Sex-specific genetic architecture and fitness consequences of subtly dimorphic traits in the long-lived Alpine swift

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Abstract

Previous research has been disproportionately focused on the evolution and maintenance of male secondary sexual traits in species with polygynous mating systems and pronounced sexual dimorphism (SD), where sexual selection plays an obvious role. Further, the evolution of SD is seen as a potential resolution of intra-locus sexual conflict, which has the potential to be especially strong in species with weak SD. Consequently, our understanding of sexual selection and sexual conflict has remained incomplete.

In this thesis, I contributed to addressing these gaps using a quantitative genetic approach to investigate how shared genetic architecture may drive sex-specific responses to selection in a bird previously characterized as monomorphic, the Alpine swift *Tachymarptis melba*. I first quantified SD in morphometric traits and suggest that the Alpine swift is rather subtly dimorphic. I found that fork length and body mass have the potential to be shaped by sexual selection and that their SD has changed over the past two decades. Thus, I further investigated these two traits. In regard to fork length, I found a cross-sex genetic correlation nearing one suggesting a strong genetic constraint, directional selection suggesting a possible role of mutual selection, and an absence of microevolution change in either sex despite phenotypic changes in females. An explanation for this change in morphology counter to evolutionary predictions—directional selection coupled with a strong cross-sex genetic correlation would be expected to result in shared evolutionary trajectories between the sexes—goes beyond the scope of this thesis. In regard to body mass, I found shared genetic architecture and that the shape of selection differed between the sexes suggesting the possible presence of an intra-locus sexual conflict. As SD in body mass has increased over the past two decades, I suggest that this may reflect a weakening of the genetic constraints imposed on this trait and that body mass therefore has the potential to evolve to sex-specific fitness optima. These results further suggest a need to consider the impact of pairing decisions, which could result in the observed pattern of reproductive success. Hence, I considered the fitness consequences of mate switching ('divorce'), as this is the only way for these otherwise monogamous birds to modify pairing decisions and potentially increase individual reproductive success. I found that divorce was most likely to occur after poor reproductive success, suggesting that these birds follow a '*win-stay lose-switch*' decision making paradigm, and that the benefits of divorce outweigh the costs of mate replacement itself. However, heritability was low in both sexes, suggested little scope for evolutionary change in this behaviour.

Overall, my thesis highlights the need to consider both sexes in studies of sexual selection and to broaden our current scope of model organisms to explicitly include species with cryptic SD, as only then can we reach a more complete understanding of these complex evolutionary processes.

Résumé

La majorité des études sur l'évolution et le maintien des caractères sexuels secondaires mâles ont été réalisés chez les espèces ayant des systèmes d'accouplement polygynes et un dimorphisme sexuel (SD) prononcé, où la sélection sexuelle joue un rôle important. L'évolution du SD est souvent considérée comme une résolution potentielle des conflits sexuels intralocus, et qui pourrait être particulièrement fort chez les espèces à faible SD. Néanmoins nous n'avons que peu d'information pour ce type d'espèce, et notre compréhension de la sélection sexuelle et des conflits sexuels demeure incomplète.

Ainsi l'objectif de ma thèse était de contribuer à combler ces lacunes en utilisant une approche de génétique quantitative. J'ai étudié comment une architecture génétique partagée pourrait conduire à des réponses à la sélection propres à chaque sexe chez un oiseau historiquement considéré comme étant monomorphique, le martinet à ventre blanc (Tachymarptis melba). J'ai d'abord quantifié le SD de traits morphométriques et découvert que le martinet présente un dimorphisme subtil. J'ai constaté que la longueur de la fourche de la queue et la masse corporelle auraient pu être influencées par la sélection sexuelle avec un SD ayant évolué au cours des deux dernières décennies. En approfondissant l'étude ces deux traits j'ai pu mettre en évidence que (1) la longueur de la fourche présente une corrélation génétique intersexe proche de 1, suggérant une forte contrainte génétique, une sélection directionnelle avec un rôle possible de la sélection mutuelle, et une tendance vers des microévolutif chez les deux sexes, malgré des changements phénotypiques uniquement observés chez les femelles. L'incohérence apparente mis en évidence ici entre les prédictions évolutionnistes — la sélection directionnelle jumelée à une forte corrélation génétique intersexe devrait se traduire par une trajectoire évolutive partagée entre les sexes — et les observations dépasse le cadre de cette thèse. (2) Pour la masse corporelle, l'architecture génétique et la forme de la sélection diffèrent entre les sexes, suggérant la présence possible d'un conflit sexuel intralocus. Avec l'augmentation du DS dans la masse corporelle au cours des deux dernières décennies, je suggère que cela pourrait refléter un affaiblissement des contraintes génétiques sur ce trait. Ce changement pourrait ainsi permettre une évolution de la masse vers des optima spécifiques à chaque sexe. Ces résultats mettent en lumière la nécessité de considérer l'impact des décisions d'appariement sur les tendances de succès reproductif observé. J'ai donc étudié les conséquences en succès reproductif des changements de partenaires (« divorce »), car c'est le seul moyen pour ces oiseaux monogames, de modifier leurs décisions d'appariement et potentiellement d'augmenter leur succès reproductif individuel. J'ai ainsi pu constater que le divorce est plus courant après un faible succès reproductif, suivant « win-stay lose-switch » (gagner-rester, perdre-changer), avec des avantages du divorce surpassant sur les coûts du remplacement du partenaire. Cependant, l'héritabilité faible de ce comportement chez les deux sexes suggère une évolution limitée de ce trait.

En somme, mon travail souligne l'importance d'intégrer les deux sexes dans les études de sélection sexuelle et d'élargir les modèles biologiques actuellement étudiés pour inclure spécifiquement les espèces à faible dimorphisme sexuel. Cela permettrait d'obtenir une compréhension plus complète de ces processus évolutifs complexes.

Declaration

Reproducibility statement

This thesis was written using Quarto (Allaire et al. 2022) and the R Statistical Software v4.3.1, Beagle Scouts (R Core Team 2023), as well as the R packages listed in Table E.1. The R code required to generate this thesis is archived on GitHub `github.com/MNDumas/PhD-Thesis`, with data and code required to reproduce each data chapter hosted on OSF.

Author declaration

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma at any university or equivalent institution and that, to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

The ideas, development, data analyses and visualizations, as well as the written content of all papers and chapters presented in this thesis were my own work, working under the supervision of Julien Martin and Pierre Bize. The inclusion of co-authors reflects the fact that the work came from active collaboration between researchers, and acknowledges the value of team-based research. This thesis was written in manuscript style and I have renumbered sections of submitted or published papers in order to generate a consistent presentation within the thesis.

Co-authorship statement

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

- Michela N. Dumas (MND): University of Ottawa, Canada
- Sophia St Lawrence (SSL): University of Ottawa, Canada
- Giulia Masoero (GM): Swiss Ornithological Institute, Switzerland & University of Ottawa, Canada
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- Julien G.A. Martin (JGAM): University of Ottawa, Canada

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Additional works

Though not directly integrated into this thesis, I am grateful to have had the opportunity to be a part of additional research projects, some of which have been published in peer-reviewed journals at the time of submission of this thesis:

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

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Chapter 1

General Introduction

Explaining the staggering diversity of phenotypic traits that exist in the natural world remains one of the central aims of evolutionary biology. Amongst these traits, the most extreme and bizarre are near-universally attributed to sexual selection (Figure 1.1). First proposed by Charles Darwin to explain the evolution of exaggerated and sexually dimorphic traits which could not be explained by natural selection alone (i.e., which hampered survival), sexual selection was defined as "the advantage which certain individuals have over others of the same sex and species, in exclusive relation to reproduction" p.256 (Darwin 1871). In other words, sexual selection arises as a result of individual variations in the ability to attract mates or repel rivals and thus achieve higher fitness, measured as the total number of offspring an individual contributes to the next generation over their lifetime (Westneat and Fox 2010). It has been suggested that sexual selection may prevent extinction by purging deleterious mutations and fixing beneficial ones (Whitlock and Agrawal 2009), and may even be accelerating adaptation in certain environments (Cally et al. 2019; Godwin et al. 2020). Hence, sexual selection plays an essential role in shaping the evolution of species, with the potential to shape population dynamics.

Though Darwin's view of sexual selection was largely limited to pre-copulatory selection (i.e., mating success, Darwin 1871), theory has since expanded to include post-copulatory selection (i.e., fertilization success, Andersson 1994). Sexual selection can further encompass traits relating to parental care (e.g., territory defence and nest building, Trivers 1972; or offspring provisioning, Clutton-Brock 1991) in species showing extended parental care to their offspring. Sexually selected traits (be they behavioural, physiological, or morphological) are thus any trait that increases reproductive success by providing an advantage in the competition for mates (Shuker 2010). This encompasses secondary sexual traits broadly categorized by function as those attracting mates (ornaments) or those repelling rivals (weapons) (Andersson 1994). Sexual selection may be characterized as either inter- or intra-sexual (Andersson 1994): inter-sexual selection occurs when individuals of one sex (generally females) mate preferentially with individuals of the other sex displaying favoured traits, while intra-sexual selection occurs when individuals of one sex (generally males) compete amongst themselves for access to mates and for the fertilization of gametes.

(a) Cichlid *Lamprologus calipterus*

(b) Elk *Cervus canadensis*

(c) Peafowl *Pavo cristatus*

(d) Stalk-eyed fly *Diopsis stuckenbergi*

Figure 1.1.: Examples of bizarre and sexually dimorphic traits found in nature: a) male cichlid *Lamprologus calipterus* are 12 times the size of their female counterparts (photo credited to Gilles Garrier); b) only male elk *Cervus canadensis* grow antlers; c) male peafowl *Pavo cristatus* have elaborate and extravagant trains; d) the bizarrely long eyestalks of the stalk-eyed fly *Diopsis stuckenbergi* are much longer in males than in females (photo credited to Mark Moffett).

For example, in peafowl *Pavo cristatus*, sexual selection has favoured the evolution of elaborate male trains by female preferences, perhaps one of the most well-known examples of pre-copulatory inter-sexual selection. Peahens mate preferentially with males displaying the most elaborate trains (as defined by size, number and brightness of eyespots on each feather, Petrie et al. 1991), which correlate positively with male immune function and offspring survival (Petrie 1994). These trains may also be costly, thus ensuring the honesty of this signal (e.g., colouration as an indicator of developmental stability per Loyau et al. 2007; but see Askew 2014; Thavarajah et al. 2016). Despite quite a bit of recent controversy on this topic (Penn and Számadó 2020), Zahavi's (1975) Handicap Principle is often cited in this context: secondary sexual signals which are preferred by females but increase male mortality can only be expressed and maintained by 'high-quality' males, explaining the evolution of such extreme phenotypes. In the giant rhinoceros beetles *Trypoxylus dichotomus*, sexual selection has favoured the evolution of a long weaponized horn in males, used in intra-sexual combat. Males with longer horns are more likely to win contests against rival males and therefore achieve higher reproductive success (Hongo 2007). Though these large horns do not incur survival costs, their evolution is constrained by mechanical limits—horns that are too long are prone to breakage (McCullough 2014). In the case of intra-sexual post-copulatory selection, some of the most well-known examples of sperm competition take place in insects, where males increase their chances of being the one to fertilize a female's eggs by engaging in mate guarding behaviours, deploying mating plugs, or even by removing the sperm of other males entirely (Parker 1970). In the case of inter-sexual post-copulatory selection, females have been shown to bias fertilization success of preferred males by ejecting stored sperm of less preferred mates (e.g., female fowl *Gallus gallus domesticus* eject sperm of subdominant males, Pizzari and Birkhead 2000). Such examples of inter- and intra-sexual selection are numerous in the literature, both at the pre- and post-copulatory levels, with the bulk of research centred on the males of polygynous and strongly sexually dimorphic species (Andersson 1994).

This bias may be in part attributed to the rigid nature of 'Darwinian sex-roles', wherein aggressive and showy males were considered to be the sole targets of sexual selection, while passive and choosy females were relegated to agents of selection. This view has been entrenched in the literature for decades, having been corroborated both theoretically (e.g., Trivers' (1972) General Framework for Sexual Selection) and experimentally (e.g., Bateman's (1948) Principle, but see Hoquet et al., (2020) for a rebuttal). Likewise, the opportunity for sexual selection may be stronger in polygamous than monogamous mating systems (Andersson 1994), as fierce competition is expected to generate more intense selection. Indeed, sexual dimorphism and polygynous mating systems are widely acknowledged correlates of strong sexual selection. Sexual selection does seem to play an obvious role in these cases and has, for example, resulted in some researchers considering model species of sexual selection to be those with "conspicuous sexual dimorphism in structure or behaviour" (Andersson and Simmons 2006). Research in recent decades has made it abundantly clear that female choice and male-male competition can lead to the evolution of extravagant ornamental traits in males (Andersson 1982; Andersson 1994), at both the pre- and post-copulatory levels. And yet, is it not possible for sexual selection to also take place in species with subtle sexual dimorphisms? Are females truly only accessories in the evolution of sexually selected traits and in the contest for reproductive success?

Significant efforts have been made in recent decades to address these biases in our understanding of how sexual selection operates within and between the sexes by considering the nature of sexual selection in females (reviewed in: Clutton-Brock 2007, 2009; Hare and Simmons 2019; Rosvall 2011). Researchers have increasingly been targeting species with female-specific ornaments (Amundsen 2001), the ornamented males of monogamous species (Regosin and Pruett-Jones 2001) and species where both males and females are similarly and extravagantly ornamented (Clutton-Brock 2009). Indeed, in the wattled jacana *Jacana jacana*, larger and brighter coloured females are more successful at defending territories and acquiring mates (Emlen and Wrege 2004), and, in sympatric populations, northern jacana *J. spinosa* females are so successful in intra-sexual conflicts that they can monopolize males of both *J. spinosa* and *J. jacana* (Lipshutz 2017). In the dance fly *Rhamphomyia tarsata*, females with larger abdominal air sacs are preferred by males, which may honestly signal fecundity (LeBas et al. 2003). Many such examples of sexual selection acting on females of sex-role reversed species are found in the literature, where this reversal is defined as being analogous to Darwinian sex roles, with males being choosy and females rather being showy and competitive (Eens and Pinxten 2000).

Of particular recent interest are cases of sexual selection in mutually ornamented species, wherein ornamental traits may be expressed to similar degrees in both sexes (Kraaijeveld et al. 2007). For example, in the crested auklet *Aethla cristatella*, both sexes have long ornamental feather crests, and individuals of both sexes with longer crests outcompete those with shorter crests and are preferred as mates (Jones and Hunter 1993). Likewise, in the king penguin *Aptenodytes patagonicus*, both sexes have conspicuously coloured auricular feather patches and keratin beak spots used in mutual mate choice (Dobson et al. 2011; Nolan et al. 2010). These ornaments appear however to signal different aspects of individual condition in each sex (i.e., beak coloration as a signal of body condition and oxidative stress in opposite directions between the sexes, Viblanc et al. 2016). Thus, examples of inter- and intra-sexual selection exist in both sex-role reversed and mutually ornamented species (Figure 1.2), highlighting the diverse and widespread nature of sexually selected traits in both sexes. However, there remains a persistent gap in our understand of how sexual selection operates within and between the sexes in species with little apparent sexual dimorphism. In particular, the evolution of sexual dimorphism is seen as a potential resolution of sexual conflict, suggesting that this conflict, when present, may be especially strong in species with weak or subtle sexual dimorphisms.

(a) Wattled jacana *Jacana jacana*

(b) Crested auklet *Aethla cristatella*

(c) Dance fly *Rhamphomyia tarsata*

(d) King penguin *Aptenodytes patagonicus*

Figure 1.2.: Examples of sexually selected traits in sex-role reversed and mutually ornamented species: a) female wattled jacana *Jacana jacana* are brighter and more aggressive than males, who are responsible for the brunt of incubation and parental care duties (photo credited to Cherie Pittillo), b) both sexes of the crested auklet *Aethla cristatella* have long ornamental feather crests (photo credited to Ian L. Jones); c) female dance flies *Rhamphomyia tarsata* with larger abdominal air sacs are prefered as mates (photo credited to Heather Proctor); d) both sexes of the king penguin *Aptenodytes patagonicus* have conspicuously coloured auricular feather patches and keratin beak spots used in mutual mate choice (photo credited to Pierre Bize).

1.1. *Sexual Conflict*

Sexual conflict occurs when sex-specific selection, reflecting the sexes' different reproductive strategies, results in different fitness optimums for each sex (Bonduriansky 2016). Indeed, the reproductive interests of males and females are not always aligned and thus cannot be simultaneously satisfied (Parker 1979), and sex-specific selection on shared traits can translate to a fitness benefit for one sex but a fitness cost for the other sex. This divergence in reproductive interests has ultimately been ascribed to anisogamy (the production of gametes of different sizes; small and cheap sperm vs. large and costly eggs), which will itself result in biased parental care, freeing up the 'less-caring sex' (often males) to pursue additional matings. While the concept of sexual conflict has been well established (Arnqvist and Rowe 2005), it cannot be understated that in sexually reproducing species with obligate outcrossing, both partners must cooperate to some extent. This is most notable in species where both parents must provide significant parental care, such as in most monogamous birds (reviewed in Clutton-Brock 1991). The scope for sexual conflicts in species with little apparent sexual dimorphism where both parents must cooperate to raise their offspring is hence expected to be strong, should the sexes diverge in their evolutionary interests, altought this aspect has received little formal attention.

