Individual variation in nest-defence behaviour and its link with survival and reproduction in the long-lived Alpine swift

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Abstract

Given the limitations in resources that individuals can allocate to life-history traits, trade-offs are expected to occur between survival and reproduction in the wild. According to the pace-of-life syndrome (POLS) hypothesis, these trade-offs may also be accompanied by changes in behavioural traits, such as the degree to which individuals defend their offspring, because such behaviours carry risks that reduce survival while increasing reproductive success. The POLS hypothesis predicts that individuals with a 'fast' lifestyle should take more risks (e.g., stay with their offspring to defend them) and, in return, achieve higher reproductive success but have a shorter lifespan than individuals with a 'slow' lifestyle.

Using a dataset with more than 20 years of measurements from a Swiss population of Alpine swifts (*Tachymarptis melba*), I investigated how nest defence behaviours change over the course of an individual's lifespan and how these behaviours influence survival and reproductive success. This long-lived bird breeds mostly in urban colonies in Switzerland, where it may be exposed to aerial and terrestrial nest predators. Both parents incubate and raise their nestlings, allowing us to quantify nest defence behaviour based on their reaction to a human intruder approaching the nest. Responses ranged from flying away, to remaining motionless on the nest, to showing aggression toward the intruder. Analyses of intra-individual variation in nest defence behaviour across age revealed that breeding female Alpine swifts were more likely to stay on the nest and defend their offspring compared to males. Both sexes became less likely to fly away as they aged, up to around 10 years old, after which this effect reached a plateau. This pattern suggests increased investment into offspring survival as individuals age, until reaching a peak, or alternatively, that adults learn to be more defensive after the onset of reproduction. However, analyses of the relationships between reproductive traits (clutch initiation date, clutch size, brood size at fledging, and lifetime reproductive success) and nest defence behaviours in male and female Alpine swifts showed no evidence of correlations. This suggests that nest defence behaviour

has minimal detectable effects on nestling survival and adult fitness in our study system and is therefore unlikely to be under selection.

Overall, my study highlights variations in behaviours between and within individuals of a wild bird species living close to humans: nest defence behaviour varied with age, and females showed higher levels of defence behaviour. However, as there is no evidence that thisvariation confer fitness advantages, the idea that natural selection accounts for the observed natural variation in behavioural traits in this population is not supported. Therefore, this study provides no support for the POLS hypothesis, which suggests that nest defence behaviours covary with life history traits such as reproductive success and survival.

Résumé

Étant donné la limitation des ressources que les individus peuvent consacrer à leur maintenance et leur reproduction, on s'attend à ce qu'il y ait des compromis entre la survie et la reproduction en milieu naturel. Selon l'hypothèse du syndrome du rythme de vie (POLS), ces compromis devraient également s'accompagner de changements dans les traits comportementaux, de sorte que les individus ayant un mode de vie « rapide » devraient se reproduire davantage, être plus agressifs et vivre moins longtemps que les individus ayant un mode de vie « lent ». Les comportements de défense du nid, définis comme une réponse comportementale envers les prédateurs ou les humains, devraient s'inscrire dans ce continuum POLS. En effet, le degré auquel les individus défendent leur progéniture, étant donné que ces comportements comportent des risques qui réduisent la survie, pourrait avoir des impacts potentiels sur leur reproduction et leur durée de vie tout en augmentant leur succès reproductif. L'hypothèse prédit que les individus ayant un mode de vie « rapide » devraient prendre plus de risques (par exemple, rester avec leur progéniture pour la défendre) et, en retour, obtenir un succès reproductif plus élevé, mais avoir une durée de vie plus courte que les individus ayant un mode de vie « lent ».

À partir d'une étude à long terme menée pendant plus de 20 ans sur une population de martinets à ventre blanc (Tachymarptis melba) en Suisse, j'ai étudié comment les comportements de défense du nid changent au cours de la durée de vie d'un individu, ainsi que leurs impacts sur la survie et le succès reproducteur. Cet oiseau longévif se reproduit principalement dans des colonies urbaines en Suisse, où il peut être exposé à des prédateurs aériens et terrestre. Les deux parents couvent et élèvent leurs oisillons. Leur comportement de défense du nid a donc été quantifié en fonction de leur réaction à l'approche d'un intrus humain, et variait entre s'envoler, rester immobile sur le nid ou montrer de l'agressivité envers l'intrus.

Les analyses des variations intra-individuelles dans les comportements de défense du nid en fonction de l'âge montrent que les femelles reproductrices du martinet alpin étaient plus susceptibles de rester sur le nid et de défendre leur progéniture que les mâles. Les deux sexes étaient moins enclins à s'envoler en vieillissant, jusqu'à l'âge de 10 ans, après quoi cet effet atteint un plateau. Cela suggère un investissement accru dans la survie de la progéniture à mesure que les individus vieillissent, jusqu'à atteindre un pic, ou que les adultes apprennent à se défendre après avoir commencé à se reproduire. Cependant, l'analyse des relations entre les traits reproductifs (date de début de la couvée, taille de la couvée, taille de la couvée à l'envol et succès reproductif au cours de la vie) et les comportements de défense du nid chez les martinets alpins mâles et femelles n'a révélé aucune corrélation. Cela suggère que le comportement de défense du nid a des effets détectables minimes sur la survie des oisillons et la condition physique des adultes dans notre système d'étude et qu'il n'est donc pas soumis à la sélection.

Dans l'ensemble, mon étude met en évidence des variations comportementales entre les individus d'une espèce d'oiseau sauvage vivant à proximité de l'homme : le comportement de défense du nid variait en fonction de l'âge, et les femelles faisaient preuve d'un niveau de défense plus élevé que les males. Cependant, n'ayant pas montré que ces variations offraient des avantages en termes de valeur sélective, l'hypothèse selon laquelle la sélection naturelle expliquerait la variation naturelle observée dans les traits comportementaux de cette population n'est pas supportée. Par conséquent, cette étude ne vient pas étayer l'hypothèse POLS, qui suggère que les comportements de défense du nid covarient avec des traits du cycle de vie tels que le succès reproductif et la survie.

Declaration

I declare that this work was done by me under supervision of Julien Martin, Pierre Bize and Michela Dumas. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

The following people and institutions contributed to the study included in this thesis:

- Michela N. Dumas (MND): University of Ottawa, Canada
- Pierre Bize (PB): Swiss Ornithological Institute, Switzerland
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I appreciate nature, who created so many beautiful puzzles. We're just trying to pull apart a small one among them, and it's already fascinating.

Finally thank to myself for holding myself together, not giving up and being consistent to what I chose to do.

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Introduction

The life history of animals can be described by how fast they grow, when they start reproducing, how much they invest into reproduction, and how long they live. Organisms are, however, facing limited time and resources to invest in growth, reproduction and maintenance (Stearns 1992). As a result, organisms must balance (i.e. trade-off) how time and energy are attributed to each specific process to maximize fitness (Stearns 1992). Thus, studying trade-offs are fundamental to our understanding of evolution in nature (Stearns 1992).

