., Marzluff, J., Møller, A. P., Nakagawa, S., Phillips, R. A., Radford, A. N., Roulin, A., Török, J., Valencia, J., … Griesser, M. (2016). Life span and reproductive cost explain interspecific variation in the optimal onset of reproduction. *Evolution*, *70*(2), 296–313. https://doi.org/10.1111/evo.12853

Mousseau, T. A., & Fox, C. W. (Eds.). (1998). *Maternal Effects As Adaptations*. Oxford University Press. https://doi.org/10.1093/oso/9780195111637.001.0001

Nussey, D. H., Coulson, T., Festa-Bianchet, M., & Gaillard, J.-M. (2008). Measuring senescence in wild animal populations: Towards a longitudinal approach. *Functional Ecology*, *22*(3), 393–406. https://doi.org/10.1111/j.1365-2435.2008.01408.x

Nussey, D. H., Kruuk, L. E. B., Morris, A., Clements, M. N., Pemberton, J. M., & Clutton-Brock, T. H. (2009). Inter- and Intrasexual Variation in Aging Patterns across Reproductive Traits in a Wild Red Deer Population. *The American Naturalist*, *174*(3), 342–357. https://doi.org/10.1086/603615

Owen, J. P., Nelson, A. C., & Clayton, D. H. (2010). Ecological immunology of bird-ectoparasite systems. *Trends in Parasitology*, *26*(11), 530–539. https://doi.org/10.1016/j.pt.2010.06.005

Priest, N. K., Mackowiak, B., & Promislow, D. E. L. (2002). The Role of Parental Age Effects on the Evolution of Aging. *Evolution*, *56*(5), 927–935. https://doi.org/10.1111/j.0014-3820.2002.tb01405.x

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

R Core Team. (2022). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.* https://www.r-project.org/

Radwan, J. (2003). Male age, germline mutations and the benefits of polyandry. *Ecology Letters*, *6*(7), 581–586. https://doi.org/10.1046/j.1461-0248.2003.00484.x

Reichert, S., Berger, V., Jackson, J., Chapman, S. N., Htut, W., Mar, K. U., & Lummaa, V. (2020). Maternal age at birth shapes offspring life-history trajectory across generations in long-lived Asian elephants. *Journal of Animal Ecology*, *89*(4), 996–1007. https://doi.org/10.1111/1365-2656.13049

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., Bogdanova, M. I., & Monaghan, P. (2010). Parent age, lifespan and offspring survival: Structured variation in life history in a wild population. *Journal of Animal Ecology*, *79*(4), 851–862. https://doi.org/10.1111/j.1365-2656.2010.01669.x

Rödel, H. G., Von Holst, D., & Kraus, C. (2009). Family legacies: Short- and long-term fitness consequences of early-life conditions in female European rabbits. *Journal of Animal Ecology*, *78*(4), 789–797. https://doi.org/10.1111/j.1365-2656.2009.01537.x

Saino, N., Ambrosini, R., Martinelli, R., & Moller, A. P. (2002). Mate Fidelity, Senescence in Breeding Performance and Reproductive Trade-Offs in the Barn Swallow. *Journal of Animal Ecology*, *71*(2), 309–319. https://doi.org/10.1046/j.1365-2656.2002.00600.x

Saino, N., Calza, S., & Moller, A. pape. (1997). Immunocompetence of Nestling Barn Swallows in Relation to Brood Size and Parental Effort. *Journal of Animal Ecology*, *66*(6), 827–836. https://doi.org/10.2307/5998

Schroeder, J., Nakagawa, S., Rees, M., Mannarelli, M.-E., & Burke, T. (2015). Reduced fitness

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

ORIGINAL UNEDITED MANUSCRIPT

in progeny from old parents in a natural population. *Proceedings of the National Academy of Sciences*, *112*(13), 4021–4025. https://doi.org/10.1073/pnas.1422715112

Simon, W. (2023). *mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation* [Computer software]. https://CRAN.R-project.org/package=mgcv

Smiseth, P. T. (2019). Parental Care. In B. Fath (Ed.), *Encyclopedia of Ecology (Second Edition)* (pp. 301–309). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.10560-3

Sparks, A. M., Hammers, M., Komdeur, J., Burke, T., Richardson, D. S., & Dugdale, H. L. (2022). Sex-dependent effects of parental age on offspring fitness in a cooperatively breeding bird. *Evolution Letters*, *6*(6), 438–449. https://doi.org/10.1002/evl3.300