Two forms of sexual conflict have been described: inter-locus and intra-locus (Bonduriansky 2016). On one hand, inter-locus sexual conflict occurs as a result of different fitness optima over the outcome of male-female interactions and involves genes at different loci. Bateman's experiment on mating rate in *Drosophila melanogaster* (Bateman 1948) is often cited as a classical example of inter-locus conflict. While a male's fitness may increase linearly with each additional mating, a female's fitness would rather peak at a much smaller number of matings, whenever her finite number of eggs within a reproductive cycle has been fertilized. Hence, males are selected to continuously seek additional matings, while females are selected to resist additional matings once their eggs have been fertilized.

On the other hand, intra-locus sexual conflict occurs as a result of shared genetic architecture for a trait expressed in both sexes (Bonduriansky 2016), which can be investigated by estimating its cross-sex genetic correlation (r_{fm}: Lande 1980). In brief, a null r_{fm} suggests no shared genetic architecture, while an r_{fm} approaching 1 (negative or positive) would rather suggest that the sexes share much of the same genetic architecture. Cross-sex genetic correlations can accelerate or hinder evolution depending on the strength and direction of selection acting on each sex. For instance, an r_{fm} approaching 1 coupled with sexually antagonist selection (i.e., selection of opposite signs) would result in a genetic constraint impeding the independent evolution of the sexes and hence possibly slow or even prevent the evolution of sexual dimorphism (e.g., strong cross-sex correlation for tarsus length in the collared flycatcher *Ficedula albicollis* displaced the female optimum by 200%, Merilä et al. 1998). Although the evolution of sexual dimorphism is seen as a resolution of intra-locus sexual conflict, it is still unclear whether such conflict present a transient or permanent constraint on the adaptive divergence of the sexes.

1.2. *Mate Choice and Individual Quality & Condition*

Central to the question of mate choice (and of the signalling function of phenotypic traits) lies variations in the relative quality and condition of individuals. If all individuals were of equivalent 'quality' and hence associated with equivalent fitness, there would be no need to choose a particular mate: being 'choosy' would result only in costs, and not in net fitness benefits. The costs of mate choice are primarily the time and effort needed to locate and select a mate, which implies lost opportunities to find food or additional mates, and an increased parasite load as well as an increased risk of predation or injury. The benefits of mate choice may include direct benefits in terms of access to territories for foraging, and indirect benefits such as offspring with 'better' or more diverse genes. Complicating the matter further, mate choice need not be a static event. Even in socially or genetically monogamous species, some individuals seek additional mating opportunities in the form of extra-pair copulations or abandon a current partner entirely in favour of a new partner ('divorce') (Choudhury 1995). Divorce is generally considered to be adaptive (i.e., conferring net fitness benefits) (Culina et al. 2015) though its causes and consequences often remain unclear, most notably regarding the genetic basis of this behaviour. Because the fitness components of divorce (and its costs and benefits) likely depend on an individual's life-history traits, the specific decision rules governing divorce have the potential to evolve by sexual selection, assuming that such variation underlying the trait is heritable. In any case, the benefits of mate choice are all contingent upon discerning such a nebulous 'high quality' mate.

Individuals may signal aspects of quality and/or condition through greater expression of phenotypic traits, with those of lower quality and/or condition unable to do so due to associated viability costs (Zahavi 1975; but see Roulin 2016 for a review of honest signalling in traits that are not costly to produce but rather to wear) and limited resource availabilities. Indeed, resources within an environment are typically finite, and thus cannot simultaneously maximize the expression of all traits of all individuals within a population (Stearns 1989). Thus, trade-offs, defined as an increase in one trait which improves fitness resulting in a decrease in another trait which also improves fitness (Flatt and Heyland 2011), will occur. These trade-off strategies are possible between functions (i.e., reproductive senescence, a trade-off between self-maintenance and reproductive output, Nussey et al. 2008) or between traits (i.e., condition-dependent ornamentation in three-spined stickleback *Gasterosteus aculeatus* males, Candolin 1999).

As illustrated by Wilson & Nussey (2009), the absence of formal definitions for the terms "individual quality" and "individual condition" has resulted in subtly different usages by different researchers. Wilson & Nussey (2009) suggest that quality can be defined as "being an axis of among-individual heterogeneity that is positively correlated with fitness." However, if one defines individual quality as higher fitness, then individuals of higher quality have higher fitness by definition. Thus, defining quality in terms of fitness is rather circular and not necessarily informative. Hill (2011) provides an alternative definition, using the term 'individual condition' to encompass genotypic and phenotypic quality, such that it is "the relative capacity to maintain optimal functionality of essential cellular processes," or "the capacity to withstand challenge," in the current environment. Hence, individual quality and condition are generally considered to hinge upon an individual's available pool of resources, and/or to the efficiency with which individuals allocate these resources to the production and maintenance of competing traits (Rowe and Houle 1996).

Following these general definitions, individual quality is used here to encompass genetic and developmental quality (i.e., good genes, good environmental conditions during early development promoting developmental stability), dictating the maximal resource pool available to individuals. In other words, quality refers to inter-individual differences which remain stable over an individual's life, and which may influence fitness through different means (e.g., stronger immune system, larger maximal resource pool allowing increased reproduction and survival). Condition then refers to intra-individual fluctuations in the allocation of available resources between competing traits, which may impact fitness. Hill (2011) further defines condition-dependent traits as a "feature of an organism that varies in expression depending on the capacity to withstand environmental challenges."

An important caveat in measuring individual condition arises from the need to control for inter-individual variations in body size and/or quality. Body condition indexes (BCIs) are commonly expressed as ratios (i.e., relationship between body mass and a measure of body length), although other methods have been used (e.g., mass relative to a population 'standard' Stevenson and Woods 2006). The aim of these BCIs is to measure the pools of resources available to individuals in the form of stored fat, and to document among individual differences in these stores after controlling for body size (Stevenson and Woods 2006). There exists a wealth of research on the applicability of such condition indices, and ample discussions as to their use, limitations, and species-specific differences (Labocha et al. 2014; Labocha and Hayes 2012; Peig and Green 2009, 2010). Further complicating this matter is the impact of individual condition on choice: individuals who are of 'low' condition will not necessarily make the same mate choice decisions as individuals of 'high' condition, potentially leading to condition-dependent selection and evolution. For example, female canaries *Serinus canaria* experiencing poorly diversified food environments (low individual condition) were less selective than females with a more highly diversified diet (high individual condition) (Lerch et al. 2011; see Cotton et al. 2006 for a review of variations in mating decisions as a result of female condition). Hence, the study of secondary sexual traits requires an understanding of the relationships between individual quality, condition, body size, and the secondary sexual trait in both sexes, as well as its consequences on fitness.

1.3. *Thesis Objectives*

In this thesis, I investigated how sexual selection operates within and between the sexes in a long-lived bird with little apparent sexual dimorphism, the Alpine swift *Tachymarptis melba*. In *Chapter 2*, I quantified subtle sexual dimoprhism in morphometric traits and assessed the sex-specific allometric scaling of morphometric traits over two decades to identify traits likely to be (or to have been) under sexual selection in one or both sexes. I then investigated the genetic constraints and selective pressures acting on the most sexually dimorphic trait (fork length) and the only female-biased trait (body mass) identified in *Chapter 2*. Hence, in *Chapter 3*, I investigated sex-specific selection, heritability and possible genetic constraints acting on fork length, a trait which has historically been considered to be under sexual selection in males. In *Chapter 4*, I investigated the causes of variation of adult body mass in both sexes as well as the possibility for sexual conflict over this highly labile trait. In *Chapter 5*, I investigated the predictors and consequences of mate switching behaviours ('divorce') in both sexes, as this behaviour presents the only opportunity for these otherwise monogamous birds to modify their initial mating decision and hence may generate additional opportunities for sexual selection. Finally, in *Chapter 6*, I bring together the conclusions and results gathered throughout the primary studies of my thesis and suggest further avenues of research as well as some specific evolutionary conclusions arising from each previous chapter.

1.4. *General Methods*

(a) Alpine swift *Tachymarptis melba* in flight

(b) *Stadtkirche* in Biel

Figure 1.3.: Photos of: a) Alpine swift in flight. The characteristic long narrow wings, achromatic throat and breast patches as well as forked tail are visible. Photo credited to Gordon Speirs. b) *Stadtkirche* in Biel, Switzerland, which houses one of the colonies being monitored. Photo credited to the City Church of Biel.

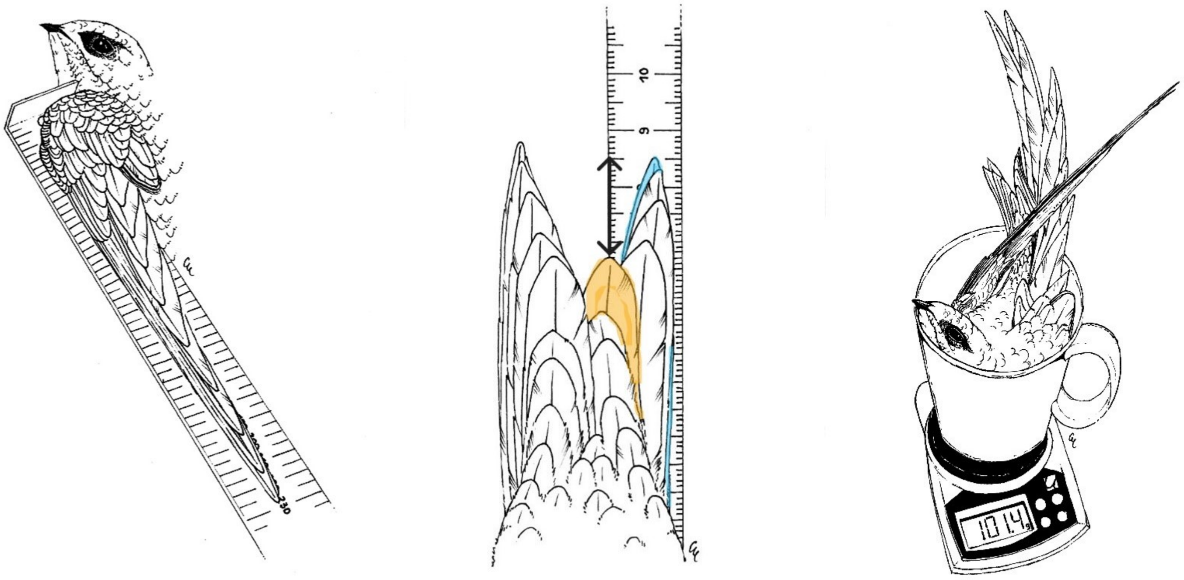
Alpine swifts are a remarkable and long-lived (lifespan: median of 7 years, maximum of up to 26 years, Moullec et al. 2023) bird capable of spending over 200 days in continuous flight (Liechti et al. 2013). Indeed, swifts only routinely land during the breeding season, in order to lay their eggs and raise their chicks in nests. Other species of swifts such as the common swift *Apus apus* have likewise been documented engaging in these incredible feats of athleticism, remaining in the air for up to 10 months out of the year (Hedenström et al. 2016). Swifts are incredibly well suited to a life spent almost entirely in flight, with their characteristic long and narrow wings enabling breakneck speeds, and short legs suited for clinging to cliff faces rather than walking (which, like the retractable wheels of a plane, are kept tight to their body during flight such that they disappearing entirely, and explaining the family name of Apodidae—"without feet") (Figure 1.3). Swifts are obligate insectivores, feeding exclusives on insects they catch in flight: despite how small their beaks appear, their mouths are a gaping void ready to engulf hundreds of insect prey in a day. Owing to their highly aerial lifestyle, the biology and ecology of Alpine swifts remain poorly understood outside of the breeding season. As with other highly aerial birds, traits relating to aerodynamic abilities (i.e., speed, agility, manoeuvrability) such as the shape of the tail are expected to be under strong natural (Thomas 1993) and sexual (Fitzpatrick 1999; Fitzpatrick 1998) selection.

(a) Regurgitated food bolus (b) Nest with eggs (c) 0-day old chicks

(d) Adult brooding 5-day old chicks (e) 25-day old chicks (f) 45-day old chicks

Figure 1.4.: General biology of the Alpine swift: a) Regurgitate food bolus containing different species of insects caught in flight and glued together with saliva to be fed to the chicks. Photo credited to Pierre Bize.; b) Nest with eggs. A piece of transparent plastic is visible, having been collected as nesting material. Photo credited to Michela Dumas. C) Hatchlings (0 days). Photo credited to Michela Dumas.; d) Parent brooding 5-day old chicks. Photo credited to Pierre Bize.; e) 25-day old nestlings parasitized by the blood-sucking louse-fly *Crataerina melbae*. Photo credited to Michela Dumas.; f) 45-day old nestlings, with adult-like plumage save for their short wings and tails. Photo credited to Michela Dumas.

Up to a hundred pairs will nest on cliffs, or in the roof spaces of tall buildings when breeding in urban settings. Swifts construct their nests entirely with dry (or even fresh) materials (e.g., feathers, plant matter, and nowadays even plastics) collected in flight that they then glue together using saliva (Lack 1956). Swifts typically build upon nest structures from previous years, as nest building is a time consuming and energetically costly behaviour. Swifts share their nests with the blood-sucking louse fly *Crataerina melbae* (Bize et al. 2004; Bize et al. 2005), an ectoparasite with an important impact on the health of chicks and adults (Cigler et al., 2023). Both parents care for their single yearly clutch of 1-4 eggs (incubation: approx. 18 days; fledging: 50-70 days after hatching) (Bize et al. 2004) (Figure 1.4). Swifts begin breeding on average at 2.8 years of age for females and 3.2 years of age for males and breed each year until their death (Tettamanti et al. 2012), often with the same partner and in the same nest from one year to the next. As with other species of swifts, Alpine swifts may leave their natal colony to reproduce in a neighbouring colony (i.e., natal dispersal), but they then remain faithful to their breeding colony (i.e., no breeding dispersal).



(a) Wing length

(b) Tail & fork length

(c) Body mass

Figure 1.5.: Alpine swift a) wing, b) tail and c) mass measurements illustrated by Martina Cadin. The outer tail feather is highlighted in blue while the inner tail feather is highlighted in orange. The fork length is depicted with a black arrow. When being measured, all tail feathers (inner rectrices R1 to outer R5) are carefully folded over each other such that the fork length is measured from the tip of the inner tail feather (R1) to the tip of the outer tail feather (R5) on both the left and right sides of the body. These measures are then averaged such that a single measure of fork length is used per individual per year captured.

Several Swiss urban-nesting colonies have been followed at the individual level for over two decades, with for instance 30-40 pairs per year in the colony located in the building *Landvogteischloss* in Baden, 60-100 pairs per year in the colony located in the building *Stadtkirche* in Biel, and 40-55 pairs per year in the colony located in the building *Bieltor* in Solothurn. This intensive monitoring has resulted in an outstanding database detailing reproductive success, morphology, pairing decisions and relatedness, which I have built upon during my 2022 and 2023 field seasons. Birds are permanently identified by ringing them as nestlings or at their first capture if not already ringed as nestlings. Throughout the breeding season, parents are caught by hand at the nest while brooding the eggs or chicks and later feeding the chicks, and their yearly reproductive success is determined (clutch size, number of hatchlings and fledglings). Individuals are weighed to the nearest tenth of a gram using a digital scale (Figure 1.5), measured to the nearest millimetre using a ruler (e.g., wing, tail and fork lengths, Figure 1.5) or tenth of a millimetre using a caliper (e.g., sternum length) and sexed (DNA taken from blood or feathers, Griffiths et al. 1998). Nestling morphometric measures and body weight are collected at regular intervals throughout their development (Masoero et al. 2024). Adult morphometric measures are taken once per individual per year captured, and weight and molt scores are recorded at each capture. Though swifts appear monomorphic to human observers, subtle sexual dimorphisms have been recorded (e.g., females are 1% heavier than males, Dumas et al. 2024c; males have 7% more deeply forked tails than females, Dumas et al. 2024b; and ageing trajectories of biometric traits are sex-specific, Moullec et al. 2023).

Throughout my thesis, I use state of the art quantitative genetic analyses to estimate the relative contributions of genetic and environmental factors on phenotypic variation (Kruuk et al. 2008). These mixed effects models linked to a pedigree (‘animal models’) allow for statistical inferences about the additive genetic variance (heritability) of traits expressed in both sexes as well as the genetic correlation(s) between the sexes. Heritability in the strict sense is defined as the fraction of the total phenotypic variance of a trait (V_P) which is due to the additive genetic effects of genes (V_A): $h^2 = V_A / V_P$. In the context of the evolution of traits, phenotypic change depends primarily on the heritable fraction of the trait, the genetic constraints arising from cross-sex (or cross-trait) correlations, and the strength of the sex-specific selection acting on the trait. Selection is generally estimated by relating individual measurements (i.e., plumage coloration) to relative fitness (i.e., number of offspring) following the Lande-Arnold approach for correlated traits (Lande and Arnold 1983).