Trade-offs are not limited to life history traits (Krebs and Davies 2009). Since life-history trade-offs depend on the allocation of energy and time, trade-offs encompass a wide diversity of traits, such as physiological, morphological and behavioural traits. For instance, nestling magpies (*Pica pica)* exhibit a trade-off between a physiological response and a morphological trait (Soler et al. 2003): it was found that, when experimentally exposed to an immune challenge, nestling magpies had a lower growth rate compared to control ones (Soler et al. 2003). Although there are many potential trade-offs across traits, we observe a non-random interaction of trade-offs across species (Stearns 1992; Ricklefs and Wikelski 2002). Some species seem to display trade-offs prominently favouring fast development and high reproduction rates at the expense of survival, whereas others prominently display trade-offs favouring slow development, slow reproduction rates, and long lifespans (Stearns 1992). This is leading to different strategies along a slow-fast continuum, with species growing fast, reproducing early and dying young, versus species with slower growth, late maturation and long-life (Ricklefs and Wikelski 2002). For example, great tits (*Parus major*) start to reproduce at one year old, produce large clutches of eggs and live 2-3 years, whereas wandering albatrosses (*Diomedea exulans*) start to reproduce at 10 years old, produce one egg every other year and live over 60 years (Weimerskirch 2018). When comparing Northern versus Southern hemisphere bird species, Ghalambor and Martin (2001) have found that Southern species on average have higher survival, lower fecundity and take less risk when facing a predator than Northern species.

Réale et al. (2010) suggested that the slow-fast continuum observed among species in terms of life-history strategy can be extended from species to individuals, given that individuals within a species can vary in their life-history strategies and trade-offs. These authors also pointed out that energy acquisition in animals depends on behaviours (foraging, exploration, ...), and therefore they suggested that behavioural variation may be at the source of trade-offs. Hence, one might expect to see differences in behavioural traits along the slow-fast continuum, with short lived individuals exploring more and moving faster than slow individuals that explore more slowly and more thoroughly. For example, a previous study on male collared flycatchers (*Ficedula albicollis*) has found that their risk-taking behavior was positively related to reproductive investment and negatively related to survival (Jablonszky et al. 2018). Another study on great tits (*Parus major*) found that females who produce more hissing calls (a form of antipredator nest defence) lay their eggs earlier and have smaller clutch sizes than females who produce fewer hissing calls (Thys et al. 2021).

Risk-taking behaviours, defined as behaviours that increase risks of injuries and decrease survival probability when facing predators and threats to life can be found in all animal species. Risk-taking behaviour, often measured as the probability to stay rather than flee, and even behave aggressively, in response to a predator model, has been shown to vary considerably among species (Ghalambor and Martin 2001) and individuals (van Oers et al. 2004). It can be measured in the context of foraging behaviour by measuring the time spent foraging in riskier areas (Verbeek et al. 1994), or by measuring how parents respond to a predator close to their nest (Montgomerie and Weatherhead 1988). For most avian species, defend against predators directly to protect their nest and offsprings during their growth. For instance, blackbirds (*Turdus merula*) tend to call when predators are approaching, while aggressive individuals may approach predators closely and dive at them or strike to attack (Knight 1986). Such behaviour often puts parents at risk of being injured or killed. Since predators are the main cause of reproduction failure in birds (Ricklefs 1969; Martin 1995), nest defence against predators is an important part of parental investment and is expected to highly influences fitness and be involved in survival vs reproduction trade-offs. For example, in great tits (*Parus major*) females that produce more hissing calls (a form of antipredator nest defence) lay their eggs earlier and have smaller clutch sizes than females that produce fewer hissing calls (Thys et al. 2021)

Individuals' risk-taking behaviour is also expected to vary with age. Indeed, young and naive individuals must familiarise themselves with predators and learn how to defend against them through experience. Hence, during the first reproductive attempts, we expect that parents should show improvement at offspring defence behaviours as suggested by Ortega et al. (2017). In addition, the cost of taking risks in term of future reproduction changes with age. Taking more risk decrease survival probability and thus decrease the probability of future reproduction. Williams (1966) defined the residual reproductive value as the sum of all expected future reproduction weighted by the survival probability to each future reproductive event. A young individual is thus expected to have a high residual reproductive value. Because individuals displaying high risk-taking behaviours are facing high costs in terms of future reproduction (i.e., death; Roff 1993), it is expected that younger individuals be less aggressive during their first(s) reproductive attempts. By contrast, as individuals get older and their survival probability decreases, they have less to lose in terms of future reproduction and are thus expected to invest more in current reproduction (Pianka and Parker 1975). Thus, in terms of nest-defence behaviour it is expected that older individuals would take more risk defending against predators given that they have a lower residual reproductive value. However, older individuals might struggle to express highly demanding behaviours due to senescence. Senescence is defined as a within-individual decrease of physiological function and could potentially lead to increase in mortality and decrease in reproductive traits (Williams 1957). Old individuals might struggle to defend against predators due to senescence (Williams 1957; Kirkwood 1977; Ricklefs 2008) and they might be expected to decrease defence against predators. If the effect of senescence is minor, we might not see such a decrease happen. Finally, previous studies have also shown evidence of terminal investment in senescent birds, with individuals showing strong increase of parental investment in their last reproductive attempt (Clutton-Brock 1984; Velando et al. 2006). This could be considered as an extreme case of when individuals have zero residual reproductive value, they completely invest into their current reproduction.

When studying age-related changes in traits, one should be careful to separate within-individual effects from among-individual variation at the population level. When studying age-related variation using natural variation in age in a non-controlled population, it is possible that selective appearance and/or disappearance hinder the detection of the within-individual effect behaviour (van de Pol and Verhulst 2006). Selective disappearance happens when mortality is strongly associated with the trait of interest leading to an over/under representation of individuals with a given value of the trait at later ages. If more aggressive individuals have a shorter lifespan due to higher risk-taking behaviour, it could lead to an apparent decrease in aggressiveness with age at the population level. For example, at the population level, common terns (*Sterna hirundo)* increased their reproductive traits with age (Zhang et al. 2015). However, longer lived individuals had higher breeding probability leading to selective disappearance and the selective disappearance explained partially the population effect (Zhang et al. 2015). Opposite to selective disappearance, selective appearance happens when individuals appear in the data at different ages because of their trait value. For example, if age at first reproduction is correlated with aggression (e.g. less aggressive individuals start to reproduce younger than more aggressive one) then a study focusing on reproductive individuals would detect an increase in aggression at the population level with age. Consequently, we must consider selective appearance and selective disappearance effect in addition to within-individual variation when we analyse the pattern of nest defence behaviours with age in natural populations.

Overall, nest defence behaviours likely appear in most avian species, can be sex specific, can be influenced by environmental conditions and age and have potential effects on reproduction success and survival (Martin 1995). However, how risk-taking changes over the course of the life of an individual remains understudied, nor do we know whether individuals who take greater risks faster lived compared to those taking less risk.

Here, we analyze the relationship between nest defence behaviours and reproduction in a long-lived bird, the Alpine swift (*Tachymarptis melba*). Alpine swifts are monomorphic long-lived migratory birds both parents provide similar parental care. Swifts recruit in the population at two or three years old when they start to reproduce. Swifts might not reproduce in their natal colony but are highly faithful to their breeding colonies (Bize et al. 2017) andbreeding nests each years afterthey start to reproduce (Dumas et al. 2025b). In urban colonies swift nests are easily accessible facilitating their study. The Alpine swift study system is ideal to ask questions related to nest-defence at the individual level. Nest defence behaviour has been shown to be a repeatable and heritable trait in Alpine swifts, with a heritability (posterior mode [lower 95% HPDI; upper 95% HPDI] of 0.235 [0.089; 0.346] (Bize et al. 2011; Bize et al. 2017). A previous study has also found a negative correlation between nest defence behaviour and natal dispersal propensity, with birds leaving the nest (not defending) having a lower probability to disperse after fledging (Bize et al. 2017).