Stearns, S. C. (1977). The Evolution of Life History Traits: A Critique of the Theory and a Review of the Data. *Annual Review of Ecology and Systematics*, *8*, 145–171. https://doi.org/10.1146/annurev.es.08.110177.001045

Stott, I., Salguero-Gómez, R., Jones, O. R., Ezard, T. H. G., Gamelon, M., Lachish, S., Lebreton, J.-D., Simmonds, E. G., Gaillard, J.-M., & Hodgson, D. J. (2024). Life histories are not just fast or slow. *Trends in Ecology & Evolution*, *39*(9), 830–840. https://doi.org/10.1016/j.tree.2024.06.001

Tettamanti, F., Witvliet, W., & Bize, P. (2012). Selection on age at first and at last reproduction in the long-lived Alpine Swift Apus melba. *Ibis*, *154*(2), 338–344. https://doi.org/10.1111/j.1474-919X.2012.01215.x

Torres, R., Drummond, H., & Velando, A. (2011). Parental Age and Lifespan Influence Offspring Recruitment: A Long-Term Study in a Seabird. *PLOS ONE*, *6*(11), e27245. https://doi.org/10.1371/journal.pone.0027245

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

van de Pol, M., Verhulst, S., Pfister, A. E. C. A., & DeAngelis, E. D. L. (2006). Age-Dependent Traits: A New Statistical Model to Separate Within- and Between-Individual Effects. *The American Naturalist*, *167*(5), 766–773. https://doi.org/10.1086/503331

Vasilieva, N. A., & Tchabovsky, A. V. (2020). Early predictors of female lifetime reproductive success in a solitary hibernator: Evidence for "silver spoon" effect. *Oecologia*, *193*(1), 77–87. https://doi.org/10.1007/s00442-020-04649-1

Vaupel, J. W., Manton, K. G., & Stallard, E. (1979). The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography*, *16*(3), 439–454. https://doi.org/10.2307/2061224

Wang, M.-H., & vom Saal, F. S. (2000). Maternal age and traits in offspring. *Nature*, *407*(6803), 469–470. https://doi.org/10.1038/35035156

Weladji, R. B., Gaillard, J.-M., Yoccoz, N. G., Holand, Ø., Mysterud, A., Loison, A., Nieminen, M., & Stenseth, N. C. (2006). Good reindeer mothers live longer and become better in raising offspring. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1591), 1239–1244. https://doi.org/10.1098/rspb.2005.3393

Weladji, R. B., Mysterud, A., Holand, Ø., & Lenvik, D. (2002). Age-related reproductive effort in reindeer (Rangifer tarandus): Evidence of senescence. *Oecologia*, *131*(1), 79–82. https://doi.org/10.1007/s00442-001-0864-6

Wen, S., Xiong, Y., Li, L., Huang, H., & Xie, Y. (2023). The effect of advanced paternal age on the lifespan of male offspring in an ancient Chinese genealogical data set. *Maturitas*, *168*, 44–48. https://doi.org/10.1016/j.maturitas.2022.10.008

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis.* (Springer-Verlag New

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025

York.). https://ggplot2.tidyverse.org

Wikel, S. K. (Ed.). (1996). *The immunology of host-ectoparasitic arthropod relationships.* Oxon, UK : CAB International. https://www.cabi.org/isc/abstract/19970500344

Wikel, S. K. (1999). Modulation of the Host Immune System by Ectoparasitic Arthropods: Blood-feeding and tissue-dwelling arthropods manipulate host defenses to their advantage. *BioScience*, *49*(4), 311–320. https://doi.org/10.2307/1313614

Wilkin, T. A., & Sheldon, B. C. (2009). Sex differences in the persistence of natal environmental effects on life histories. *Current Biology*, *19*(23), 1998–2002. https://doi.org/10.1016/j.cub.2009.09.065

Wolf, J. B., & Brodie, E. D. (1998). The Coadaptation of Parental and Offspring Characters. *Evolution*, *52*(2), 299–308. https://doi.org/10.2307/2411068

Zimmer, I., Ropert-Coudert, Y., Kato, A., Ancel, A., & Chiaradia, A. (2011). Does Foraging Performance Change with Age in Female Little Penguins (Eudyptula minor)? *PLOS ONE*, *6*(1), e16098. https://doi.org/10.1371/journal.pone.0016098

ORIGINAL UNEDITED MANUSCRIPT

Downloaded from https://academic.oup.com/evolut/advance-article/doi/10.1093/evolut/qpaf181/8258963 by Turku University user on 07 October 2025