The availability of detailed pedigrees is still relatively rare in wild populations, requiring significant time and effort, and allowing us to explore various and exciting questions about the evolution of traits in both sexes using the Alpine swift as a model species. Indeed, long-term studies allow the study of processes rather than static events (e.g., ageing), and how these processes change (e.g., microevolution in response to climate change) (Sheldon et al. 2022). Throughout this thesis, I use a social pedigree compiled from behavioural observations of parents caught at the nest while brooding the eggs or chicks and later feeding their chicks. These behavioural observations are sufficient to construct a reliable social pedigree as very low extra-pair paternity (EPP) has been recorded in this population (<5%; C. M. Meier and P. Bize, manuscript in preparation). Note also that Charmantier and Réale (2005) showed that misassigned paternities have a negligeable impact on heritability estimates in cases were EPP rates are under 20%. Thought the Alpine swift is the model species used in this thesis, the questions I investigated may more broadly be applicable to any subtly dimorphic species. My thesis sheds new light on the evolution of sexual dimorphism and the effects of intra-locus sexual conflicts as well as the genetic basis of pairing decisions in both sexes of a wild population. Given the importance of sexual selection in shaping population dynamics, and the relative scarcity of long-term studies able to answer such questions using quantitative genetics, my thesis fills an important gap in our understanding of how sexual selection operates within and between the sexes in nature.

Chapter 2

Chapter 2: Temporal changes in sex-specific cryptic sexual dimorphism and allometric scaling in the long-lived Alpine swift *Tachymarptis melba*

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Preamble

As it will quickly become apparent, the order of the following data chapters does not correspond to the chronological order in which they were completed. These data chapters were rearranged in order to facilitate the progression of the ideas presented within this thesis. The chronological order of completion also reflects, to some extent, the chapters I found most captivating. Overall, figuring out the somewhat-complex analyses contained in this thesis was generally more fun than writing.

As the Alpine swift has historically been considered to be monomorphic, it was first necessary to quantify any potential sexual dimorphism in morphometric traits, which was the general aim of this chapter. Although relatively straightforward, and the last chapter to be completed, the findings outlined here are foundational to the following data chapters.

Abstract

Morphological differences between the sexes are frequently reported in wild populations, ranging from subtle to extreme. These differences can extend beyond body size itself and result in differences in the size and/or shape of specific traits in relation to overall body size, as revealed by allometric scaling. Sexually selected traits have historically been expected to display positive allometric scaling (i.e., relatively larger trait size in bigger individuals), although recent works rather suggest that sexually selected traits can also display negative allometric scaling (i.e., relatively larger trait size in smaller individuals). We used a long-term dataset to quantify the sexual dimorphism and sex-specific allometric scaling of morphometric traits in a wild bird generally characterized as monomorphic, the Alpine swift. We identified subtle sexual dimorphisms suggesting that the Alpine swift is rather a cryptically dimorphic species. Fork length was the most sexually dimorphic trait, with males displaying 7% longer forks than females. Interestingly, we found that the extent of this sexual dimorphism has changed over the course of the study, such that male and female feather traits have become more similar. We further identified sex- and trait-specific allometric scaling, as well as possible sex-specific changes in allometric scaling of fork length over the course of the study. The negative allometric scaling of morphometric traits in the Alpine swift suggests that selection has favoured reduced investment into these body structures for larger individuals in both sexes. In line with the Functional Allometry Hypothesis, this results is coherent with the suggestion that sexually selected traits can display negative allometric scaling.

2.1. Introduction

Males and females of a given species often differ in their behaviour, physiology and/or morphology (Fairbairn 2007; sexual dimorphism (SD): Shine 1989). The extent of these differences can vary widely, from the subtle to the extreme, even within closely related groups. For instance, the tail-feather shape of “bee” hummingbirds ranges from sexually monomorphic in some species to extravagantly dimorphic with a striking elongation of the outer tail feathers of males only in other species (Clark and Rankin 2019). Much of the work done on sexual dimorphism has dealt with sexual size dimorphism (SSD) in particular, as body size is often (though not always) one of the most conspicuous traits differing between the sexes. The cichlid fish *Lamprologus callipterus* is one such case, with males reaching body sizes an impressive 12 times larger than that of females (Schütz and Taborsky 2005).

Differences in morphology between males and females can inform us as to the ecological relationships of both sexes and the evolutionary conditions that have shaped sex-specific morphology. Indeed, SSD is generally thought to arise as a result of sexual selection, fecundity selection, or inter-sexual niche divergence (Owens and Hartley 1998; Shine 1989). Larger body size in males than females of many species may have evolved as a result of male-male combat for access to females because the winners of such contests have increased mating opportunities and hence greater fitness (Fairbairn 2007). In many fish and bird species, females tend to be the larger sex owing to the fact that larger females lay more eggs and thus produce more offspring than smaller females (Fairbairn 2007). In raptors and seabirds, SSD may reduce inter-sexual food competition through niche divergence (Krüger 2005) as in the barn owl *Tyto alba*, with the sexes specializing on the capture of differing prey species (Pande and Dahanukar 2012). Importantly, these proposed explanations for the evolution of SSD need not be mutually exclusive.

Coupled with these overall body size differences, there can also be sex differences in the size and/or shape of specific morphological structures. Allometry describes how specific morphological structures scale with the body size of an organism and can be used to quantify the relative investment of individuals into these traits in relation to their body size. We describe here static allometry, or variation in shape among individuals of the same species at adulthood. In the case of isometric allometry, the relative trait size is constant for all body sizes, suggesting equal resource allocation between traits across sizes. In the case of positive allometry, trait size is relatively larger for larger body sizes, while in the case of negative allometry, trait size is relatively smaller for larger body sizes. Historically, when studying species with extravagant ornaments and weapons, secondary sexual traits have been expected to demonstrate strong positive allometry in one sex only (Emlen 2008; Kodric-Brown et al. 2006), with relatively larger traits conferring their bearers an advantage in the contest for reproductive success (Green 1992). However, more recent findings—including on species with weak sexual dimorphism—have highlighted that sexually selected traits, as well as those under natural selection alone, may display positive, negative or isometric scaling (Bonduriansky 2006), in either or both sexes (e.g., positive allometry of the bill in both sexes of the common moorhen *Gallinula chloropos*, Petrie 1988). Thus, when studying species with weak sexual dimorphism, we have no marked expectations as to the steepness of the allometric slopes in either sex. In addition, allometric scaling is generally only assessed at a single given point in time assuming that it remains stable through time. However, studies investigating the evolution of allometric scaling have, in laboratory settings, shown that it can be altered under artificial selection (Harrison 2015; Tobler and Nijhout 2010). It remains unclear how stable allometric scaling may be in the wild.

Here, we use a long-term dataset to quantify sexual dimorphism of morphometric traits (body mass, sternum length, wing length, outer and inner tail feather length, fork length) and their allometric scaling in both sexes of the Alpine swift *Tachymarptis melba*. We expected fork length to be the most dimorphic trait and for it to be more strongly expressed in males, as this trait has historically been expected to be under strong sexual selection in swifts and swallows (Hasegawa and Arai 2020). We also compared sexual dimorphism between breeding and non-breeding individuals, with the expectation that traits under sexual selection should be more strongly expressed in sexually mature individuals as compared to immature individuals. In addition, preliminary results have highlighted changes in swift morphology over the last two decades: wing length at adulthood appears to have increased in both sexes and growth during early life may have accelerated. Hence, we also assessed changes in sexual dimorphism over the past two decades. We then investigated the sex-specific allometric scaling of feather traits in relation to two indices of body size, sternum (with and without correcting for mass) and wing length, as well as changes in allometric scaling over time and how this may differ between the sexes. We expected traits relating to fork depth to scale more steeply in males than in females as a potential indicator of the impact of sexual selection on this trait, although we make no predictions as to weather this scaling would be negative, isometric, or positive. We further expected to detect sex-specific differences in allometric scaling between the two periods, reflecting sex-specific changes in morphology over the course of the study.

2.2. Materials & Methods

2.2.1. *Study Species & Site*

The Alpine swift is a long-lived and colonially nesting bird, with a median lifespan of 7 years and a maximal known lifespan of 26 years (Moullec et al. 2023). They have been shown to spend over six consecutive months in flight (Liechti et al. 2013), and only land during the breeding season which takes place from May to August. During this time, colonies of a few to a hundred pairs will nest on cliff walls or under the roof spaces of tall buildings. Both parents will incubate their single yearly clutch of 1-4 eggs for 18-21 days, and then provision their nestling for up to seventy days, at which point chicks reach independence and fledge (Bize et al. 2004). Intensive individual monitoring has been carried out in two urban Alpine swift colonies in the Swiss cities of Biel (60-100 breeding pairs) and Solothurn (40-55 breeding pairs) since 1999 and 2000, respectively, where all the individuals are banded for permanent identification the first time they are captured, either as nestlings or as new recruits immigrating to the breeding colony.

Throughout the breeding season, adults are caught at the nest. Individuals are weighed to the nearest tenth of a gram using a digital scale and sexed using DNA extracted from blood or feather samples (Griffiths et al. 1998). Morphometric measurements are taken to the nearest millimeter using a ruler (e.g., wing, outer tail feather and fork length) or to the nearest tenth of a millimeter using a caliper (e.g., sternum length). Sternum length serves as a measure of skeletal size in the Alpine swift since their tarsi are too short to be reliably measured, as with other members of the Apodidae family. Skeletal growth ceases well before fledgling, at approximately 35-40 days of age (Masoero et al. 2024), and hence sternum length was averaged across all post-fledgling lifetime captures for a given individual ($R = 0.95$: repeatability conditioned on sex was estimated based on 3872 observations from 1145 individuals using the R package *rptR*, Stoffel et al. 2017). Fork length was measured as the distance between the tip of the inner tail feather (retrice R1) and the tip of the outer tail feather (retrice R5). Outer tail feather length and fork length are thus measured on both the right and left sides of the body and then averaged to yield a single estimate per individual, reducing measurement error. The inner tail feather length was calculated as the difference between the outer tail feather length and the fork length. Morphometric measures are taken once per individual per year captured, and body mass was recorded at each capture event throughout the breeding season.

Both male and female Alpine swifts have cryptic tawny plumage, with the characteristic white throat and breast patches. As is the case for most swifts, Alpine swifts have historically been considered as monomorphic. Indeed, no differences between the sexes are apparent in the field, ensuring that data collection is done blind to the sex of the individual. However, slight sexual dimorphisms in morphometric traits have been recently documented in other species of swift (e.g., male pallid swifts *Apus pallidus* have longer wings than females, Boano et al. 2015; male common swifts *Apus apus* have more deeply forked tails than females, Jukema et al. 2023), suggesting that there is a need to carefully reconsider sexual dimorphisms in morphometric traits in swifts.

2.2.2. *Statistical analyses*

All statistical analyses presented below were conducted in R version 4.3.1 "Beagle Scouts" (R Core Team 2023). All morphometric variables were mean-centered and scaled to a variance of 1, pooled across the sexes, and then log transformed for the allometric analyses. Year as a continuous variable was also mean-centered and scaled to a variance of 1. When included in the analyses, quadratic effects were calculated using orthogonal polynomials. All models were first tested with the inclusion of all biologically relevant interaction terms and quadratic effects; non-statistically significant interaction terms (Engqvist 2005) and non-statistically significant quadratic effects (Faraway 2014) were dropped from the final models and are reported only in the supplemental (Table A.3, Table A.5). Interaction terms which approached statistical significance (p-value < 0.08) where retained in the main body of the paper. Data presented in these analyses spans 1999-2021.

2.2.3. *Sexual dimorphism*

In a first part, we investigated the extent of sexual dimorphism in the Alpine swift. The traits considered were body mass, sternum length, wing length, outer tail feather length, inner tail feather length, and fork length. We expected that some traits (i.e., fork length) would be male-biased while others (i.e., body mass) would be female-biased. Given that preliminary results suggest changes in swift morphology over the past two decades (e.g., wing and tail lengths have increased in both sexes, Masoero et al., in prep), we considered sex-specific changes in these morphological traits over the course of the study. To help us identify traits likely to be (or to have been) under sexual selection, we also considered the effect of breeding status, with the expectation that traits under sexual selection would be expressed more strongly in breeding individuals than non-breeding individuals (typically juveniles who may not have yet reached sexual maturity). Alpine swifts start reproducing between 2 to 4 years of age (Tettamanti et al. 2012).

Body mass in the Alpine swift has previously been shown to be a highly labile trait sensitive to short term climatic variability (Dumas et al. 2024c). Owing to the fact that individuals are not caught (and hence weighed) on the same days or at the same time, we adjusted mass estimates statistically to account for this variation. Mass was adjusted for each individual each year based on the average weather within a year, at 14h00 (median capture time) and on June 13th (median capture date reflecting the stored energy available for reproduction) following the methodology outlined by Dumas et al. (2024c), adapted to a frequentist rather than Bayesian approach. Though this approach does not allow us to carry over the error from the adjustment as with the Bayesian approach, the error on these estimates is very small, as indicated by the qualitatively and quantitatively similar results of Dumas et al. (2024c) with both statistics.

We fit a series of linear mixed effects models with each morphometric trait as a function of sex (2-level factor: male vs female), year (continuous variable), colony (2-level factor: Biel vs Solothurn), and breeding status (2-level factor: breeding vs non-breeding). We included an interaction term between sex and year to investigate whether each morphometric trait changed in the same ways in both sexes over the course of the study. We also included a sex by colony interaction term to assess whether morphological traits differed between the colonies as a function of the sex of the individuals. We further included breeding status by sex and breeding status by year interaction terms to assess whether the expression of each trait differed between sexes in accordance with breeding status or changed over the course of the study. Finally, we included a three-way interaction between breeding status, sex and year to investigate whether these sex-specific differences changed over the course of the study. Individual identity and the year of measurement were included as random effects to account for repeated measurements at the individual and year level respectively.

In addition, we simplified these models in order to increase power by contrasting dimorphism between the first and second halves of the study, 1999-2010 and 2011-2021. Hence, we ran the same series of linear mixed effects models described above with period (2-level factor: period 1999-2010 vs period 2011-2021) as a fixed effect in place of year as a continuous variable (Table A.1). We obtained qualitatively similar results with both approaches. We further expressed sexual dimorphism as the percentage of difference in male to female morphology, using the formula (mean male trait – female mean trait) / mean female trait * 100 for both periods (1999-2010 & 2011-2021) in order to obtain estimates of overall dimorphism in each period as well as overall (Table A.2).

2.2.4. *Allometry*

In a second part, we investigated the sex-specific allometric scaling of morphometric traits to better understand the sex-specific investment of different-sized individuals into various body structures. Only breeding individuals were considered in these analyses. Despite remaining debates in the literature, the use of regressions to examine sexual dimorphism and trait scaling is widely accepted for such analyses, as they enable the normalization of data and control for confounding variables (Packard and Broadman, 1999). We investigated allometric scaling in relation to sternum length (a measure of skeletal size), sternum length corrected for body mass (a measure of body condition), and to wing length (a measure of body size). Scaling in relation to sternum length and to sternum length corrected for body mass are reported only in the supplemental (Table A.4 and Table A.5, respectively). We expected stronger scaling in relation to wing length than sternum length, as wing length may be a more relevant measure of body size when considering the ecology of highly aerial species like the Alpine swift than skeletal size. As preliminary results have suggested that these body structures changed over time, we also considered how their allometric scaling may have changed over time.

We fit a series of linear mixed effects models with each (log-transformed) trait as a function of (log-transformed) wing or sternum length (or sternum length corrected for mass), with sex (2-level factor: males vs females), colony (2-level factor: Biel vs Solothurn) and year (continuous variable) as fixed effects. We included an interaction term between sex and year to investigate whether the allometric scaling of each morphometric trait changed in the same ways in both sexes over the course of the study, and between sex and sternum or wing length to assess whether the sexes differed in their relative investment into each trait. We also included a sex by colony interaction term to assess whether morphological traits differed between the colonies as a function of the sex of the individuals. Finally, we included a three-way interaction between sternum or wing length, sex and year to investigate how these sex-specific differences in silhouette changed over the course of the study. Individual identity and the year of measurement were included as random effects to account for repeated measurements at the individual and year level respectively. As with the previous set of analyses quantifying sexual dimorphism, we refitted models of allometric scaling by replacing year (continuous variable) with period (2-level factor: 1999-2010 vs 2011-2021) in order to increase power.

2.2.5. *Ethical Note*

Swifts were caught at the nest by hand and handled for 5-15 minutes before being released at the colony site. To minimize stress, we avoided capturing swifts during sever weather events, and the bulk of captures took place between 9h00 and 18h00 so as to avoid disturbances during periods of intense social activity at dusk and dawn (Meier et al. 2018). All handlers were trained by

PB or senior members of the field team. All work was conducted in accordance with international standards on animal welfare and in compliance with Swiss local and national regulations (ringing permit 2235 and project 72 delivered by the Swiss Federal Office for the Environment to PB).

2.3. Results

2.3.1. *Sexual dimorphism*

We identified sexual dimorphism in morphometric traits ranging from weak (<2%) to moderate (7%), with fork length as the most sexually dimorphic trait (Table 2.1, Table A.1, Table A.2). Over the entire course of the study, body mass was female-biased, with females being 1% heavier than males, and sternum length, wing length, outer tail feather length, and fork length were male-biased, being 2%, 1%, 2%, and 7% longer in males than in females, respectively (Table 2.1, Table A.2). There were no statistically significant differences between the sexes in inner tail feather length (Table 2.1, Table A.2). Individuals from Solothurn had longer sternums, longer inner tail feathers and shorter fork lengths than those from Biel (Table 2.1). There were no statistically significant differences in body mass, wing length, or outer tail feather length between colonies (Table 2.1).