We split the work in two parts. First, we assessed within-individual variation, as well as selective appearance and disappearance (i.e. between-individual variation), of nest defence behaviours in relation to age. The Alpine swift is long-lived species, and thus we expected that adult Alpine swifts should be more likely to flee rather than stay at their nest and defend it aggressively during the first reproductive attempts. In addition, we expected nest-defence behaviours to increase with age due to the decrease in residual reproductive value. We also expected to see individuals with higher levels of nest defence behaviour have shorter lifespan compared with those that show lower level of nest defence behaviour. Second, we investigated the relationship between reproductive traits and nest defence behaviours. Following the POLS hypothesis, we expected individuals with higher level of nest defence behaviour to lay eggs earlier, have larger clutch size and brood size at fledgling, and have higher lifetime reproductive success.

Methodology

Study species & site

Field work was conducted from 1999 to 2024 in two colonies located in Switzerland (Biel: 47°10′ N, 7°12′ E; Solothurn: 47°12′ N, 7°32′ E), 21km from each other. I was involved in the field work in 2024 summer as a part of my master's project. Those two colonies are part of a wider study including another seven colonies throughout Switzerland. The Alpine swift is a long-distance migratory bird that breeds in Europe between April/May and September/October and spends the rest of the year (non-breeding) in sub-Saharan Africa (Meier et al. 2020). Alpine swifts start breeding at two to three years old (Tettamanti 2012) and have a median lifespan of seven years of age (Moullec et al. 2023), with the oldest Alpine swift reported reaching 26 years old (Bize 2012).

During the breeding season, this colonial bird nests on cliffs and in the roof spaces of tall buildings. Swifts are monogamous, and both parents incubate their eggs (usually one to four per clutch) for about 20 days and feed the chicks until fledging at 50–70 days of age (Bize et al. 2003). Swifts return each year to reproduce in the same colony (Bize et al. 2006) and do not disperse once they have settled into a breeding site (Bize et al. 2017). This high site fidelity makes it possible to collect long-term reproductive data for the same individuals within a colony (Masoero et al. 2024; Dumas et al. 2025a; Moullec et al. 2025).

Adult Alpine swifts produce one clutch per year until their year of disappearance, which is interpreted as their year of death (Bize et al. 2009; Tettamanti 2012). The probability of recapturing breeding adults during incubation or hatching is essentially 1.0 at our study site (Bize et al. 2006); consequently, individuals that are no longer observed when breeding are considered dead. Male and female swifts do not differ in life expectancy (Bize et al. 2009; Moullec et al. 2023), they are socially monomorphic, and both sexes provide similar parental care during incubation and nestling feeding. However, previous studies have shown subtle differences in the life history trade-off between reproduction and survival (Bize et al. 2008), as well as trait-specific rates of senescence, in male and female Alpine swifts (Moullec et al. 2023). Following POLS theory, we might therefore expect these subtle sex differences in life history to be associated with sex differences in behaviour, with these behavioural differences also likely to depend on age.

Every year during the breeding season, the two colonies were visited regularly to record reproductive traits such as laying date, clutch size, and brood size at hatching and fledging. Alpine swift adults were captured by hand while they were incubating or brooding nestlings. Adult body mass was measured in grams using a digital scale to the nearest 1 g each time they were captured. Wing length, tail length, and fork length were measured with a ruler to the nearest 1 mm at the first capture each year. Sternum length was measured using a calliper to the nearest 0.1 mm, also at the first capture each year.

Eggs were marked to record their hatching date, and chicks were ringed with an aluminium numbered band 10 days after hatching. Nestling biometrics (body mass, wing length, tail length, fork length, sternum length, and parasite load) were measured throughout their development at 10, 20, 30, 40, and 50 days of age. As swifts are visually monomorphic (Dumas et al. 2025b), genetic markers were used to determine their sex (Griffiths et al., 1998). DNA was extracted from blood samples or feathers collected from adult birds (Griffiths et al., 1998).

Nest-defence behaviour

Alpine swifts can experience nest predation by aerial predators such as corvids, or by terrestrial predators such as rats (*Rattus sp.*) and stone martens (*Martes foina*). For example, one nearby colony, located in the *Jesuitenkirche* building in the city of Solothurn, only 200 m from our monitored colony in the *Bieltor* building, went completely extinct in the 1990s, with more than 100 breeding pairs disappearing following predation by a stone marten on eggs, nestlings, and adults (Pierre Bize, personal communication). In our monitored colony *Stadtkirche* in Biel, Alpine swift nests were exposed to predation by jackdaws (*Coloeus monedula*) in the early 2000s to 2010 (Pierre Bize, personal communication). Nest-defence behaviours of Alpine swifts have been recorded each year since 2003 by scoring how breeding individuals respond to a human approaching the nest. Because humans are major predators for many species, we interpret these responses as proxies for nest-defence behaviour against predators. Methods relying on how animals respond to a human approach are frequently used to quantify animal vigilance and flight initiation distance (Hammer et al. 2023; Dsouza et al. 2025) or nest-defence behaviour in birds (Hollander et al. 2008). A study on Eurasian kestrels (*Falco tinnunculus*) also found that nest-defence responses toward human match those shown toward predators (Carrillo & Aparicio 2001).

In Alpine swifts, parental behaviour was ranked on a 0–2 scale based on how individuals respond to an approaching observer (Bize et al. 2011, 2017). Individuals that immediately leave the nest when the observer approaches receive a score of 0. Those that remain in the nest as the observer approaches but leave when capture is attempted, receive a score of 0.5. Individuals that remain still throughout the entire process receive a score of 1. If individuals stay immobile during the approach but become aggressive during capture (e.g., wing flapping, pecking), they receive a score of 1.5. Individuals that display aggression immediately receive a score of 2. Higher behavioural scores indicate greater defensiveness toward intruders at the nest (Bize et al. 2017).

Statistical analysis

Statistical analyses were performed in R version 4.4.1 (R Core Team 2024). We used data collected between 2003-2024 and included only individuals who were recruited into the population as breeding adults, of know sex, and of exact known age and age at first reproduction (5331 observations of behaviour scores, 831 individuals). Quadratic effects were estimated using the *poly ()* function in R. The numeric variables were scaled to mean of 0 and variance of 1 before analyses. Given that the following analysis combined models fitted with a frequentist approach and others fitted with a Bayesian approach, we followed suggestions by Muff *et al.* (2022) and always refer to the strength of evidence rather than statistical significance for all our results.

To analyze changes in nest defence behaviours in response to individual age, we fitted a cumulative linked mixed model (clmm) using the R package *ordinal* (Christensen 2023). To evaluate the relation between age and nest defence behaviour at the population level, with behaviour scores as the dependent variable and age (linear and quadratic effects), sex, colony and time since the start of the study as fixed effects. Individual identity (ring number) and year were included as random effects to account for repeated measurements. Since 81.6% of the behaviour observations were measured by the same observer, we did not include the observer identity as a random effect. We also included an interaction term between colony and time since the start of the study to assess changes in behaviour scores differing between the colonies over the course of the study. Previous studies on Alpine swifts have reported that the change of behaviour scores since the start of the study differed between colonies (Bize et al. 2011, 2017).

Age specific changes in nest defence behaviour

We evaluated how nest defence behaviour changed with age both at the population level and the within individual level simultaneously and separated potential effects of selective appearance and disappearance. To do so, we applied a within individual centering approach with quadratic effects of age (Fay et al. 2022). We fitted nest defence behaviour as the dependent variable, with the individual mean of age and age squared, the within-individual centered age and centered age squared (calculated by subtracting the individual mean from each measurement), sex, colony and time since the start of the study as fixed effects. We included the colony and time since the start of the study interaction term as fixed effects, and individual identity and year as random effects. In this model, the individual mean of age and age squared explain changes at the population level (among-individual variation) driven by demographic effects, while the centered age and centered age squared explain within-individual variation with age driven by ageing.

To investigate the selective appearance and disappearance (van de Pol and Verhulst 2006), we fitted another model with the nest defence behaviour in response to age (linear and quadratic effect), age at first reproduction, lifespan, sex and an interaction term of time since the start of the study and colony as fixed effects, year of measurement and individual identity as random effects. The dataset was restricted to individuals of known age at first reproduction and known lifespan (3405 observations of behaviour score, 599 individuals). In this model, age at first reproduction represents selective appearance, while lifespan represents selective disappearance.

Nest-defence behaviour and reproductive traits

To estimate the correlation between reproductive traits (clutch size, clutch initiation date, brood size at fledgling and lifetime reproductive success) and behaviour, we fitted a series of bivariate models using the R package *MCMCglmm* (Hadfield 2010). Lifetime reproductive success was calculated as the sum of brood size at fledgling of each individual through their lifetime and log transformed. We ran each model separately for males and females (Males: 2428 observations, 371 individuals; females: 2903 observations, 460 individuals). In each model, the nest defence behaviour and one of the reproductive traits were fitted as response variables, with age (linear and quadratic effect estimated with the polynomial function) and colony as fixed effects on both traits. We fitted individual identity and year as random effects on both traits to estimate the between individual and between year correlations. We calculated the correlation coefficients as COV (A, B) / (sqrt (V_A *V_B)) where V_A and V_B were the variance of variable A and B respectively and COV (A, B) was their covariance from the posterior samples of the model. For both random effects, we used the following non-informative prior: V = diag (2), nu = 1.002. Since the nest defence behaviour was modeled as an ordinal trait, we also fixed the residual variance to 1 for the behaviour (prior: V = diag(2), nu=1.002, fix=2; Nakagawa and Schielzeth 2010). For lifetime reproductive success models, we kept the same fixed and random effect structure for the behaviour but fitted only colony as a fixed effect and individual identity as a random effect since there was only one measurement of lifetime reproductive success per individual. In addition, since lifetime reproductive success had only one measurement per individual, we forced the among-individual variance that should be estimated at the residual level to be estimate at the among-individual level by fixing the residual variance to a really small value (prior for residual variance: V = diag(2)*c(0.001,1), nu=1.002, fix=1). For clutch initiation date and clutch size, the models were run for 4.2×10^5 iterations, with a burn-in of 20,000 and a thinning interval of 100. For brood size at fledgling and lifetime reproductive success for males, the models were run for 1.2×10^6 iterations, with a burn-in of 20,000 and a thinning interval of 1000. For lifetime reproductive success for females, the models were run for 5.02×10^6 iterations, with a burn-in of 20,000 and a thinning interval of 5000. The models passed the Heidelberg stationary test and had autocorrelation level between retained iterations lower than 0.1.

Results

Age-related variation in nest defence behaviour

At the population level, nest defence behaviour increased non-linearly with age (strong evidence for linear and quadratic effects of age; Table 1), with individuals becoming more prone to taking risk during their first years of breeding before reaching a plateau after 12 years of age (Figure 1). On average, males were more likely to fly away from the nest than females, and individuals in Biel were more likely to stay in their nests than those in Solothurn (Table 1). Individuals became less prone to fly away over the course of the study, with a faster decrease in behaviour score for those from Biel than Solothurn (evidence for an interaction between colony and year; Table 1).

Using a within-individual centering approach with quadratic effects (Fay et al. 2022), we found an effect of age only at the within individual level. Nest defence behaviour scores increased throughout age at the within-individual level (linear and quadratic effects of age; Table 2, Figure 2). As reported at the population level (Table 1), females were more prone to stay in their nests than males, and individuals in Biel were more likely to stay in their nests than those in Solothurn (Table 2). The behaviour scores decreased over the course of the study (Table 2, Figure 3), with behaviour scores of individuals from Biel decreasing faster than those from Solothurn (Table 2). At the between individual level, we found no relationship between age and nest-defence behaviour, and in turn no support for selective appearance or disappearance. This finding is further supported by models on age at first reproduction and lifespan. We found no evidence for effects of either age at first reproduction or lifespan on behaviour scores. The output of this model is reported in the supplementary (Table S1).

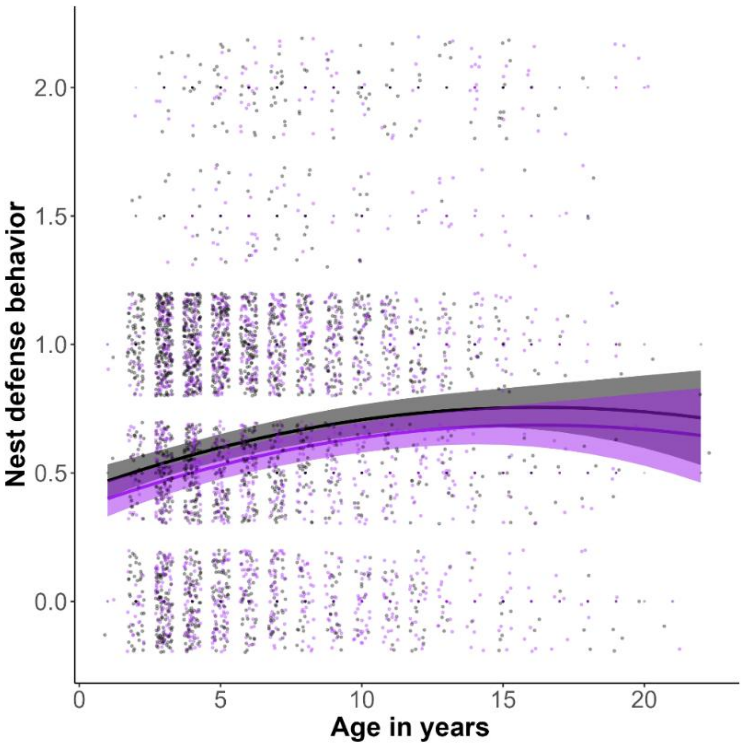

Figure 1: Age-related change in nest defence behaviour in male and female (displayed as purple and black, respectively) Alpine swifts breeding in two urban colonies in the cities of Biel and Solothurn, Switzerland. Regression lines derived from a linear mixed effect model with behaviour as a numeric variable are displayed with 95% confidence interval. Jittered dots reflect the raw data, with nest defence behaviour scores of 0 to 2 mirroring increase in risk-taking in response to human observers approaching the nest (0 = fly away, 1 = stay at the nest, and 2 = behave aggressively toward the observer).