We also report slight changes in sexual dimorphism over the course of the study in some traits only (Table 2.1, Table A.1). Indeed, there were statistically significant changes in sexual dimorphism over the course of the study in body mass, wing length, outer tail feather length, and fork length (Table 2.1, Table A.2). Fork length increased non-linearly in both sexes over the course of the study (increase followed by an attenuation of the effect), with a greater increase in length in females than in males (Table 2.1). This greater increase in female than male fork length resulted in an attenuation of the sexual dimorphism in this trait, with males having 8.2% longer forks than females in the first period of the study decreasing to 6.7% in the second period of the study (Table A.1, Table A.2). Wing length and outer tail feather length increased linearly in both sexes over the course of the study, with a greater increase in the length of these traits in females than in males (Table 2.1), likewise resulting in a slight decrease in sexual dimorphism from one period to the next (Table A.1, Table A.2). Body mass increased linearly in both sexes over the course of the study, with females presenting a greater increase in body mass than males (Table 2.1), resulting in a slight increase in sexual dimorphism from one period to the next (Table A.1, Table A.2). Sexual dimorphism in sternum length was maintained over the course of the study, with a slight decrease in sternum length in both sexes over the course of the study (Table 2.1). Inner tail feather length decreased slightly and non-linearly in both sexes (decrease followed by an attenuation of the effect) over the course of the study (Table 2.1).

Breeding individuals of both sexes were heavier, had longer wings, longer outer and inner tail feathers, as well as longer forks than non-breeding individuals (Table 2.1). This increase in trait length between non-breeders and breeders was greater in females than in males for wing length and outer tail feather length (Table 2.1). Non-breeding individuals had a greater increase in trait length over the course of the study than breeders for body mass (followed by an attenuation of the effect) and wing length (Table 2.1). There were no statistically significant differences between breeders and non-breeders in sternum length (Table 2.1).

Table 2.1.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the sexual dimorphism in morphometric traits: body mass, sternum length, wing length, outer and inner tail feather length, and fork length. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T-Value**	**P-Value**
Mass[1]				
Intercept	-0.15	0.14	-1.08	0.290
Sex [M]	**-0.17**	**0.06**	**-3.13**	**0.002**
Colony	-0.07	0.04	-1.80	0.072
Year	**32.04**	**10.19**	**3.14**	**0.005**
Year ˆ2	-3.23	9.70	-0.33	0.742
Breeding Status	**0.13**	**0.02**	**6.79**	**< 0.001**
Sex [M] : Year	**-25.47**	**2.44**	**-10.43**	**< 0.001**
Sex [M] : Year ˆ2	**-5.82**	**2.04**	**-2.85**	**0.004**
Sex [M] : Breeding Status	-0.01	0.03	-0.53	0.596
Year : Breeding Status	**-9.18**	**1.75**	**-5.24**	**< 0.001**
Year ˆ2 : Breeding Status	**-3.39**	**1.45**	**-2.33**	**0.020**
Sex [M] : Year : Breeding Status	**9.01**	**2.30**	**3.91**	**< 0.001**
Sex [M] : Year ˆ2 : Breeding Status	**7.28**	**2.04**	**3.57**	**< 0.001**

Sternum Length[2]

Intercept	**-0.33**	**0.04**	**-9.12**	**< 0.001**
Sex [M]	**0.53**	**0.03**	**20.68**	**< 0.001**
Colony	**0.18**	**0.03**	**6.85**	**< 0.001**
Year	**-0.05**	**0.01**	**-3.77**	**0.001**
Breeding Status	0.05	0.03	1.46	0.146

Wing Length[3]

Intercept	**-0.45**	**0.05**	**-9.23**	**< 0.001**
Sex [M]	**0.60**	**0.06**	**10.73**	**< 0.001**
Colony	0.01	0.05	0.30	0.762
Year	**0.31**	**0.03**	**9.31**	**< 0.001**
Breeding Status	**0.27**	**0.02**	**11.01**	**< 0.001**
Sex [M] : Year	**-0.10**	**0.02**	**-3.85**	**< 0.001**
Sex [M] : Breeding Status	**-0.10**	**0.03**	**-3.12**	**0.002**
Year : Breeding Status	**-0.12**	**0.02**	**-5.72**	**< 0.001**

Outer Tail Feather Length[4]

Intercept	**-0.58**	**0.05**	**-11.46**	**< 0.001**
Sex [M]	**0.64**	**0.06**	**10.74**	**< 0.001**
Colony	0.07	0.05	1.53	0.126
Year	**0.08**	**0.03**	**2.76**	**0.007**
Breeding Status	**0.33**	**0.03**	**11.59**	**< 0.001**
Sex [M] : Year	**-0.14**	**0.03**	**-4.70**	**< 0.001**
Sex [M] : Breeding Status	**-0.09**	**0.04**	**-2.23**	**0.026**

Inner Tail Feather Length[5]

Intercept	**-0.22**	**0.05**	**-4.25**	**< 0.001**
Sex [M]	0.02	0.05	0.43	0.665
Colony	**0.29**	**0.05**	**6.09**	**< 0.001**
Year	**-7.12**	**2.21**	**-3.23**	**0.003**

Year ^2	**8.16**	**1.96**	**4.17**	**< 0.001**
Breeding Status	**0.12**	**0.03**	**4.62**	**< 0.001**
Fork Length[6]				
Intercept	**-0.44**	**0.05**	**-9.08**	**< 0.001**
Sex [M]	**0.67**	**0.05**	**14.78**	**< 0.001**
Colony	**-0.18**	**0.05**	**-4.06**	**< 0.001**
Year	**11.36**	**2.39**	**4.76**	**< 0.001**
Year ^2	**-10.42**	**2.05**	**-5.08**	**< 0.001**
Breeding Status	**0.24**	**0.02**	**10.28**	**< 0.001**
Sex [M] : Year	**-7.71**	**2.08**	**-3.70**	**< 0.001**
Sex [M] : Year ^2	-2.17	1.52	-1.42	0.155

[1]Number of: Observations: 4195; Individuals: 1079; Years: 24 [2]Number of: Observations: 5355; Years: 24 [3]Number of: Observations: 5333; Individuals: 1450; Years: 24 [4]Number of: Observations: 5284; Individuals: 1447; Years: 24 [5]Number of: Observations: 5263; Individuals: 1445; Years: 24 [6]Number of: Observations: 5282; Individuals: 1445; Years: 24

2.3.2. *Allometry*

Unsurprisingly, the exact allometric scaling of morphometric traits differed regarding the reference trait used, with traits scaling more steeply to wing length (Table 2.2) than sternum length (Table A.3) or sternum length corrected for body mass (Table A.4). That said, the allometric scaling estimates were largely negative in both sexes regardless of the scaling reference trait used (Table 2.2, Table A.3, Table A.4, Table A.5). The allometric scaling of fork length differed between the sexes in relation to wing length, with a possible change in this scaling over the course of the study (Table 2.2). Females' fork lengths scaled more steeply than that of males over the course of the study (Table 2.2), though this difference was only statistically significant when considering the two periods of the study rather than year as a continuous variable (Table A.6). Sex differences and sex-specific changes in dimorphism over the course of the study as well as colony differences in these morphometric traits were in line with the previously described results on sexual dimorphism (Table 2.1).

Table 2.2.: Linear (LMM) mixed-effects models assessing the allometric scaling of morphometric traits in relation to wing length on a log-log scale: outer and inner tail feather length, as well as relative and absolute fork depth. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T-Value**	**P-Value**
Outer Tail Feather Length[1]				
Intercept	**-0.17**	**0.04**	**-4.29**	**< 0.001**
Sex [M]	**0.34**	**0.04**	**8.14**	**< 0.001**
Wing	**0.41**	**0.02**	**26.24**	**< 0.001**
Year	-0.01	0.03	-0.29	0.776
Colony [Solothurn]	0.08	0.04	1.81	0.071
Sex [M] : Year	**-0.09**	**0.03**	**-3.33**	**< 0.001**
Inner Tail Feather Length[2]				
Intercept	-0.03	0.04	-0.64	0.521
Sex [M]	**-0.14**	**0.04**	**-3.08**	**0.002**
Wing	**0.33**	**0.02**	**17.38**	**< 0.001**
Year	**-9.38**	**1.95**	**-4.80**	**< 0.001**
Year ^2	**7.83**	**1.77**	**4.43**	**< 0.001**
Colony [Solothurn]	**0.29**	**0.05**	**6.52**	**< 0.001**
Fork Length[3]				
Intercept	**-0.15**	**0.05**	**-3.36**	**0.001**
Sex [M]	**0.51**	**0.05**	**11.15**	**< 0.001**
Wing	**0.24**	**0.02**	**10.36**	**< 0.001**
Year	**6.85**	**2.31**	**2.96**	**0.005**
Year ^2	**-9.50**	**2.04**	**-4.66**	**< 0.001**
Colony [Solothurn]	**-0.18**	**0.05**	**-3.88**	**< 0.001**
Sex [M] : Wing	-0.02	0.03	-0.56	0.579
Sex [M] : Year	**-4.30**	**2.00**	**-2.15**	**0.031**
Sex [M] : Year ^2	-1.79	1.51	-1.19	0.235

Wing : Year	-1.26	1.25	-1.01	0.312
Wing : Year ^2	1.67	1.02	1.64	0.101
Sex [M] : Wing : Year	2.87	1.78	1.61	0.108
Sex [M] : Wing : Year ^2	-2.61	1.48	-1.77	0.078

[1] Number of: Observations: 4534; Individuals: 1302; Years: 24 [2] Number of: Observations: 4520; Individuals: 1300; Years: 24 [3] Number of: Observations: 4527; Individuals: 1300; Years: 24

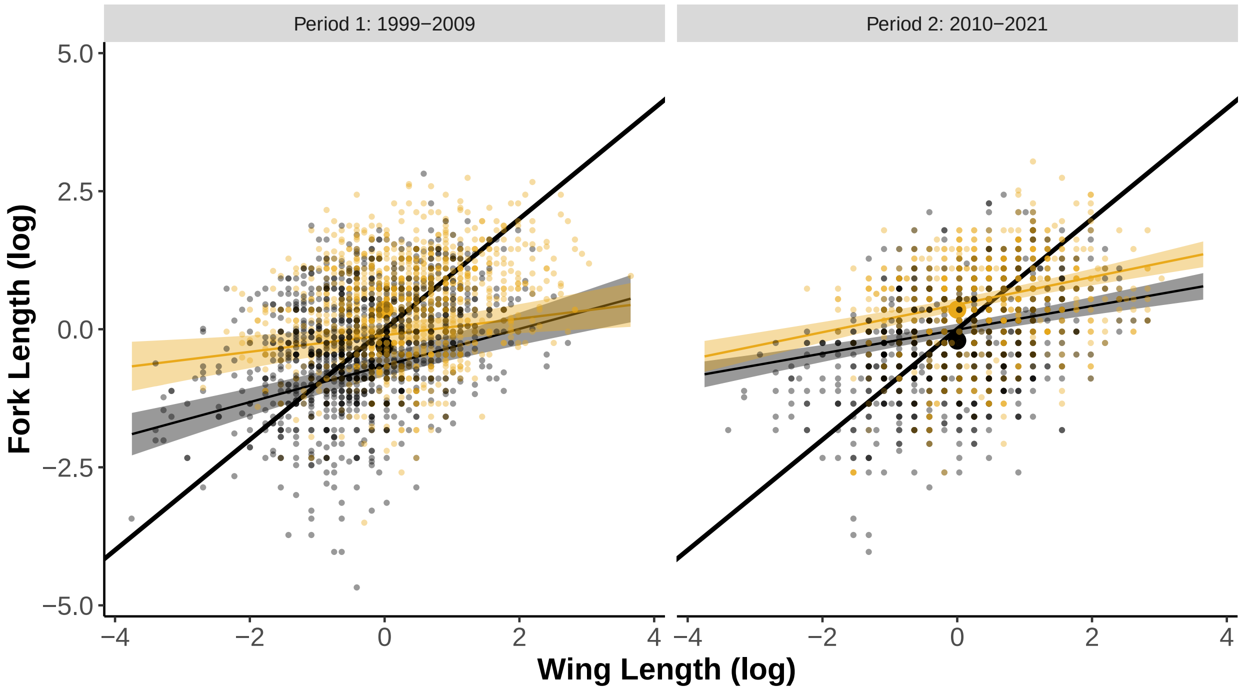

Figure 2.1.: Sex-specific changes in allometric scaling of fork length. Lines and confidence intervals are based off of predicted values with female swifts in black, and male swifts in gold based on the model with year as a continuous variable (split between periods for visualization only). The data points correspond to the raw data. Mean fork length per sex per period are displayed. The solid black lines denote isometry.

2.4. Discussion

In this study, we identified sexual dimorphisms of morphometric traits in a bird previously characterised as monomorphic and conclude that the Alpine swift is rather a cryptically dimorphic species. Interestingly, we found that the extent of this sexual dimorphism has changed over the course of the study, such that male and female feather traits have become more similar, but that females are getting heavier such as to increase the sexual dimorphism in body mass. We further identified sex- and trait-specific allometric scaling, as well as possible sex-specific changes in allometric scaling of fork length over the course of the study.

On average, feather traits were male-biased, with fork length being the most dimorphic trait, and body mass as the only female-biased trait. Subtle sexual dimorphism has also been reported in other swift species (e.g., common swifts *Apus apus*, Jukema et al. 2023; plain swift *Apus unicolor*, Garcia-Del-Rey et al. 2008; pallid swifts *Apus pallidus*, Boano et al. 2015), suggesting that sexual dimorphisms in swifts may be more common than previously reported. This sexual dimorphism may have arisen, at least partially, as a result of sexual selection. In particular, fork length has historically been considered to be under strong sexual selection in swifts and swallows (Hasegawa and Arai 2020) and is likely involved in aerial courtship displays. In the Alpine swift, fork length is under directional selection, as females with longer forks lay heavier eggs, and males with longer forks have more surviving fledgling proportionate to clutch size (Dumas et al. 2024b). In addition, morphometric traits (with the exception of sternum length) were over-expressed in breeding individuals of both sexes, further suggesting a possible role of sexual selection acting on these traits.

However, the degree of sexual dimorphism in Alpine swift feather traits decreased over the course of the study. Notably, wing, outer tail feather and fork lengths increased more in females than in males over the course of the study such that these traits became more similar between the sexes. The strongest reduction in SSD was for fork length, with a reduction of nearly 20% in the past 2 decades. Morphometric changes have been documented in the Alpine swift, with notable increases in adult wing and outer tail feather length (Masoero et al., in prep). These changes appear to be driven by a combination of demographic effects (newly recruited females have longer wings and tails), plasticity (feather growth in early life has accelerated) and microevolution (breeding values have increased over the course of the study) (Masoero et al., in prep). This may point to changes in the environment resulting in shifting sex-specific selective pressures but remains to be investigated further.

Body mass was the only female-biased trait, possibly as a result of viability selection with larger females being able to invest more resources into various aspects of egg laying. Indeed, heavier females lay their clutches sooner (Dumas et al. 2024c). Our results suggest that the sexual dimorphism in body mass has increased slightly over the course of the study, becoming even more female-biased (albeit still small). Body mass appears to be under positive directional selection in females (trending towards stabilizing selection), and under negative directional selection in males (trending towards diversifying selection) (Dumas et al. 2024c). This increase in female body mass, coupled with their relatively shorter wings, could results in increased wing load as compared to males, with implications for sex-specific flight patterns and hence foraging niches. Indeed, male and female pallid swifts reportedly forage on prey species of different sizes (Fernandes et al. 2023), althought there is currently no information on foraging strategies and niches in the Alpine swift. In the wandering albatrosses *Diomedea exulans*, males have greater wing loading than females and are more likely to take off during strong winds than females, suggesting different foraging strategies and niches (Clay et al. 2020). Sternum length has likewise decreased in both sexes over the course of the study, despite remaining on average longer in males than in females and maintaining male-biased dimorphism. As the sternum serves as the point of attachment for pectoral flight muscles, this could serve to further reinforce these sex-differences in expected wing loading capacities.

Allometric scaling was largely negative in both sexes, though this relation was stronger when scaling to wing length than sternum length (or sternum length corrected for body mass). It appears unsurprising for morphometric traits to scale more steeply to wing length than to sternum length, as wing length encapsulates variation both in skeletal size and feather length, with the later relating more directly to all other feather traits. Indeed, wing and tail length are strongly positively correlated at the genetic level, and both wing length and sternum length are moderately positively correlated with body mass at the genetic level (Masoero et al., in prep). The importance of choosing an appropriate reference characteristic has been noted by Fox et al. (2015), who likewise found differing allometric scaling based on the choice of reference trait in the desert hairy scorpion *Hadrurus arizonensis*. Fox et al. (2015) advocate for the use of a neutral reference character (i.e., without sexual dimorphism and independent of nutritional state), which proves difficult in the Alpine swift. Although sternum length and wing length show similar trends in trait- and sex-specific scaling, and consistently indicative of negative allometric scaling, we therefore interpret these results with caution. Negative allometric scaling suggests that larger individuals invest relatively less into a given body structure, or that the costs of increasing these body structures are greater than the benefits for larger body sizes. In regards to fork length in particular, this negative scaling suggests that longer wings do not act as a compensatory trait for more deeply forked tails as it has been suggested in other species with deeply forked tails (Fitzpatrick 1999). Sexual selection often acts on the allometric intercept (i.e., sexual dimorphism independent of body size) rather than the allometric slope (Bonduriansky 2006). Hence, and as discussed elsewhere in the literature (e.g., Bonduriansky 2006; Cuervo and Møller 2009; Rodríguez and Eberhard 2019), negative allometric scaling does not rule out sexual selection as a driver of shape dimorphism in the Alpine swift. In addition, Rodriguez & Eberhard (2019) have suggested that allometric scaling may be best predicted by the function of the trait, with weapons being the trait most likely to evolve positive allometry. Under this ‘functional allometry’ hypothesis (Rodríguez and Eberhard 2019), courtship signals would rather be expected to display negative allometric scaling. Hence, negative allometric scaling of fork length would be in line with its expected function as a signal of individual condition used in courtship in both sexes (Dumas et al. 2024a).

Furthermore, the sex-specific scaling of fork length may have changed over the course of the study. To the best of our knowledge, this is the first study to report possible changes in sex-specific allometric scaling over time in a wild bird. As with the attenuation of the sexual dimorphism in feather traits, this change suggests an attenuation of allometric scaling. Indeed, females with short wings have proportionately longer forks now than at the start of the study, while no such changes in relative trait size occurred for long winged females. However, we must interpret these results with caution as this change in sex-specific scaling was statistically significant only while simplifying the model to contrast the first and second period of the study, rather than by treating year as a continuous variable ($p = 0.078$). This discrepancy between both approaches may reflect a lack of power to accurately detect a signal when modelling year as a continuous variable as a result of increased error due to the collinearity with other variables, and also potential non-linear changes in trait sizes. None the less, both approaches suggest the same direction of change in allometric scaling. Although this change in the relative investment into fork length in relation to body size remains to be investigated, such a change may reflect environmental changes selecting for greater maneuverability, either via longer wings and/or more deeply forked tails in females.

To conclude, the Alpine swift is a weakly dimorphic species, with sex- and trait-specific allometric scaling. Fork length was the trait with the greatest sexual dimorphism (7%), with longer fork lengths in breeders than non-breeders. Negative allometric scaling of fork in relation to wing length coupled with previous evidence of positive selection on fork length (Dumas et al. 2024b) suggests that fork length may be under sexual selection in this highly aerial bird. This result is coherent with previous results suggesting the evolution of deeply forked tails by sexual selection in aerial birds such as swifts and swallows (Hasegawa and Arai 2020; Møller et al. 1998). Our results are consistent with current trends in allometric scaling, suggesting that negative allometric scaling can occur for sexually selected traits. Although we identified changes in dimorphism as well as possible sex-specific changes in allometric scaling of fork length over the course of the study, an explanation for these changes is beyond the scope of the present study and will require further investigation. Crucially, more studies on scaling relationships for traits lacking extreme exaggeration are needed to evaluate the relative variation of morphological traits and resulting evolutionary consequences in both sexes.

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Chapter 3

Chapter 3: Shared genetic architecture and sex-specific fitness consequences of forked tails in the Alpine swift *Tachymarptis melba*

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Preamble

Ones' research proposal has been jokingly described to me as 'everything you won't do during your PhD.' My thesis very much fits the mold, with only the general shape of my proposal making it to this final version (and mostly only to introduce the concepts herein!). That said, studying fork length was always in the cards, as this trait is a likely contender for sexual selection and a good place to start. It's also pretty fun to measure fork and tail length on swifts: head down, swaddled into a bird-burrito so that they don't injure themselves (or you with their sharp little foot-daggers), and (gently) pinned between your knees. The results presented in this chapter are only a first step in understanding the sex-specific evolution of this trait, with several more fascinating questions to follow up on!

Abstract

The evolution of deeply forked tails in highly aerial birds has been suggested to be driven by sexual and viability selection. Using over 20 years of data on the Alpine swift, we investigated the sex-specific predictors and fitness consequences of deeply forked tails, as well as the role of genetics in shaping the evolutionary trajectory of this trait. In the Alpine swift, fork length shows moderate sexual dimorphism, being 7% longer in males than in females. Longer forks were associated with increased reproductive success in males and larger eggs in females, suggesting that this trait may be mutually selected and signal aspects of individual condition in both sexes. In addition, fork length was heritable and strongly genetically correlated between the sexes, with effectively the same genetic architecture expressed in both sexes. However, genetic constraints between the sexes are unlikely to explain the changes in fork length observed over the course of the study, as fork length increased more in females than in males. Further studies will be required to understand why male fork length has not became further elaborated, despite positive directional selection on this heritable trait.

3.1. Introduction

Sexual dimorphism is widespread in the animal kingdom, encapsulating differences between the sexes in behaviour, physiology or morphology, and ranging from subtle to extreme while favouring one sex or the other (Fairbairn 2007). Sexual dimorphism is expected to arise when the strength and shape of selection on the sexes differs (Shine 1989), reflecting adaptive differences in the optimal value of the trait for each sex (Fairbairn 2007). For instance, both sexes of the barn swallow *Hirundo rustica* have elongated tail streamers resulting in deeply forked tails. Deeply forked tails are expected to impact maneuverability and agility, both of which play a crucial role in foraging and predator escape in highly aerial species. The tail streamers of the barn swallow appear to be elaborated past the natural selection optimum in males (Møller et al. 1998) thereby increasing drag and incurring aerodynamic costs (Evans and Thomas 1992), and are considered a classical example of sexual selection. Males with more deeply forked tails have higher levels of circulating testosterone and are preferred as mates by females, but also suffer increased mortality (Møller et al. 1998). Despite controversy around the relative roles of natural vs. sexual selection in driving tail length and shape, especially in swallows (Aparicio and Møller 2012; Evans et al. 2012), deeply forked tails may arise in both sexes as a product of both natural and sexual selection.

Because traits expressed in both sexes typically have their origin in shared genetic architecture (Poissant et al. 2010; Roff 1996), genetic constraints in the form of intra-locus sexual conflict could impede the evolution of sex-specific phenotypic optima (Bonduriansky and Chenoweth 2009). Intra-locus sexual conflicts may be commonplace—especially so in cases of weak or subtle sexual dimorphism where the conflict could be ongoing—and can be assessed by estimating the cross-sex genetic correlation (r_{fm}, Lande 1980) and sex-specific selection acting on a shared trait. While an r_{fm} approaching one (positive or negative) suggests the presence of shared genetic architecture between the sexes, and thus constraints on sex-specific evolution, a null correlation suggests little shared genetic architecture and thus that both sexes may evolve to their own sex-specific optima unhindered (Poissant et al. 2010). Intra-locus sexual conflict is expected in cases where a positive r_{fm} approaching one is coupled with sexually antagonistic selection or where a negative r_{fm} approaching one is coupled with sexually concordant selection (Kruuk et al. 2008). Intra-locus sexual conflict has chiefly been reported in lab-based population, namely studies on *Drosophila melanogaster* (Long and Rice 2007; Rice and Chippindale 2001), though it has also been identified in wild populations such collared flycatchers *Ficedula albicollis*, (Merilä et al. 1997, 1998) and mountain goats *Oreamnos americanus* (Mainguy et al. 2009).

Such genetic constraints have been put forth as one of the explanations for monomorphism, wherein secondary sexual traits are expressed in the non-signaling sex as a result of strong genetic correlations between the sexes. In these cases, one sex would be expected to benefit from the over-elaboration of the trait, while the other sex would only bear the costs. Indeed, this argument has been used by some to explain the evolution of tail streamers in female barn swallows (Cuervo et al. 1996), wherein tail streamers that are longer than the aerodynamic optimum are sexually selected in males and may be over expressed in females solely due to the genetic constraint. In line with this expectation, experimentally elongated tail steamers in female barn swallows resulted in decreased reproductive success in the year following the manipulation, suggesting long-term parental investment or flight efficacy costs (Cuervo et al. 2003).

As an alternative to the genetic correlation hypothesis, monomorphic traits could evolve as a result of mutual selection (Kokko and Johnstone 2002), wherein the trait would be sexually selected in both sexes. Under mutual mate choice, deeply forked tails could act as a signal of individual condition in both sexes, with individuals of higher condition able to carry the costs of more deeply forked tails. Mutual selection is predicted to occur most often in monogamous species with bi-parental care, though its prevalence remains uncertain (Kokko and Johnstone 2002). Crested auklets *Aethia cristatella* of both sexes prefer mates with longer feather crests (Jones and Hunter 1999), and longer tail streamers were associated with higher reproductive success in both sexes of an East Mediterranean population of barn swallows *H. r. transitive* (Vortman et al. 2011).

The aim of this study was to investigate the sex-specific fitness consequences and genetic architecture of relatively deeply forked tails in a wild population of Alpine swifts *Tachymarptis melba*, a highly aerial insectivore. We first quantified the sex-specific reproductive and viability selection acting on fork length. Given that the allometric scaling of fork length to wing length is sex-specific (Dumas et al. 2024b), we also considered direct and indirect selection acting on fork length and wing length in both sexes. Although this appears unlikely to be the case in the Alpine swift, longer wings have been identified as potential compensatory traits for deeply forked tails by minimizing their aerodynamic costs (Fitzpatrick 1999). We expected longer forks to provide benefits for males but not females in terms of reproductive success, and costs for both sexes in terms of survival, consistent with general theory on traits subject to sexual selection. Despite the bulk of studies on fork length being on swallows, recent works have provided some support for the role of sexual selection in driving the evolutionary of more deeply forked tails in male swifts (Hasegawa and Arai 2020; Jukema et al. 2023). Because sexual conflict at the genetic level requires the traits in question to be heritable, we then quantified the additive genetic variance and heritability of fork length in both sexes. We additionally assessed the importance of genetic constraints on the evolution of sexual dimorphism in fork length by estimating the cross-sex genetic correlation, with the expectation that such a correlation would be strongly positive. Finally, we evaluated the microevolutionary trajectory of fork length over the course of the study.

3.2. Materials & Methods

3.2.1. *Study Species & Site*

The Alpine swift is a long-lived (lifespan: median approx. 7 years, maximum 26 years, Bize et al. 2006a; Moullec et al. 2023) and colonially nesting bird. They live a highly aerial lifestyle, capable of remaining in constant flight for over six months at a time (Liechti et al. 2013) and landing only during the breeding period. Colonies of a few to a hundred pairs will nest on cliffs or in the roof spaces of tall buildings when nesting in urban settings. Alpine swifts nest from May to August, with both parents incubating their 1-4 eggs for approximately 18 days (Bize et al. 2004). Chicks take approximately 50 to 70 days from hatching to fledging, during which time both parents will brood and feed them (Bize et al. 2004). As such, males and females are expected to have similar parental allocation into reproduction, with the exception of egg laying for which females alone pay the energetic costs (e.g., females show a more pronounced decrease in body mass over the season than males, Dumas et al. 2024c).

Since 1999 and 2000 respectively, two urban-nesting colonies have been intensively monitored in the Swiss cities of Biel (60-100 breeding pairs) and Solothurn (40-55 breeding pairs). In both colonies, birds are individually identified by permanently ringing them as nestlings or at their first capture at adulthood if not already ringed as nestlings. Parents are caught by hand at the nest, their identity is recorded, and their yearly reproductive success is determined (clutch size, brood size at hatching and fledgling). As no extra-pair paternity (EPP) has been recorded in this population (C. M. Meier & P. Bize, personal comm.), these behavioural observations are sufficient for pair-bond identification and to construct a detailed social pedigree. Individuals are measured to the nearest millimetre using a ruler (e.g., wing, tail and fork lengths) or tenth of a millimetre using a caliper (e.g., sternum length) and sexed (DNA taken from blood or feathers, Griffiths et al. 1998). Fork length is measured as the distance between the tip of the inner tail feather and the tip of the outer tail feathers on both the left and right sides of the body, and then averaged. The inner tail feather is calculated as the difference between the outer tail feather and the fork length. These feather traits are measured once per individual per year captured.

Although Alpine swifts have historically been considered to be monomorphic like most swifts, subtle sexual dimorphisms are present (e.g., females are 1% heavier than males, Dumas et al. 2024c; males have 7% longer forks than females, Dumas et al. 2024b). Despite the presence of these slight sexual dimorphism, Alpine swifts appear monomorphic to human observers, and hence field measurements are taken blind to the sex of the individuals. Fork length in other swifts ranges from monomorphic in the plain swift *Apus unicolor* (Garcia-Del-Rey et al. 2008), to minorly dimorphic in the common swift *Apus apus* (Jukema et al. 2023), to strongly dimorphic in the black swift *Cypseloides niger borealis* (Gunn et al. 2018), with males having more deeply forked tails than females. Sexual dimorphism in other feather and morphometric traits have also been documented in some species (e.g., male pallid swifts *Apus pallidus* have longer wings than females, Boano et al. 2015).

3.2.2. *Statistical analyses*

All statistical analyses were conducted in R version 4.3.1 "Beagle Scouts" (R Core Team 2023), using the R packages *lmerTest* (Kuznetsova et al. 2017) and *MCMCglmm* (Hadfield 2010). Deeply forked tails can be produced by one of two mechanisms: lengthening of outer tail feathers and/or shortening of inner tail feathers. Hence, for all models, we examined fork length as well as the relative fork depth, determined as the ratio of fork length to the inner or outer tail feathers. Results from all three approaches were qualitatively similar and hence only the fork length models are included in the manuscript, while the relative fork depth models are reported in the supplemental. Absolute and relative fork depths were mean-centered and scaled to a variance of 1, pooled across the sexes. Year, as a continuous variable, was also mean-centered and scaled to a variance of 1. When included in the analyses, quadratic effects were calculated using orthogonal polynomials. All models were first tested with the inclusion of all biologically relevant interaction terms and quadratic effects; non-statistically significant interaction terms (Engqvist 2005) and non-statistically significant quadratic effects (Faraway 2014) were dropped from the final models and are reported only in the supplemental. Data presented in these analyses spans 1999-2021.

3.2.3. *Selection analyses*

In a first part, we investigated the fitness consequences of relatively deeply forked tails in both sexes. We ran a series of linear and generalized linear mixed effects models to investigate the fitness consequences of fork length on measures of reproductive success and overwinter survival. We considered direct and indirect selection acting on fork length and wing length, as the sexes differ in their relative fork to wing lengths, with wing length seen as a potential compensatory trait for more deeply forked tails. We further considered both female and male traits as selection may operate differently on each sex. Overwinter survival was estimated for breeding individuals only based on yearly records of capture, as the probability of recapturing birds in this population is nearly one (Bize et al. 2006a).

Reproductive success traits considered were clutch size (Poisson distribution, log-link), brood size at hatching (Poisson distribution, log-link) and at fledgling (Poisson distribution, log-link), and the weighted proportion of surviving fledglings (binomial distribution, logit-link). The weighted proportion of surviving fledglings was modelled as brood size at fledging over clutch size. Surviving fledglings are defined as those that successfully leave the colony.

Since non-breeding individuals have typically not yet reached sexual maturity, we also considered the relation between fork length and breeding status (binomial distribution, logit-link). In addition, we considered the relation between fork length and egg laying date (Gaussian distribution), as laying date is strongly related to fitness in the Alpine swift (de Villemereuil et al. 2020) despite not being a fitness component *per se*. Laying date was modeled as day of the year and mean-centered and scaled to a variance of 1. Finally, we considered the relation between fork length and egg volume (Gaussian distribution), as previous studies have identified a trade-off between egg size and deeply forked tails in swifts and swallows (females with more deeply forked tails produced smaller eggs, Hasegawa and Arai 2017, 2018). Egg volume was calculated as egg length x egg width^2 x $\pi/6$ following Bize et al. (2002).

For each reproductive parameter, we fitted a model with reproductive success as a function of female and male fork length, female and male wing length, and the colony. Female and male identity as well as the year were included as random effects to account for repeated measurements on the individual and yearly levels, respectively. These models were conducted at the pair level, as reproductive success requires concerted effort from both parents with both parents providing care to their offspring at all stages. Models were fitted with both linear and quadratic effects for male and female fork length and wing length, but the quadratic term was dropped from the final model as these were not statistically significant (Table B.2).

The breeding status (binomial distribution, logit-link) and overwinter survival models (binomial distribution, logit-link) were run at the individual level, and thus included sex as a fixed effect. We fitted breeding status as a function of sex, fork length (linear and quadratic terms), and colony, with individual identity and year as random effects to account for repeated measures. We also included the two-way interaction term between sex and fork length (linear and quadratic), but these were removed the final model as they were not statistically significant (Table B.2). We fitted overwinter survival as a function of sex, fork length, and colony, with individual identity and year as random effects to account for repeated measures. We also included the two-way interaction term between sex and fork length but it was removed from the final model as it was not statistically significant (Table B.2).

3.2.4. *Quantitative genetic analyses*

In a second part, we investigated the predictors of fork length in female and male Alpine swifts. We assessed the sexual dimorphism in fork length, with the expectation that males would have more deeply forked tails than females, as shown in previous work on the Alpine swift (Dumas et al. 2024a), and since previous studies have suggested a sexually selected role of deeply forked tails in males (Hasegawa and Arai 2020). As Alpine swifts have been subject to rapid morphometric changes over the past two decades (e.g., wing and tail lengths have increased in both sexes, Masoero et al., in prep), we considered sex-specific changes in fork length over the course of the study. As such, we fitted a generalized linear mixed effects model with fork length as a function of sex, the year (linear and quadratic), and colony as fixed effects, with an interaction term between sex and year to investigate whether fork length changed in the same ways over the course of the study in both sexes. We further considered the effect of male and female age (linear and quadratic) on fork length, as previous studies on the Alpine swift have revealed sex specific ageing trajectories of morphometric traits (Moullec et al. 2023). Since the quantitative genetic analyses results with and without the age effects were qualitatively similar, and including individual age decreases the available sample size by approximately 30%, we report age effects only in the supplemental (Table B.6, Table B.7).