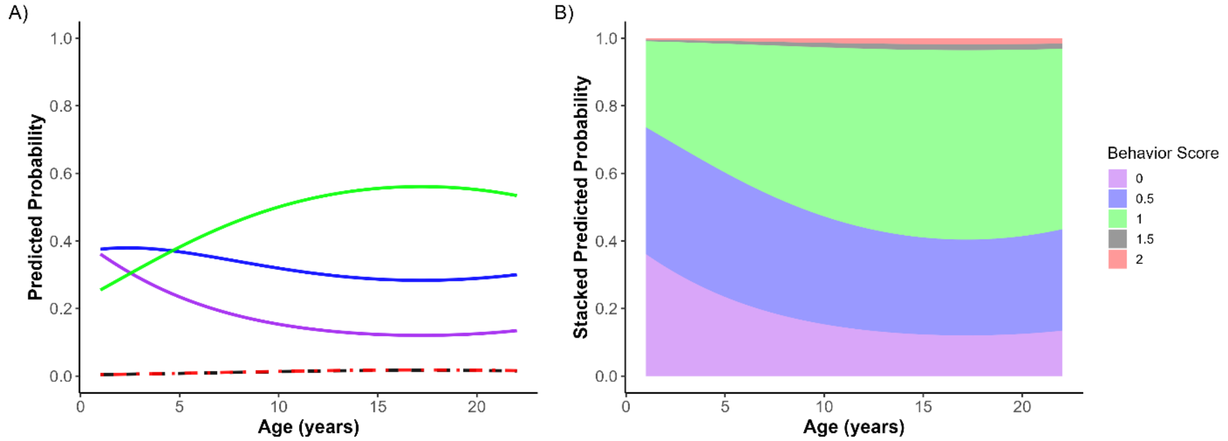

Figure 2: Predicted probability distribution and stacked predicted probability distribution of nest defence behaviour scores in response to scaled age in Alpine swifts. A: Colored lines represent the predicted probabilities for each score (purple=0, blue=0.5, green=1, black=1.5, red=2). B: Colored areas represent the predicted probabilities for each score (purple=0, blue=0.5, green=1, black=1.5, red=2). Predictions were derived from a cumulative link mixed model (Table 1).

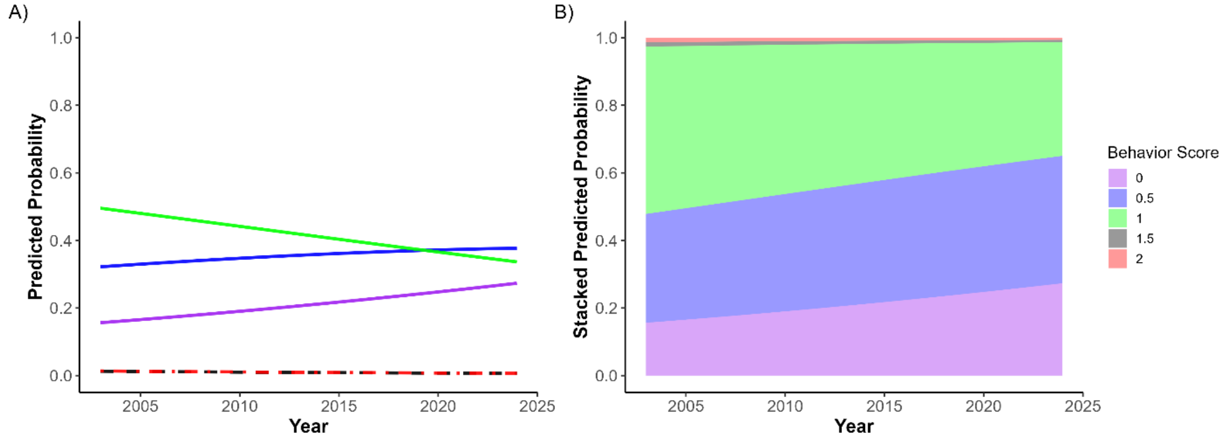

Figure 3: Predicted probability distribution and stacked predicted probability distribution of nest defence behaviour scores in response to study years in Alpine swifts. A: Colored lines represent the predicted probabilities for each score (purple=0, blue=0.5, green=1, black=1.5, red=2). B: Colored areas represent the predicted probabilities for each score (purple=0, blue=0.5, green=1, black=1.5, red=2). Predictions were derived from a cumulative link mixed model (Table 1).

Table 1: Estimates, standard errors, Z values and P values (clmm model fit using the R package *ordinal*) for the relationship between nest-defence behaviour scores and fixed and random effects for adult Alpine swifts. Estimates with P values less than 0.05 are considered to show evidence of an effect and are bolded. Female is the reference level for sex. Solothurn is the reference level for colony. Time since start of study and age were scaled.

	Estimate	**Standard Error**	**Z-value**	**P-value**
Number of observations: 5331; number of individuals: 818; number of years: 22				
Age	**25.14**	**3.68**	**6.83**	**<0.001**
Age^2	**-6.75**	**3.01**	**-2.24**	**0.025**
Sex (Male)	**-0.37**	**0.13**	**-2.77**	**0.006**
Colony (Biel)	**0.58**	**0.14**	**4.08**	**<0.001**
Time since start of study	**-0.23**	**0.11**	**-2.16**	**0.031**
Colony (Biel): Time since start of study	**-0.34**	**0.12**	**-2.84**	**0.005**
Random effects	Variance		Standard deviation	
Individual identity	2.27		1.51	
Year	0.04		0.20	
Cutpoints				
0|0.5	**-1.31**	**0.14**	**-9.56**	**<0.001**
0.5|1	**0.29**	**0.14**	**2.11**	**0.035**
1|1.5	**3.98**	**0.16**	**24.55**	**<0.001**
1.5|2	**4.66**	**0.18**	**26.48**	**<0.001**

Table 2: Estimates, standard errors, Z values and P values (clmm model fit using the R package *ordinal*) for the relationships between behaviour scores and population and individual level effects for adult Alpine swifts. Estimates with P values less than 0.05 are considered to show evidence of an effect and are bolded. Female is the reference level for sex. Solothurn is the reference level for colony. The age and time since the start of the study were scaled.