We estimated quantitative genetic parameters of fork length by including pedigree data (an 'animal model,' Kruuk et al. 2008). Animal models allow users to decompose total variance between environmental and genetic sources, and hence make inferences about the evolutionary potential of a trait (Kruuk et al. 2008; Wilson and Nussey 2009). We estimated the following sex-specific variance components: additive genetic variance (individual identity linked to the pedigree), permanent environment variance (individual identity), yearly variance (year of observation) and residual variance. In addition, we estimated the cross-sex genetic and yearly covariances and correlations, to assess the presence of genetic constraints on the evolutionary potential of fork length. Variance parameters were estimated as the median, mean and posterior mode following Pick et al. (2023) and reported with their 95% highest posterior density intervals (HPDI) (the mean and posterior mode are reported in the supplemental only, Table B.9). Variance ratio estimates were calculated as the proportion of total phenotypic variation explained by the given variance parameter, i.e., heritability conditioned on the fixed effects was estimated as the sex-specific additive genetic variance divided by the (conditional) total phenotypic variance. The pruned social pedigree used in this study was 5 generations deep and included data on 1396 individuals, with 590 maternities and 571 paternities

(Table B.5). The social pedigree statistics were determined using the R package *pedantics* (Morrissey 2023).

For the residuals and the permanent environment effect, for which cross-sex correlations cannot be estimated, we used standard priors with V = diag(2), nu = 1.002. For the additive genetic and year effects, we used expanded priors, adapted for models estimating cross-sex correlations (i.e., V = diag(2) * 0.02, nu = 3, alpha.mu = rep(0, 2), and alpha.V = diag(2) * 1000). The model had a burn-in period of 50000 iterations and was sampled every 2000 iterations for a total effective sample size of 1500. Plot traces were visually assessed, and absolute autocorrelation values were verified to be <0.1. We verified chain convergence for each parameter using the Heidelberger and Welch's convergence diagnostic (heidel.diag function) as recommended by Hadfield (2010); all converged well.

In addition, we refitted the previous animal model without the inclusion of year as a fixed effect in order to assess whether or not there have been genetic changes in this trait over the course of the study. To do so, we estimated the predicted breeding values (PBVs) of female and male fork length using best linear unbiased predictors (BLUPs) based on individual phenotypic information as well as that of relatives (Henderson, 1950). We then fit the female-trait and male-trait breeding values as a function of the year of birth of each individual (linear and quadratic) to investigate changes in PBVs over the course of the study. The quadratic effect of the year of birth was non-statistically significant and hence was dropped from the model. These linear regressions were fit on the PBVs of each posterior sample from the animal model, allowing us to estimate the posterior distribution (median) of the slope (Hadfield 2010). We further simulated random breeding values following the pedigree for each posterior sample in order to estimate the changes in PBVs over time due to genetic drift, and to assess whether the change in female-trait and male-trait PBVs over time were stronger than those expected under drift alone (Hadfield 2010).

3.2.5. *Ethical note*

Adult swifts were caught at the nest between 8h00 and 20h00 (usually between 9h00 and 18h00) to avoid disturbing the adults during periods of intense social activity (dawn and dusk) (Meier et al. 2018). We minimized the number of captures and disturbances during severe weather events to avoid extra stress to the birds. To further limit stress to the birds, swifts were placed in cloth bags and handled quickly, typically 5-15 minutes depending on data collection. All individuals were released at the colony site. All handlers were trained by PB or senior members of the field team. All work was conducted in accordance with international standards on animal welfare and in compliance with Swiss local and national regulations (ringing permit 2235 & project 72 delivered to Pierre Bize by the Swiss Federal Office for the Environment).

3.3. Results

3.3.1. *Selection analyses*

On average, there were more breeding females than breeding males, and breeders had longer forks than non-breeders with a non-linear increase in breeding probability in relation to fork length (Table 3.1). Female but not male fork and wing lengths had a positive effect on egg volume (Table 3.1). There were no detectable effects of either female or male fork length or wing length on egg laying date (Table 3.1). Likewise, there was no detectable selection on female or male fork length or wing length in relation to clutch size (Table 3.1). However, males with longer forks had larger brood sizes at hatching and fledgling as well as a greater weighted proportion of surviving fledglings than males with shorter forks (Table 3.1, Figure 3.1). In addition, males with shorter wings had larger brood sizes at hatching than males with longer wings (Table 3.1). There were no statistically significant effects of female fork length or wing length in relation to brood size at hatching nor fledgling, or to the weighted proportion of surviving fledglings (Table 3.1). There were no statistically significant differences in overwinter survival in relation to sex, fork length or wing length (Table 3.1). There were statistically significant colony differences for all measures of reproductive success as well as breeding status, laying date and overwinter survival, with more breeding individuals, earlier laying dates, larger eggs, larger clutch and brood sizes (hatching, fledgling, weighted proportion of surviving fledglings) as well as greater overwinter survival in Solothurn as compared to Biel (Table 3.1). These results were qualitatively similar when looking at the relative fork depth (ratio of fork length to inner or outer tail feather length) rather than absolute fork length (Table B.3), and when removing wing length from the models (Table B.4).

Table 3.1.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between fork length and breeding status (binomial distribution), laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), the weighted proportion of surviving fledglings (binomial distribution) and overwinter survival (binomial distribution). The T-Value is reported for the laying date model, while the Z-Value is reported for all other models. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T- or Z-Value**	**P-Value**
Breeding Status[1]				
Intercept	**2.8**	**0.21**	**13**	**< 0.001**
Sex [M]	**-0.55**	**0.12**	**-4.5**	**< 0.001**
Fork Length	**17**	**4.3**	**4.0**	**< 0.001**
Fork Length ^2	**-12**	**3.1**	**-3.8**	**< 0.001**
Wing length	**28**	**4.5**	**6.3**	**< 0.001**
Wing Length ^2	**-11**	**3.7**	**-3.0**	**0.0027**
Colony [Solothurn]	**-0.28**	**0.12**	**-2.5**	**0.014**
Laying Date[2]				
Intercept	0.18	0.12	1.4	0.16
Female Fork Length	-0.028	0.024	-1.2	0.23
Male Fork Length	-0.030	0.021	-1.4	0.15
Female Wing Length	-0.035	0.025	-1.4	0.15
Male Wing Length	0.023	0.021	1.1	0.26
Colony [Solothurn]	**-0.34**	**0.051**	**-6.7**	**< 0.001**
Egg Volume[3]				
Intercept	**5.8**	**0.027**	**210**	**< 0.001**
Female Fork Length	**0.046**	**0.012**	**3.9**	**< 0.001**
Male Fork Length	0.011	0.0086	1.3	0.19
Female Wing Length	**0.035**	**0.013**	**2.6**	**0.0097**
Male Wing Length	0.011	0.0094	1.2	0.22

Colony [Solothurn]	**0.074**	**0.035**	**2.1**	**0.038**
Clutch Size[4]				
Intercept	**0.99**	**0.019**	**52**	**< 0.001**
Female Fork Length	0.0074	0.015	0.50	0.62
Male Fork Length	0.0035	0.014	0.24	0.81
Female Wing Length	0.0036	0.015	0.24	0.81
Male Wing Length	0.0047	0.014	0.33	0.74
Colony [Solothurn]	0.048	0.028	1.7	0.083
Brood Size at Hatching[5]				
Intercept	**0.63**	**0.042**	**15**	**< 0.001**
Female Fork Length	0.015	0.018	0.85	0.40
Male Fork Length	**0.047**	**0.018**	**2.7**	**0.0076**
Female Wing Length	0.0017	0.018	0.093	0.93
Male Wing Length	**-0.043**	**0.017**	**-2.5**	**0.013**
Colony [Solothurn]	**0.18**	**0.035**	**5.2**	**< 0.001**
Brood Size at Fledgling[6]				
Intercept	**0.34**	**0.063**	**5.4**	**< 0.001**
Female Fork Length	0.027	0.021	1.3	0.20
Male Fork Length	**0.042**	**0.021**	**2.0**	**0.042**
Female Wing Length	0.012	0.021	0.55	0.58
Male Wing Length	-0.033	0.021	-1.6	0.11
Colony [Solothurn]	**0.22**	**0.042**	**5.3**	**< 0.001**
Weighted Proportion of Surviving Fledglings[7]				
Intercept	0.22	0.17	1.3	0.19
Female Fork Length	0.082	0.056	1.5	0.15
Male Fork Length	**0.16**	**0.053**	**3.1**	**0.0020**
Female Wing Length	0.024	0.058	0.40	0.69
Male Wing Length	-0.10	0.057	-1.8	0.079

Colony [Solothurn]	**0.59**	**0.14**	**4.3**	**< 0.001**
Overwinter Survival[8]				
Intercept	**-0.71**	**0.22**	**-3.2**	**0.0016**
Sex [M]	-0.067	0.074	-0.91	0.36
Fork Length	0.0035	0.041	0.087	0.93
Wing Length	0.056	0.040	1.4	0.16
Colony [Solothurn]	**-0.34**	**0.073**	**-4.6**	**< 0.001**

[1] Number of: Observations: 5337; Individuals: 1444; Years: 24 [2] Number of: Observations: 1941; Females: 611; Males: 576; Years: 24 [3] Number of: Observations: 5047; Nests: 1655; Females: 593; Males: 554; Years: 23 [4] Number of: Observations: 1939; Females: 613; Males: 578; Years: 24 [5] Number of: Observations: 1949; Females: 613; Males: 578; Years: 24 [6] Number of: Observations: 1946; Females: 613; Males: 577; Years: 24 [7] Number of: Observations: 1934; Females: 612; Males: 577; Years: 24 [8] Number of: Observations: 4585; Individuals: 1300; Years: 24

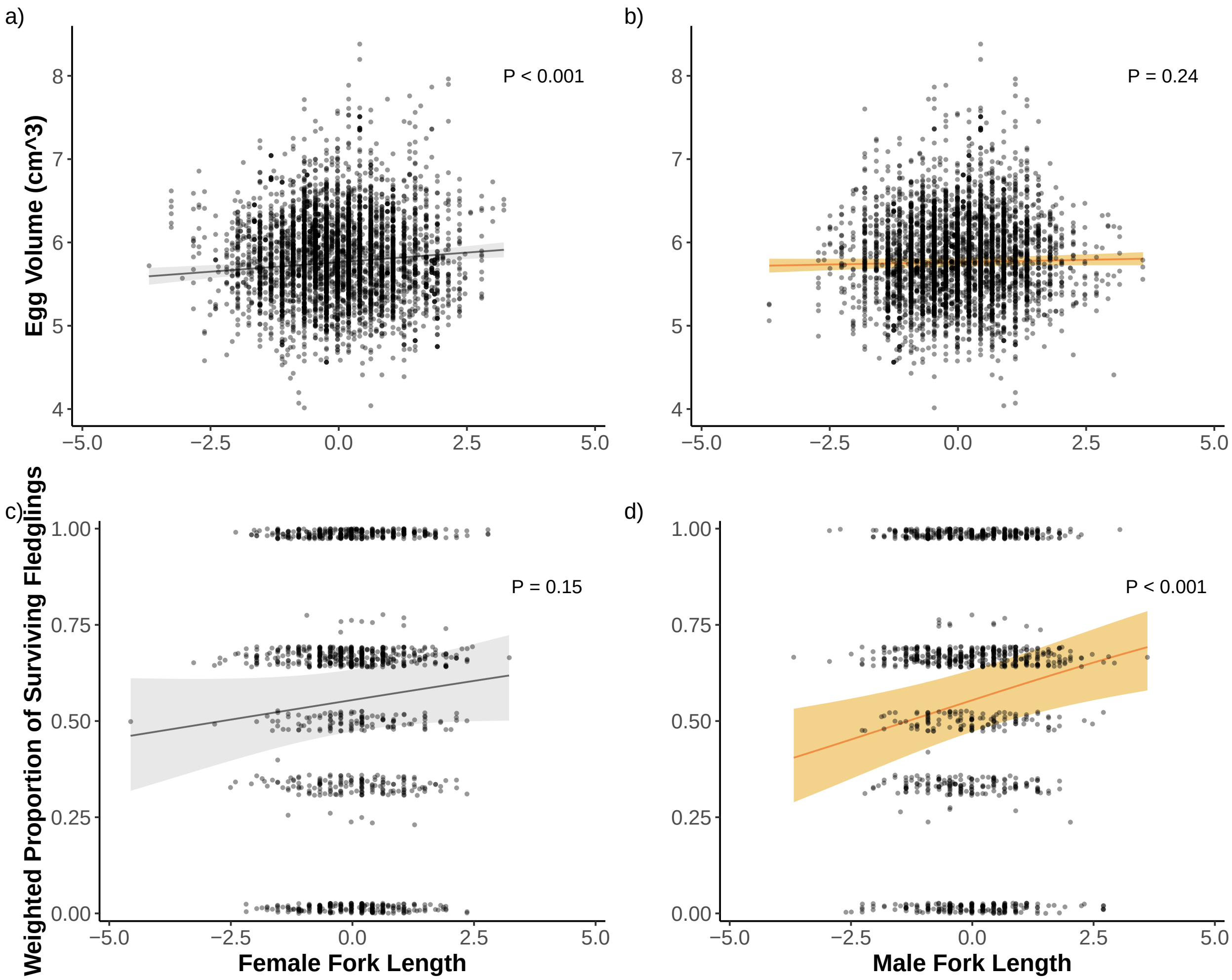

Figure 3.1.: Association between female (left) and male (right) fork length and egg volume (panels a and b) as well as the weighted proportion of surviving fledglings (panels c and d) in a Swiss population of Alpine swifts (data spans 1999-2021). The data points correspond to the raw data.

3.3.2. *Quantitative genetic analyses*

This population of Alpine swifts showed moderate sexual dimorphism in fork length (Table 3.2), with males' fork length being on average 7% longer than that of females. Average fork length was of 24.1 mm in males and 22.5 mm in females (raw data, Table B.1). The inner tail feather length was comparable between sexes, with longer outer tail feathers in males than in females (Table B.1). On average, birds of both sexes in Biel had longer forks than birds in Solothurn (Table 3.2). Fork length has increased over time, with a more pronounced increase in females, such that fork length has become more similar between the sexes over the course of the study (Table 3.2).

We report relatively high additive genetic variance in both sexes, of 0.56 [0.45; 0.67] (median [95% HPDI]) in females and 0.44 [0.32; 0.55] in males (Table 3.3). Heritability was likewise high in both sexes, explaining 60% [51; 68] of the variance in females and 52% [41; 62] of the variance in males. Despite appearing slightly higher in females than in males, the additive genetic variance and heritability of fork length were comparable between the sexes: a model for which additive genetic variance was constrained to the same value for both sexes performing no better than one where it was permitted to vary between the sexes (Table B.8). The permanent environment explained 14% [7; 22] of the variance in females and 16% [7; 25] of the variance in males (Table 3.3). The year effect explained only a small proportion of variance in fork length accounting for 4% [2; 7] in females and 6% [3; 10] in males. There were strongly positive cross-sex genetic (0.89 [0.76; 0.99]) and year (0.95 [0.86; 0.99]) correlations in fork length (Table 3.3, Figure 3.2). The cross-sex genetic correlation was effectively 1, as a model estimating the correlation did not perform better than one where it was fixed to 1 (Table B.8). The median, mean and mode of the posterior distribution were all comparable and are reported in the supplemental (Table B.9). A model with a single estimate pooled across the sexes for each of the variance components and ratios likewise performed similarly (Table B.9). Results for the relative fork length (in relation to the inner or outer tail feather) where likewise qualitatively similar (Table B.10 & Table B.11).

The predicted breeding values of female-trait fork length and male-trait fork length may both have increased slightly over the course of the study (Figure 3.3), though the estimates were near zero and with credible intervals crossing zero (median of the slopes (with lower and upper 95% HPDI): female-trait 0.02 (-0.02; 0.06); male-trait 0.01 (-0.03; 0.04); Table B.12). The estimated rate of increase in female-trait and male-trait fork length over the study period was greater than expected under genetic drift alone in 70.1% and 61.7% of cases, respectively ($\Pr[\text{slope}_\text{e} > \text{slope}_\text{d}]$ Table B.12). As PBVs could be estimated both for individuals born before the start of data collection and individuals with no collected data based on ancestry information, we also ran the analyses with all PBVs, the results of which were qualitatively similar and presented in the supplemental (Figure B.1, Table B.12, Table B.13).

Table 3.2.: Estimates (median) and 95% credible intervals (Bayesian model in R package MCMCglmm) for the relationships between fork length and fixed effects for male and female swifts (1999-2021). Female is the reference level for sex. Biel is the reference level for colony.

	Estimate	**Lower 95% HPDI**	**Upper 95% HPDI**
Intercept	**-0.22**	**-0.32**	**-0.12**
Sex [M]	**0.63**	**0.53**	**0.71**
Year	**16**	**12**	**21**
Year^2	**-9.8**	**-13**	**-6.0**
Colony [Solothurn]	**-0.16**	**-0.27**	**-0.070**
Sex [M] : Year	**-9.1**	**-14**	**-4.7**
Sex [M] : Year^2	-2.3	-5.7	0.82

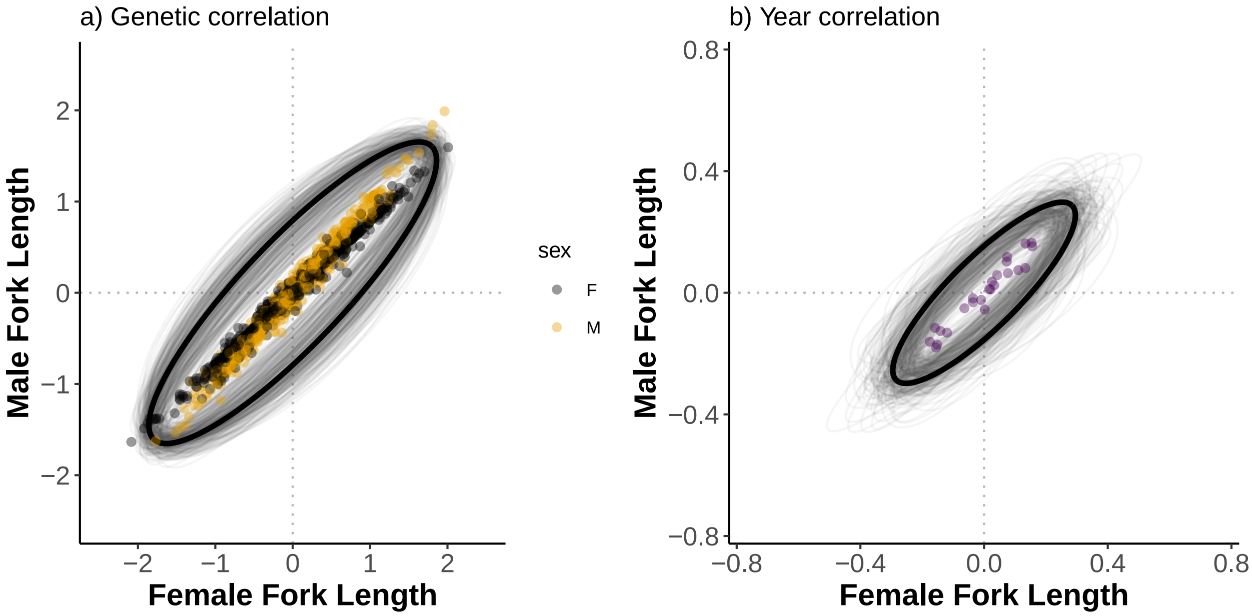

Figure 3.2.: The cross-sex a) genetic and b) yearly correlations in Alpine swift fork length. The points represent the posterior mode of the best linear unbiased predictors (BLUPs) from the MCMCglmm model (black: females; gold: males; purple: each year). Ellipses represent the correlation estimate. The bold ellipses were estimated from the posterior mode while the grey ellipses represent the uncertainty (300 randomly selected estimates from the posterior distribution). Data spans 1999-2021.

Table 3.3.: Variance component as well as variance ratio estimates (median of the posterior distribution) along with their [upper; lower] 95% HDP intervals of fork length in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios : heritability, permanent environment and year effects. We bolded estimates for which the 95% HPD interval did not cross zero, deemed statistically significant.

	Females	**Males**	***Rfm***
Additive Genetic Variance	**0.58 [0.45; 0.68]**	**0.46 [0.34; 0.56]**	**0.89 [0.76; 0.99]**
Permanent Environment	**0.13 [0.059; 0.21]**	**0.14 [0.064; 0.21]**	
Year	0.014 [0.0061; 0.027]	0.014 [0.0053; 0.026]	**0.45 [0.36; 0.54]**
Residual	**0.2 [0.19; 0.22]**	**0.2 [0.19; 0.21]**	
Heritability	**0.62 [0.53; 0.71]**	**0.57 [0.45; 0.66]**	
Permanent Environment	**0.14 [0.067; 0.23]**	**0.17 [0.067; 0.27]**	
Year	0.015 [0.0063; 0.028]	0.017 [0.0065; 0.031]	

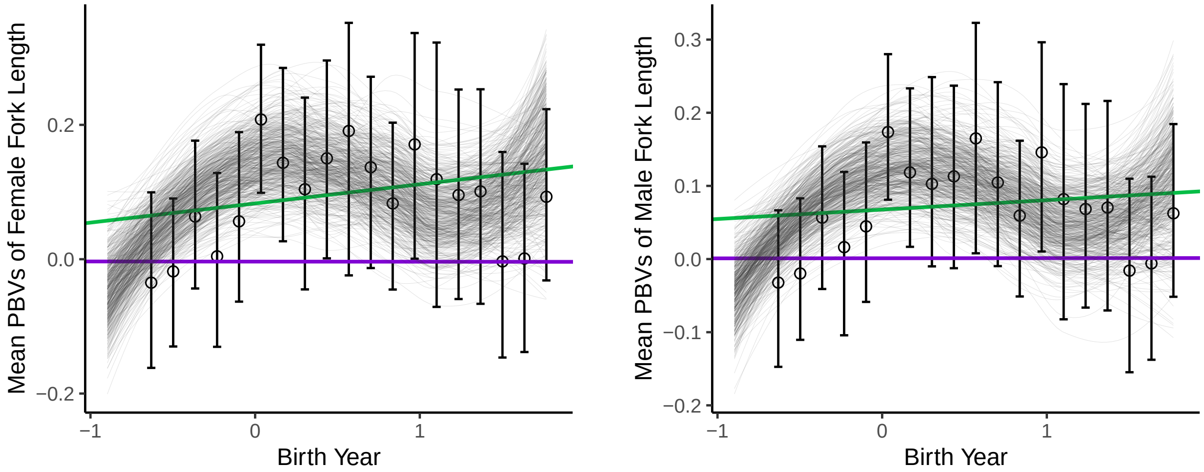

Figure 3.3.: Changes in average Alpin swift female-trait (left) and male-trait (right) predicted breeding values in relation to their year of birth (1999-2021). The green lines represent the posterior median of predicted changes from linear regressions, while the purple lines represent the changes as expected from genetic drift alone. The circles are the median of the PBVs per birth year and the bars are the associated 95% HDP intervals. The thin grey lines are a loess fit on a random draw of 500 iterations (out of 1500) from the posterior distribution of female-trait and male-trait average PBVs per birth year. The intercept for the predicted PBVs (green line) does not cross zero likely partially because individuals with birth years prior to 1999 were not removed from the data set and pedigree when running the animal model from which the PBVs were estimated.

3.4. Discussion

In this study, we investigated the predictors and fitness consequences of fork length in both sexes of a Swiss population of Alpine swifts. Fork length showed moderate sexual dimorphism, with males displaying longer forks than females. In line with the expectation that forked tails are a sexually selected signal in males, males with longer forks had greater reproductive success than those with shorter forks. Females with longer forks produced larger eggs, suggesting a greater allocation into reproduction than females with shorter forks. Taken together, these positive correlations with fitness suggest that fork length may be a mutual selected trait in both sexes. Contrary to our expectations, longer forks did not appear to incur survival costs for either sex. Finally, the length of the fork was heritable and positively genetically correlated between the sexes, with effectively the same genetic architecture in males and females.

On average, males had forks which were 7% longer than those of females (raw data). This sexual dimorphism was driven primarily by sex differences in the outer tail feather length, as the inner tail feather was effectively of the same lengths in both sexes (Table B.1). It was therefore unsurprising for analyses on the absolute and the relative fork depth (fork / outer tail feather length and fork / inner tail feather length) to be qualitatively similar. Although most swifts have historically been considered to be monomorphic, sexual dimorphism in fork length has also been reported in the common swifts (3-7%, Jukema et al. 2023), the plain swift (4%, Garcia-Del-Rey et al. 2008) and the black swift (83%, Gunn et al. 2018), suggesting that sexual dimorphism in this trait may be more widespread than previously reported. That said, sexual dimorphism in fork length in this population has decreased over the course of study, being of 8.2% in the first decade and 6.7% in the second decade (Dumas et al. 2024a). Sexual dimorphism in outer tail feather length has likewise decreased by 1.6% over the course of the study (Masoero et al., in prep).

We report that males with longer forks had greater reproductive success than those with shorter forks. Males with longer forks had larger brood sizes at hatching and fledgling as well as a greater weighted proportion of surviving fledglings than males with shorter forks. This is consistent with the expectation for fork length to be a sexually selected trait in male swifts (Hasegawa and Arai 2020). Males with more deeply forked tails likewise are reported to have greater reproductive success than those with less deeply forked tails in the barn swallow (Møller et al. 1998), with the length of the fork possibly acting as a reliable signal of offspring longevity (Møller 1994). Thought little is known about the behaviours of swifts outside of the breeding period, they likely engage in aerial courtship displays, and possibly also aerial threat displays, as has been suggested in common swifts (Lack 1956) and chimney swifts *Chaetura pelagica* (Fischer 1958). Indeed, birds of many species use their tails in agonistic and/or sexual displays (Fitzpatrick 1998). Males with more deeply forked tails may also have greater foraging success than those with less deeply forked tails, potentially specializing on different prey, and hence may be better able to provision their offspring. Male pallid swifts have been found to consume larger prey than females (Fernandes et al. 2023), suggesting that dietary niche segregation between the sexes could also be possible in the Alpine swift.

Females with longer forks produced larger eggs—and hence had greater energetic investment into reproduction—than females with shorter forks. This is contrary to what previous studies have identified in other species, with a possible trade-off between deeply forked tails and egg size having been suggested to occur in swifts and swallows (Hasegawa and Arai 2017, 2018). Females with longer forks may, like their male counterparts, have greater foraging success than those with shorter forks, perhaps as a result of the prey species available in these regions. However, although numerous studies have shown that larger eggs give rise to larger hatchlings that grow faster and are more likely to survive up to fledging (Bize et al. 2002), there was no detectable effect of female fork length on more direct measures of reproductive success (clutch size, brood size at hatching and fledgling, weighted proportion of surviving fledglings). This suggests that the previous benefit of larger eggs do not translate into higher reproductive success, and thus that longer forks may still be costly to bear for females.

Beyond serving as a possible signal of individual condition in both sexes, the length of the fork may potentially also serve as an indication of age and therefore experience. A general tendency for flight feathers to become longer with age has been reported, and tail feather length have also been shown to increase with age (e.g., older birds had longer tail feathers than younger birds in the sand martin *Riparia riparia*, Szép et al. 2019). Fork depth has also been shown to increase with age in barn swallows, as the combined result of both outer tail feather lengthening and inner tail feather shortening with age (Adámková et al. 2022). Older birds are generally considered to be more experience than younger birds and may be more skilled when it comes to migration (e.g., older whooping cranes *Grus americana* deviate less from a straight-line migration path then younger birds, Mueller et al. 2013) and breeding behaviours (e.g., older mute swans *Cygnus olor* lay earlier and have larger clutches than younger birds, McCleery et al. 2008). In our population, fork length has been shown to increase in early life in both sexes (Moullec et al. 2023, present study Table B.6), while remaining relatively stable from approximately 5 years of age onwards. As such, it is unlikely that our results are simply a reflection of age effects on reproduction.

Contrary to our expectations, we report no selection on fork length in relation to overwinter survival in either sex, suggesting that deeply forked tails did not hamper overwinter survival for either sex. However, overwinter survival may not accurately reflect the costs of deeply forked tails. Rather, fork length may incur costs during incubation or chick provisioning in terms of increased effort (e.g., increased energetic expenditure or foraging time) which will need to be investigated in future studies. Thought our study was unable to detect costs of fork length in either sex, deeply forked tails in barn swallows have been associated with increased oxidative damage (Vitousek et al. 2016), which can impair survival (Bize et al. 2014). As these costs should be especially apparent during and following migration, which represents a period of high exertion and risk, individuals with less deeply forked tails (and hence less drag) should have a clear advantage. One possible future avenue of research in the Alpine swift could then be to investigate the link between fork length and arrival to the breeding grounds, with the expectation that those with longer forks would arrive later—should there be a cost associated with deeply forked tails.

Furthermore, fork length presented comparable and moderate additive genetic variance and heritability in both sexes. This suggests that fork length has the potential to evolve in response to selection in both sexes. We found a strong positive cross-sex genetic correlation suggesting that females and males would be positively correlated in any evolutionary response. Per the genetic correlation hypothesis (Bonduriansky and Chenoweth 2009; Lande 1980; Poissant et al. 2010), this strong cross-sex genetic correlation could explain the presence of forked tails in females despite direct advantages of more deeply forked tails only being found for males. However, male fork length has remained relatively static over the course of the study, with female fork length increasing to more closely resemble that of males. Given clear reproductive benefits for males with longer forks, the strong genetic correlation across sexes, and no detected costs in either sex, we would have expected fork length to increase in a similar way in both sexes. We found small (but not statistically significant) changes at the genetic level in both sexes which followed the direction of phenotypic change, suggesting no microevolution of fork length. As such, it is unlikely for the observed changes in fork length in this population to have occurred as a result of selection and genetic constraints on fork length. Rather, this more rapid change in female than male fork length could be due to as of yet unidentified environmental causes. Though preliminary GPS data suggests that Alpine swifts forage mostly within a 15km radius surrounding the colony during the breeding period (Brighten et al., pers. com.), it remains unknown whether males and females forage in the same areas or at the same time, or if they specialize on the same insect prey. Given that male pallid swifts appear to prey on larger arthropods than females (Fernandes et al. 2023), similar sex-specific foraging niches are possible in the Alpine swift. In particular, it may be interesting to investigate possible links between fork length and sex-specific foraging strategies using GPS loggers as well as diet using a metabarcoding approach. In particular, female foraging habits may have changed over the last decades, perhaps as a result of climate change, and potentially accelerating the changes in their fork length.

To conclude, fork length is a moderately sexual dimorphic trait likely to be under sexual selection in the Alpine swift. Longer forks conferred reproductive benefits to females and males in terms of reproductive allocation and success, respectively, suggesting that fork length has the potential to signal aspects of individual condition in both sexes. The sexes effectively shared the same genetic architecture for fork length, with relatively high heritability and a cross-sex genetic correlation approximating one, suggesting that males and females should share the same evolutionary trajectory. In line with this, we identified a possible increase in breeding values in both sexes over the course of the study. It nonetheless remains unclear why female fork length increased while male fork length remained relatively static over the course of the study and finer scale studies on male and female foraging behaviour would be needed.

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Chapter 4

Chapter 4: 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

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Preamble

This chapter started as a class project with Sophie St Lawrence back in 2022 and was our second co-authored paper. Our co-working sessions were great fun, and instrumental in finding (and maintaining) motivation as I slowly figured out how to go about a PhD from my home office / bedroom (I'm sure that everyone else who started their graduate studies back in 2020 can relate). Aside from being one of the chapters I hadn't even considered when I wrote my research proposal, this is also the first chapter that gave me a real taste of the dreaded 'reviewer 2 phenomenon' (but at least I got to learn to do some cool stats in the process). After 3 rounds and 432 days spent under review, I'm both proud of how this chapter turned out and incredibly unwilling to read it again!

Abstract

In most animals, body mass varies with ecological conditions and is expected to reflect how much energy can be allocated to reproduction and survival. Because the sexes often differ in their resource acquisition and allocation strategies, variations in adult body mass and resulting consequences on fitness can differ between the sexes. Assessing the relative contributions of environmental and genetic effects (i.e., heritability)—and whether these effects and their fitness consequences are sex specific—is essential to gain insights into the evolution of sexual dimorphism and sexual conflicts. We used 20+ years of data to study the sources of variation in adult body mass and associated fitness consequences in a bird with bi-parental care, the Alpine swift *Tachymarptis melba*. Swifts appear monomorphic to human observers, though subtle dimorphisms are present. We first investigated the effects of weather conditions on adult body mass using a sliding window analysis approach. We report a positive effect of temperature and a negative effect of rainfall on adult body mass, as expected for an aerial insectivorous bird. We then quantified the additive genetic variance and heritability of body mass in both sexes and assessed the importance of genetic constraints on mass evolution by estimating the cross-sex genetic correlation. Heritability was different from zero in both sexes at ~0.30. The positive cross-sex genetic correlation and comparable additive genetic variance between the sexes suggest the possibility for evolutionary constraints when it comes to body mass. Finally, we assessed the sex-specific selection on adjusted body mass using multiple fitness components. We report directional positive and negative selection trending towards stabilizing and diversifying selection on females and males respectively in relation to the weighted proportion of surviving fledglings. Overall, these results suggest that while body mass may be able to respond to environmental conditions and evolve, genetic constraints would result in similar changes in both sexes or an overall absence of response to selection. It remains unclear whether the weak (1%) dimorphism in Alpine swift body mass we report is simply a result of the similar fitness peaks between the sexes, or of genetic constraints.

4.1. Introduction

In most animals, being heavier generally reduces vulnerability to food shortages or cold weather events and can provide a competitive advantage against other individuals. Indeed, body mass (weight) and/or body condition (weight corrected for skeletal size) may reflect energy stores (i.e., fat reserves, Labocha and Hayes 2012) and thus how much energy can be allocated to reproduction and survival. For example, in terms of reproductive allocation, heavier female yellow-bellied marmots *Marmota flaviventer* can wean more pups (Maldonado-Chaparro et al. 2015) and produce heavier pups (Monclús et al. 2014) than lighter females. In terms of survival, heavier little auk *Alle alle* adults with larger fat reserves are better able to survive periods of food shortage than those with smaller reserves (Harding et al. 2011). However, the body mass that maximizes fitness will depend on a variety of factors, including environmental conditions experienced and sex (Ronget et al. 2018).