	Estimate	**Standard Error**	**Z-value**	**P-value**
Number of observations:5331; number of individuals: 818; number of years: 22				
Age (between individual)	0.44	0.27	1.62	0.105
Age^2 (between individual)	-0.22	0.27	-0.82	0.415
Age (within individual)	**0.44**	**0.11**	**4.13**	**<0.001**
Age^2 (within individual)	**-0.22**	**0.11**	**-2.10**	**0.036**
Sex (Male)	**-0.36**	**0.14**	**-2.64**	**0.008**
Colony (Biel)	**0.56**	**0.14**	**3.91**	**<0.001**
Time since the start of the study	**-0.27**	**0.11**	**-2.39**	**0.017**
Colony (Biel): Time since the start of the study	**-0.33**	**0.12**	**-2.77**	**0.006**
Random effects	Variance		Standard deviation	
Individual identity	2.26		1.50	
Year	0.04		0.20	
Cutpoints				
0|0.5	**-1.29**	**0.14**	**-9.35**	**<0.001**
0.5|1	**0.30**	**0.14**	**2.22**	**0.026**
1|1.5	**4.00**	**0.16**	**24.47**	**<0.001**

	Estimate	**Standard Error**	**Z-value**	**P-value**
Number of observations:5331; number of individuals: 818; number of years: 22				
1.5|2	**4.68**	**0.18**	**26.41**	**<0.001**

Reproductive traits and nest defence behaviour

None of the correlations between reproductive traits (clutch initiation date, clutch size and brood size at fledgling and lifetime reproductive success) and nest defence behaviour in either males or females were found to differ from zero (Table 3). The HPDI were narrow, overlapped zero, and the estimates were relatively small (absolute value lower than 0.15) (Table 3). The sex-specific models are reported in Tables S2-S5.

Table 3: Correlation coefficients (and 95% HPDI [lower; upper]) between nest defence behaviours, reproductive traits (clutch initiation date, clutch size, brood size at fledgling and lifetime reproductive success) at the individual, year and residual level for male and female adult Alpine swifts.

	Male		**Female**	
	Individual	**Year**	**Individual**	**Year**
Clutch initiation date	-0.02 [-0.19; 0.14]	-0.39 [-0.73; 0.13]	-0.03 [-0.19; 0.09]	-0.19 [-0.57; 0.35]
Clutch size	-0.08 [-0.26; 0.08]	0.07 [-0.36; 0.52]	-0.01 [-0.15; 0.15]	0.14 [-0.27; 0.61]
Brood size at fledgling	-0.02 [-0.19; 0.20]	-0.00 [-0.42; 0.49]	-0.06 [-0.21; 0.14]	-0.02 [-0.50; 0.40]
Lifetime reproductive success	-0.09[-0.20; 0.11]	-	0.10[-0.03; 0.23]	-

Discussion

In this study investigating changes in nest defence behaviour with age and its relationships to lifespan, reproductive traits and lifetime reproductive success, we found the following main results. First, as individuals become older and more experience, they were more prone to stay on their nest in response to a human approaching. Second, nest defence behaviour score decreased through the study period. Third, there was no evidence of any correlation between nest defence behaviour and reproductive traits or lifetime reproductive success. Fourth, females were more prone than males to take risk (i.e. stay on nest or behave aggressively), and individuals in Biel were more prone than those in Solothurn to take risk.

The observed change in nest defence behaviour with age at the individual level could be explained by three non-mutually exclusive mechanisms: 1) change in parental investment towards offspring with age, 2) the learning process of nest defence behaviour with reproductive experience and 3) habituation to human approach. Alpine swifts may stay in their nests more as they get older to invest more to produce offsprings, since offsprings become more valuable to them. Montgomerie and Weatherhead (1988) pointed out that as parents have more experience when they get older, the survival probability of offsprings increases independently of parent risk taking behaviour, thus increasing the expected value of future offspring. As a result, parents increase their investment for offsprings as they are more valuable. For species that senesce, an increase in parental effort is expected as parents' survival is decreasing (Montgomerie and Weatherhead 1988). In addition, when ill or facing an immune challenge, individuals might invest more into current reproduction (Clutton-Borck 1984; Podmokla et al. 2014). Since previous studies have found evidence for senescence of Alpine swifts (Moullec et al. 2023), we could infer that Alpine swifts increase in nest defence score might be associated to an increase in parental effort as they are senescing. However, we found that nest defence behaviour scores increased with age up to 10 years old (Table 1-2; Figure 1), which is when Alpine swifts start experiencing senescence (Moullec et al. 2023). This result is inconsistent with an increase in reproductive investment with aging. This might suggest instead that adults become more familiar with predators as they get older, becoming less likely to flee and more likely to remain at the nest. Blue-footed boobies *Sula nebouxii* show a similar pattern of nest defence behaviour with age, with an increase in aggressiveness through their early life stage, that might have been driven by learning (Ortega et al. 2017). Although individuals may learn to properly defend against predators in early life, we expect this process to be fast and follow a plateau after the first few years of reproduction (Immelmann 1984). Based on previous studies about behavioural learning process of birds, most of them show rapid learning process after one capture event by human (Marzluff et al. 2010; Linhart et al. 2012; Blum et al. 2020). Since our study found the attenuation started at late life stage (around 10 years old), our result may not support the fast-learning process. Although the attenuation of the increase happened late (around 10 years old), the increase of nest defence through the early life stage could still be explained by maturation. We also found that nest defence behaviors do not differ based on individuals' age at first reproduction. Previous work has found that selection favors individuals starting reproduction earlier in Alpine swifts (Tettamanti et al. 2012). This suggests that nest defence behavior is unlikely to be associated to the selection on age at first reproduction.**4**

We found that nest defence behaviour scores changed over the course of the study at the population level in both colonies as shown in Figure 3. The predicted probability of score 0 and 0.5 increased, while score 1-2 decreased with time. As years since the start of the study increases, individuals are less likely to stay in their nests or actively defend it, and more likely to fly away during human interaction. This might be due to sensitization to human disturbance. Sensitization was defined as an increase of responsiveness caused by a repeated stimulus (Groves and Thompson 1970). Although human observers are harmless, birds were still bothered by human and being caught and measured. In addition, being kept in human hands forces them to stay away from their nests and thus leave their eggs or offsprings away from parental care. So, even if human handling has no survival cost for an adult it still has a cost associated to lower parental care and missed opportunities for other behaviours. Previous studies have also found evidence of sensitization to human handling in other avian species (Seress et al. 2017; Kluen et al. 2022). Thus, it suggests that at the population level at least, Alpine swifts are being sensitized and tend to avoid human handling more than at the start of the study.

According to previous studies on risk taking behaviour, behaviour often has an impact on reproductive traits (Clay et al. 2018; Dingemanse et al. 2020; Thys et al. 2021). Following the POLS hypothesis, we predicted that more aggressive individuals would also be more productive and live shorter compared to less aggressive ones (Réale et al. 2010). We found among-individual variations in reproductive traits (clutch initiation date, clutch size, brood size at fledgling) with effects of age, colonies and year (Table S2-S5). However, we did not find any correlations between nest defence behaviour and lifespan (Table S1) or any reproductive traits (Table 3). This clearly indicates an absence of selection for nest defence behaviour. In our study, Alpine swifts breed in colonies where nest predators are rare for most of the study years and colonies (Masoero et al. 2024). In addition, human interactions with birds during the study is kept to a minimum to decrease any potential impact of human presence and handling on the birds. Potentially, the absence of selection detected is due to a combination of low human impact and low predation event at the colonies. However, when predation events happen, they are usually quite intense potentially wiping out a colony seen in 1990 in a close by colony (PB, personal communication). We would thus expect nest defense behaviour to be under selection. The intensity and low frequency of predation event might render the detection of selection for this behaviour extremely difficult, and it would be great to be able to measure the difference in behaviour in years with and without strong predation events.

Nest defence scores were affected by sex and colony. Females are more likely to stay in nests than male, and individuals in Biel are more likely to stay in nests than those in Solothurn (Table 1). Previous study has pointed out that due to the different life history strategies between male and female, variation in female fitness is more affected by variation in reproduction, while variation in male fitness is more affected by variation in survival (Bize et al. 2008). This might suggest that females tend to protect their offsprings during the breeding season, while males are more likely to fly away to maximize their survival. A previous study on blue tit (*Cyanistes caeruleus*) also found that females are more aggressive than males during incubation (Boiten et al. 2023). They pointed out that females might have evolved to be more aggressive because they must invest more into offspring, however they did not experimentally test for it (Boiten et al. 2023). For Alpine swifts, however, female and male provide similar parental care (Bize 2009). The existence of sexual difference in nest defence behaviour still needs further study. The colony variation suggests that nest defence behaviour is affected by local breeding environment. As Bize et al. (2011) mentioned, Biel has stronger competition for nestling sites that favors individuals who take more risks (Bize et al. 2011). In addition, the decrease in behaviour score through years also differed among colonies, with individuals in Biel decreasing faster than those in Solothurn (Table 1). This might suggest a variation of sensitization in those two colonies due to different local environment. By comparing the variance of individual identity and year as random effects, we find that most of the variance is explained by individual identity rather than year, which suggests that between year variation of behaviour scores is minor. Thus, nest defence behaviour is a repeatable trait with consistent variation between individuals. As a result, the age-related change of behaviour is due to phenotypic plasticity.

In conclusion, the change of behaviour through age in adult Alpine swifts might be caused by the change of parental investment and a learning process. Over the long-term study, sensitization potentially occurred so that behaviour score decreased with year. Due to life strategy difference between males and females, nest defence behaviour varied between sex. It was also affected by local breeding environment. Since human observers and handlers are harmless for swifts, and there was little predation found in the colonies during the study years, we did not detect fitness consequence of nest defence behaviour. Overall, our study investigated the change of behaviour under human impact in two of the Alpine swift colonies located in cities. As a wild animal that been breeding in cities for hundreds of years, analysing the change and fitness consequence of their behaviour against human observers is important to understanding human interactions with wildlife species. As a next step, we could focus on the variation of nest defence behaviour within each nesting cycle, similarly to Pearson et al. (2005), to see how birds of different ages adjust their nest defence behaviour from incubation to fledgling stages since the energy allocated for a given reproduction event increases as offsprings develop and become more valuable.

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Supplementary

Table S1: Estimates, standard errors, Z values and P values (clmm model fit using the R package ordinal) for the relationships between behaviour scores and fixed and random effects for Alpine swifts' adults. Estimates with P values less than 0.05 are considered to show evidence of an effect and are bolded. Female is the reference level for sex. Solothurn is the reference level for colony. The years since the first reproduction variables are considered as factors.

	Estimate	**Standard Error**	**Z-value**	**P-value**
Number of observations: 3405; number of individuals: 599; number of years: 21				
Age	**12.47**	**4.42**	**2.82**	**0.005**
Age^2	**-8.90**	**2.89**	**-3.08**	**0.002**
Age at first reproduction	-0.11	0.08	-1.36	0.175
Lifespan	-0.01	0.11	-0.07	0.943
Sex(Male)	**-0.31**	**0.16**	**-1.97**	**0.049**
Colony(Biel)	**0.40**	**0.18**	**2.27**	**0.023**
Time since start of study	-0.13	0.16	-0.79	0.429
Colony(Biel): Time since start of study	**-0.41**	**0.16**	**-2.55**	**0.011**
Random effects	Variance		Standard deviation	
Individual identity	2.16		1.47	
Year	0.05		0.23	
Cutpoints				

	Estimate	Standard Error	Z-value	P-value
Number of observations: 3405; number of individuals: 599; number of years: 21				
0|0.5	**-1.49**	**0.18**	**-8.48**	**<0.001**
0.5|1	0.24	0.17	1.40	0.160
1|1.5	**4.08**	**0.20**	**19.99**	**<0.001**
1.5|2	**4.89**	**0.22**	**21.78**	**<0.001**

Nest defence behaviour and fitness

Females lay eggs earlier when paired with older males. There is also evidence for a positive interaction between colony and year for clutch initiation date of the partners of males in Solothurn, indicating that clutch initiation dates in Solothurn become later over the years (Table S2). Female clutch initiation date is also influenced by age, showing a pattern similar to that of males: they lay earlier as they age, but later again in their final years. Females in Biel lay eggs later than those in Solothurn, while clutch initiation dates in Solothurn become progressively later each year compared with Biel (Table S2).

There is strong evidence for a relation between male clutch size and age, increasing at first and then declining as males grow older. Males in Biel have smaller clutch sizes than those in Solothurn. In both Biel and Solothurn, clutch size is associated with the interaction between colony and year (Table S3). Females show a similar pattern: they lay more eggs early in life, and clutch size decreases as they age. Birds in Biel lay fewer eggs than those in Solothurn. Female clutch size is also positively correlated with the interaction between colony and year (Table S3).

Both female and male brood size at fledging follow the same increase-then-decrease pattern (Table S4). Males in Biel have smaller brood sizes at fledging compared with those in Solothurn. Brood size at fledging in males is positively correlated with the interaction between colony and year.

Table S2: Estimates (posterior mode) and 95% HPDI intervals (bivariate Bayesian model fit using the R package *MCMCglmm*) for the relationships between behaviour score and female and male clutch initiation day in response to fixed effects and random effects variance and covariance for adult Alpine swifts. Estimates with 95% HPDI intervals that exclude 0 were deemed to show evidence of an effect and were bolded. Solothurn is the reference level for colony. Clutch initiation day, age and year were scaled.

	Male			Female		
	Esti-mates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Esti-mates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Clutch initiation date effects						
Intercept	-0.14	-0.44	0.18	-0.12	-0.44	0.17
Age	**-16.87**	**-19.51**	**-14.31**	**-22.08**	**-24.84**	**-19.20**
Age2	**12.29**	**10.30**	**14.52**	**17.53**	**15.25**	**19.69**
Time since start of study	0.09	-0.01	0.20	0.25	-0.07	0.58
Colony(Biel)	0.27	-0.07	0.56	**0.22**	**0.11**	**0.33**
Colony(Biel): Time since start of study	**-0.36**	**-0.45**	**-0.27**	**-0.26**	**-0.35**	**-0.17**
V_{years}	0.48	0.22	0.82	0.48	0.23	0.82
$V_{individuals}$	0.15	0.11	0.19	0.23	0.18	0.28
Behaviour effects						
Intercept	**0.81**	**0.48**	**1.11**	**1.02**	**0.75**	**1.29**
Age	**16.42**	**8.13**	**24.53**	**22.41**	**14.05**	**30.22**
Age^2	-2.74	-9.31	3.63	**-9.64**	**-16.71**	**-2.85**
Colony(Biel)	**0.41**	**0.07**	**0.74**	**0.50**	**0.20**	**0.79**
Time since start of study	-0.10	-0.39	0.18	-0.26	-0.53	-0.00
Colony(Biel): Time since start of study	**-0.35**	**-0.63**	**-0.07**	-0.21	-0.46	0.06
V_{years}	-0.09	-0.25	0.05	0.13	0.06	0.24

$V_{\text{individuals}}$	1.50	1.13	1.87	1.39	1.06	1.72
Covariance between clutch initiation date and behaviour						
$\text{Cov}_{\text{years}}$	-0.09	-0.25	0.05	-0.03	-0.17	0.10
$\text{Cov}_{\text{individuals}}$	-0.01	-0.09	0.07	-0.03	-0.11	0.05

Table S3: Estimates (posterior mode) and 95% HPDI intervals (bivariate Bayesian model fit using the R package *MCMCglmm*) for the relationships between behaviour score and female and male clutch size in response to fixed effects and random effects variance and covariance for adult Alpine swifts. Estimates with 95% HPDI intervals that exclude 0 were deemed to show evidence of an effect and were bolded. Clutch size, age and year were scaled.

	Male			**Female**		
	Esti-mates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Esti-mates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Clutch size effects						
Intercept	0.12	-0.05	0.28	0.07	-0.10	0.26
Age	**5.94**	**2.76**	**9.39**	**15.96**	**12.47**	**19.74**
Age^2	**-5.61**	**-8.54**	**-2.76**	**-12.97**	**-15.89**	**-9.97**
Colony (Biel)	**-0.24**	**-0.37**	**-0.11**	**-0.26**	**-0.40**	**-0.13**
Colony (Biel): time since start of study	**0.12**	**0.01**	**0.23**	0.11	0.00	0.23
Time since start of study	0.04	-0.14	0.21	0.04	-0.15	0.23
$V_{individuals}$	0.19	0.14	0.24	0.30	0.24	0.37
V_{years}	0.11	0.04	0.18	0.12	0.06	0.21
Behaviour effects	**0.80**	**0.47**	**1.10**	**1.02**	**0.72**	**1.29**
Intercept	**16.68**	**8.45**	**24.37**	**22.59**	**14.29**	**30.55**
Age	-2.66	-9.45	3.74	**-9.69**	**-16.85**	**-3.12**
Age^2	**0.41**	**0.09**	**0.77**	**0.50**	**0.20**	**0.81**
Colony (Biel)	-0.11	-0.40	0.18	-0.25	-0.54	-0.00
Colony (Solothurn): year	**-0.35**	**-0.62**	**-0.07**	-0.20	-0.45	0.06

	Male			Female		
	Estimates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Estimates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Clutch size effects						
$\mathbf{V}_{\mathbf{years}}$	0.15	0.06	0.27	0.14	0.05	0.24
$\mathbf{V}_{\mathbf{individuals}}$	1.49	1.12	1.87	1.39	1.09	1.74
Covariance between clutch size and behaviour						
$\mathrm{Cov}_{\mathrm{years}}$	0.01	-0.06	0.07	0.02	-0.05	0.09
$\mathrm{Cov}_{\mathrm{individuals}}$	-0.05	-0.14	0.05	0.00	-0.09	0.10

Table S4: Estimates (posterior mode) and 95% HPDI intervals (bivariate Bayesian model fit using the R package *MCMCglmm*) for the relationships between behaviour score and female and male brood size at fledgling in response to fixed effects and random effects variance and covariance for adult Alpine swifts. Estimates with 95% HPDI intervals that exclude 0 were deemed to show evidence of an effect and were bolded. Age and year were scaled.

	Male			**Female**		
	Esti-mates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Esti-mates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Brood size at fledgling effects						
Intercept	**0.53**	**0.34**	**0.73**	**0.46**	**0.27**	**0.66**
Age	**3.65**	**0.91**	**6.54**	**6.25**	**3.29**	**9.14**
Age^2	-2.42	-4.94	0.26	**-7.86**	**-10.55**	**-5.20**
Colony(Biel)	**-0.25**	**-0.35**	**-0.15**	**-0.18**	**-0.27**	**-0.09**
Colony(Biel):time since start of study	0.01	-0.19	0.22	0.06	-0.15	0.28
Time since start of study	0.02	-0.08	0.11	-0.02	-0.11	0.06
V_{years}	0.18	0.08	0.31	0.19	0.08	0.33
$V_{individuals}$	0.08	0.05	0.11	0.08	0.06	0.11
Behaviour effects	**0.80**	**0.50**	**1.11**	**1.03**	**0.73**	**1.30**
Intercept	**16.55**	**8.62**	**24.49**	**22.65**	**14.63**	**30.73**
Age	-2.84	-9.46	3.90	**-9.55**	**-16.17**	**-2.46**
Age^2	**0.41**	**0.08**	**0.73**	**0.49**	**0.21**	**0.79**
Colony(Biel)	-0.10	-0.40	0.18	-0.25	-0.51	0.01
Colony(Biel):year	**-0.35**	**-0.62**	**-0.05**	-0.21	-0.46	0.05
V_{years}	0.01	-0.08	0.10	0.13	0.05	0.24

	Male			**Female**		
	Esti-mates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Esti-mates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Brood size at fledgling effects						
$V_{individuals}$	0.00	-0.07	0.07	1.39	1.07	1.72
Covariance between brood size at fledgling and behaviour						
Cov_{years}	0.15	0.06	0.27	-0.01	-0.09	0.07
$Cov_{individuals}$	1.49	1.12	1.88	-0.01	-0.07	0.05

Table S5: Estimates (posterior mode) and 95% HPDI intervals (bivariate Bayesian model fit using the R package *MCMCglmm*) for the relationships between behaviour score and female and male lifetime reproductive traits in response to fixed effects and random effects variance and covariance for adult Alpine swifts. Estimates with 95% HPDI intervals that exclude 0 were deemed to show evidence of an effect and were bolded. Lifetime reproductive traits, age and year were scaled.

	Male			**Female**		
	Estimates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Estimates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Lifetime reproductive success effect						
Intercept	**1.67**	**1.52**	**1.80**	**1.66**	**1.54**	**1.78**
Colony (Biel)	**0.48**	**0.23**	**0.72**	**0.41**	**0.19**	**0.62**
$V_{individuals}$	**1.00**	**0.85**	**1.17**	**1.06**	**0.91**	**0.21**
Behaviour effect						
Intercept	**0.93**	**0.57**	**1.28**	**1.12**	**0.80**	**1.47**
Age	**12.09**	**4.46**	**20.05**	**18.96**	**10.44**	**27.25**
Age^2	-3.89	-10.34	2.61	**-9.45**	**-16.66**	**-3.06**
Colony (Biel)	0.34	-0.08	0.75	**0.41**	**0.03**	**0.80**
Time since start of study	-0.08	-0.42	0.24	-0.23	-0.56	0.08
Colony (Biel): Time since start of study	**-0.40**	**-0.74**	**-0.03**	**-0.35**	**-0.68**	**0.01**
V_{years}	**0.07**	**0.00**	**0.16**	**0.07**	**0.00**	**0.16**

	Male			**Female**		
	Estimates	**Lower 95% HPDI**	**Upper 95% HPDI**	**Estimates**	**Lower 95% HPDI**	**Upper 95% HPDI**
Lifetime reproductive success effect						
$V_{individuals}$	**1.48**	**1.07**	**1.94**	**1.67**	**1.25**	**2.08**
Covariance between lifetime reproductive traits and behaviour						
$Cov_{individuals}$	**-0.08**	**0.26**	**0.12**	**0.13**	**-0.05**	**0.31**