Variations in environmental conditions have been shown to result in body mass fluctuations across a wide range of species (e.g., Georgiadis et al. 2003; Ronget et al. 2018). Indeed, meteorological conditions such as precipitation and temperature can impact the amount of available food and the energetic requirements necessary to survive. For example, higher precipitation often increases vegetation productivity, leading to heavier body weights and faster population growth rates in many ungulate species (Georgiadis et al. 2003). Conversely, periods of inclement weather (i.e., droughts, strong winds, or extreme temperatures) can result in decreased body mass and/or body condition. For instance, cold windy days have been linked to decreased flying insect abundance (Grüebler et al. 2008) and cold rainy days have been linked to decreased activity in small rodents (Lehmann and Sommersberg 1980), both of which are key prey items for numerous species. Inclement weather has likewise been associated with increased thermoregulatory costs (e.g., wet coats in birds and mammals are less insulating than dry coats, Webb and King 1984) and energetic costs (e.g., negative relationship between energy expenditure and temperature in male sage grouse *Centrocerus urophasianus*, Vehrencamp et al. 1989).

Further, energy allocation and trade-offs may differ between the sexes, resulting in sex-specific phenotypic optima. Sexual size dimorphism (SSD), a difference in the mean body size and/or mass of males and females, has been extensively studied and varies dramatically within and between taxa. In birds and mammals, males are often larger than females, while in reptiles and fish, females are generally larger than males (Fairbairn 2007). Nonetheless, within taxa, some species can present the opposite trend (reverse SSD). For example, in seabirds and raptors, females are often larger and heavier than males (Krüger 2005; Székely et al. 2000). These differences between the sexes can reflect sex-specific natural and sexual selection. For instance, in the context of sexual selection, intra-sexual competition for mates could result in different optimal sizes for males and females.

Male northern elephant seals *Mirounga angustirostris* compete over access to harems of females with body size as a sexually selected weapon (Lloyd et al. 2020). As a result, they can be 3.5 times heavier than females (Salogni et al. 2019). Conversely, in species where males compete aerially for mates, males may be lighter than females to increase their agility (Székely et al. 2000). Natural selection may also be responsible for these pronounced differences as a result of males and females specializing on different food sources (i.e., to lessen inter-sexual foraging competition through niche segregation Krüger 2005), different parental roles, and differences in fecundity selection (Székely et al. 2000). Given these sex-specific ecological roles, SSD is often considered to be adaptive (Fairbairn 2007).

In species with little apparent dimorphism, the evolution of SSD may be potentially constrained by shared genetic architecture between the sexes (Bonduriansky and Chenoweth 2009; Poissant et al. 2010). This can be estimated through the cross-sex genetic correlation (r_{fm} Lande 1980). A r_{fm} different from zero suggests the presence of shared genetic architecture between the sexes and suggests that selection acting on one sex could constrain the evolution of the other (Bonduriansky and Chenoweth 2009). In cases where a negative r_{fm} is coupled with sexually concordant selection, the evolution of SSD will not be favoured, though the mean value of the trait may evolve in both sexes. In cases where a positive r_{fm} is coupled with sexually antagonistic selection the evolution of SSD may likewise be constrained (Kruuk et al. 2008). This could lead to intra-locus sexual conflict (broadly defined as sex-specific fitness optima for a shared trait, Parker 1979), studies of which are rare in natural populations. Of those studies, most focus on highly dimorphic species (Poissant et al. 2010) and present differing results. For example, intra-locus sexual conflict over body mass has been reported in mountain goats *Oreamnus americanus* (Mainguy et al. 2009) but not in bighorn sheep *Ovis canadensis* (Poissant et al. 2008). Given that SSD may represent a resolution to an intra-locus sexual conflict, this conflict should be especially strong in species with weak sexual dimorphisms.

In this study, we investigated variation of adult body mass in the Alpine swift *Tachymarptis melba,* a weakly sexually dimorphic bird. Further, we assessed the potential for genetic constraints over the evolution of body mass by examining the sex-specific genetic architecture and selection acting on this trait. Swifts are obligate insectivores and forage exclusively in flight. As such, they can experience periods of food shortages during inclement weather events (i.e., cold and rainy conditions). Therefore, we first studied the effect of weather conditions on adult body mass. While previous studies have shown strong variation in body mass and body temperature in nestlings (Bize et al. 2007), there has been little investigation as to the effects of weather on adult body mass. We expected that adults would be lighter when measured on cold and rainy days than on warm sunny days due to lack of foraging opportunities. We then quantified the additive genetic variance and heritability of body mass in both sexes as well as the cross-sex genetic correlation using an animal model. We expected body mass to be heritable (Roff 1996), and for there to be a positive cross-sex genetic correlation between the sexes (Roff 1996), as shown in other species (Bonnet et al. 2017; Mainguy et al. 2009; Poissant et al. 2008, 2010; Robinson et al. 2009). Finally, we assessed the sex-specific selection acting on body mass using field estimates of yearly reproductive success and overwinter survival. We expected different fitness components to be positively related to body mass, but further expected these relationships to differ between the sexes should males and females show different resource acquisition and allocation strategies.

4.2. Materials & Methods

4.2.1. *Study Species & Site*

The Alpine swift is a long-lived migratory bird, with a median lifespan of 7 years (maximum: 26 years, Bize et al. 2009). They live a highly aerial lifestyle, remaining in flight for over six months at a time (Liechti et al. 2013), and landing only during the reproductive period. Colonies of a few to a hundred pairs will nest on cliffs or in the roof spaces of tall buildings. Alpine swifts nest from May to August, with both parents incubating their 1-4 eggs for approximately 18 days (Bize et al. 2004). Chicks take approximately 50 to 70 days from hatching to fledging, during which time both parents will brood and feed them (Bize et al. 2004). As such, males and females are expected to have similar parental allocation into reproduction (with the exception of egg-laying costs exclusive to females). Further, since adults return to the same breeding site throughout their life, and the probability of recapturing breeders is virtually 1 (Bize et al. 2006a), we can adequately estimate the annual survival of adults through the records of captures from year to year. In addition, weather during the breeding period can be highly variable, resulting in important yearly variations in egg-laying dates (de Villemereuil et al. 2020) as well as fluctuations in prey availability and hence mass Bize et al. (2007).

Since 1999 and 2000 respectively, two urban-nesting colonies have been studied in Biel (60-100 breeding pairs) and Solothurn (40-55 breeding pairs), Switzerland. Each breeding season, these two colonies are regularly visited to monitor each nest and determine when the first egg was laid, how many eggs were laid, and how many hatchlings and fledglings were produced. In both colonies, birds are individually identified by permanently ringing them as nestlings or at their first capture at adulthood if not already ringed as nestlings. Parents (and nestlings) are caught by hand at the nest regularly throughout the breeding season. Individuals were weighed to the nearest tenth of a gram using a digital scale, measured to the nearest millimetre using a ruler (e.g., wing length) or tenth of a millimetre using a caliper (e.g., sternum length) and sexed (DNA taken from blood or feathers Griffiths et al. 1998). Sternum and wing length were measured by the same observer (PB) each year; repeated measures on each individual show that these measures are highly repeatable ($R = 0.95$ and $R = 0.84$, respectively. Repeatability conditional on sex was estimated using the R package *rptR* Stoffel et al. 2017). Despite subtle sex differences (e.g., more deeply forked tails in males than in females), swifts appear monomorphic to human observers. As such, field measurements are taken blind to the sex of the individual.

4.2.2. *Statistical analyses*

All statistical analyses were conducted in R version 4.2.0 (R Core Team 2023). Throughout the analyses, linear and quadratic effects were calculated using orthogonal polynomials. When included in the analyses, the effects of mass, age, day of capture, hour of capture, rainfall and temperature were mean-centred and scaled to a variance of 1.

For all analyses (Environmental effects, Quantitative Genetic, and Selection analyses), models were also run with the inclusion of sternum length as a fixed effect to correct for skeletal size differences. The results obtained were qualitatively similar and are presented only in the appendix (Table C.1; Table C.5; Table C.6).

4.2.3. *Environmental effects on body mass*

Environmental conditions are expected to affect body mass in swifts since insect prey availability is highly dependent on weather (Grüebler et al. 2008). To determine the weather time period(s) that best explained variation in body mass, we used a sliding window approach fitted with the function slidingwin from the R package *climwin* (Bailey and van de Pol 2016; van de Pol et al. 2016a). The sliding window approach allows the user to simultaneously test for critical periods as well as descriptive metrics (i.e., mean, sum) and functions (i.e., linear, quadratic) that best describe the relationship between weather and biological data. We used a relative window which opened 105 days before each mass measurement and closed the day of mass measurement. We chose this opening date to include the full duration of the breeding season (May – August) for those weights taken at the end of the breeding season (e.g., for a weight on August 10th, the opening date corresponded to April 27th and hence immediately preceded the first egg laid). Adults were captured and weighed between 8h00 and 20h00, from May 1st to August 10th (1999 - 2021). Given that swifts can travel great distances within a day, we estimated daily weather data as the average of daily rainfall and daily temperature across five Swiss Meteorological Stations surrounding the colonies (Bern-Zollikofen, Cressier, Grenchen, Koppigen, Wynau). We averaged these measurements to account for daily variations across stations (e.g., strong local precipitation recorded by one of the stations).

To find the best-supported model, *climwin* compares the AICc (Akaike Information Criterion corrected for small sample sizes) value of each model relative to the base model (i.e., a model with no weather signal). This base model was fitted using the R package *lme4* (Bates et al. 2015). Our base model included sex, colony, day and hour of capture (linear and quadratic terms), and age (linear and quadratic terms) as fixed effects. Hour and day of capture were included to correct for seasonal and daily fluctuations in body mass as individuals are not captured on the same days nor at the same time. Indeed, weight in birds is known to fluctuate daily (e.g., 5 to 15%: Clark 1979). In our data set, individual variation in body mass between captures ranged from 0 to 45%. We included interactions between sex and the linear and quadratic effects of day of capture to estimate sex differences in these terms. We also included year and individual identity as random effects to account for between-year variation and repeated measurements, respectively. By comparing this model to models that included the linear and quadratic effects of mean rainfall and temperature, we were able to select the best-supported model for each environmental variable based on the delta AICc (difference in AICc between the best model and the base model) (Bailey and van de Pol 2016; van de Pol et al. 2016a).

4.2.4. *Quantitative genetic analyses*

A detailed social pedigree has been constructed over the years of the study based on behavioural observations (parents are caught at the nest while brooding the eggs or chicks, and later feeding the chicks). Extra-pair paternity (the proportion of a female's clutch sired by a male other than her social partner, EPP) approaches zero in this Alpine swift population (C. M. Meier & P. Bize, personal comm.). A molecular analysis of another Swiss colony of Alpine swifts nesting in Baden (50 breeding pairs) shows little evidence of EPP (C. M. Meier and P. Bize, manuscript in preparation). Likewise, low incidences of EPP are reported for the common swift *Apus apus* (Martins et al. 2003), which has similar ecology to the Alpine swift. Hence, behavioural observations are suitable to construct a social pedigree in the Alpine swift. Furthermore, frequent natal dispersal (10%) coupled with no breeding dispersal (Bize et al. 2017) ensures gene flow between the two colonies. Previous analyses including genetic groups have shown no heterogeneity in additive genetic variance between colonies. As such, the two colonies are treated in the analyses as a single population. The pruned social pedigree used in this study is 5 generations deep and includes data on 1159 individuals, with 533 maternities and 516 paternities (Table C.3). In our data set, individuals from Biel with at least one parent from Solothurn accounted for 5.9% of the colony, while individuals from Solothurn with at least one parent from Biel accounted for 11.8% of the colony (Table C.4). The social pedigree statistics were determined using the R package *pedantics* (Morrissey 2023).

Using the R package *MCMCglmm* (Hadfield 2010), we fitted body mass as a function of sex, hour and day of capture (linear and quadratic effects), colony as well as the weather signals (daily mean rainfall and temperature; linear and quadratic effects) extracted from the best *climwin* model detailed above (rainfall window: 6-0 days before weighing; temperature window: 1-0 days before weighing). We also included an interaction term between sex and day of capture (linear and quadratic) to assess sex differences in these terms. We also tested for an interaction between sex and colony; as this interaction was not statistically significant, it was dropped from the model (Table C.2).

We estimated the following sex-specific variance components: additive genetic variance (individual identity linked to the pedigree), permanent environment variance (individual identity), yearly variance (year of observation) and residual variance. In addition, we estimated the cross-sex genetic and yearly covariances and correlations. We did not include parental effects in the model for two reasons. First, we are studying mass in adults and parental (maternal or paternal) effects on mass are often found to become negligible at adulthood (Vedder et al. 2023). Second, including parental identity in the model would result in a strong reduction in sample size due to the incomplete maternities and paternities of individuals in the first years of the study and of immigrants.

Variance parameters were estimated as the posterior mode and reported with their 95% highest posterior density intervals (HPDI). Variance ratio estimates were calculated as the proportion of total phenotypic variation explained by the given variance parameter, i.e., heritability conditioned on the fixed effects was estimated as the sex-specific additive genetic variance divided by the total phenotypic variance, while evolvability was estimated as the additive genetic variance divided by the squared mean of the population. For the residuals and the permanent environment effect, for which cross-sex correlations cannot be estimated, we used standard priors with V = diag(2), nu = 1.002. For the additive genetic and year effects, we used expanded priors, adapted for models estimating cross-sex correlations (i.e., V = diag(2) * 0.02, nu = 3, alpha.mu = rep(0, 2), and alpha.V = diag(2) * 1000). The model had a burn-in period of 50000 iterations and was sampled every 2000 iterations for a total effective sample size of 1500. Plot traces were visually assessed, and absolute autocorrelation values were verified to be <0.1. We verified chain convergence for each parameter using the Heidelberger and Welch's convergence diagnostic (heidel.diag function) as recommended by Hadfield (2010).

4.2.5. *Adjusting mass for selection analyses*

Body mass is a highly labile trait in the Alpine swift, and highly sensitive to short term climatic variability. As individuals are not captured on the same days or at the same time, we needed to account for this additional source of between and within individual variation before fitting selection models. To do so, we adjusted mass estimates for each individual each year for the average weather within a year, at a specific time of day for a given date. We used 14h00 which is the median capture time. For the date, we adjusted body mass to two different dates; 1. on June 13th ("June mass"), which corresponds to the median capture date and is representative of mean hatching throughout the study (range: June 2nd to June 28th) and may reflect how much energy is available for reproduction; 2. August 8th ("August mass"), possibly reflecting the energy available at the end of the breeding season when chicks are approaching fledging, but prior to migration. The adjusted body mass estimates for each individual each year were obtained as predictions of a linear mixed model including fixed effects of the hour of capture (linear and quadratic), date of capture (linear and quadratic), rainfall (linear and quadratic), temperature (linear and quadratic), individual age (linear and quadratic), sternum length, and colony. The model also included random intercepts for the year of measurement and for individual identity, as well as random slopes of the date of capture (linear and quadratic) at the individual level within each year. We fit one model each for females and for males (Figure C.3). Models were fitted using the R package *MCMCglmm* (Hadfield 2010) with 1000 iterations in the final posterior output. Mass predictions conditional on random effects were obtained using the predict.MCMCglmm function using 14h00 for the time of capture, average rainfall and temperature for the given year and the specific date to obtain either June or August mass. Year specific measurements of age, sternum length and colony for each individual were also used for the predictions. Predictions were done for each iteration of the model; thus, we obtained a set of 1000 individual-year specific estimates.

4.2.6. *Selection analyses*

We used the R package *lmerTest* (Kuznetsova et al. 2017) to investigate selection for adjusted June and August mass based on measures of reproductive success and overwinter survival. June mass was used for the reproductive success models, while August mass was used for the overwinter survival model. To carry forward the error from the mass adjustment detailed above, we ran each selection model using each of the 1000 set of mass estimates in a Bayesian like approach. We obtained a posterior distribution for every statistic from the selection models, and report the posterior mode, 95% HPDI and posterior mode of the associated p-value.

For reproduction and survival selection analyses, we estimated the total selection on body mass including both direct and indirect selection. As such, we did not include other traits as covariates. However, given that laying date is strongly related to fitness (de Villemereuil et al. 2020), we also fitted a model of laying date as a function of body mass to estimate indirect selection on body mass. This model included colony, maternal and paternal June mass (linear and quadratic terms) as fixed effects and maternal and paternal identity as random effects. Laying date (Gaussian distribution) was modelled as day of the year and mean-centered and scaled to a variance of 1.

For reproductive success, we ran a series of models using the following fitness components: clutch size (Poisson distribution, log-link), brood size at hatching (Poisson distribution, log-link), brood size at fledging (Poisson distribution, log-link), and the weighted proportion of surviving fledglings (binomial distribution, logit-link). These models were conducted at the pair level, as these traits require concerted effort from both parents. Models included colony, maternal and paternal June mass (linear and quadratic terms) as fixed effects and maternal and paternal identity as random effects. The weighted proportion of surviving fledglings was modelled as brood size at fledging over clutch size. Surviving fledglings are defined as those that successfully leave the colony. To facilitate our interpretation of statistically significant quadratic effects, threshold regression models with a single breakpoint at the stationary point (i.e., minimum or maximum of the quadratic function) were fitted. The stationary point corresponds to the point where the first derivative is equal to zero.

The overwinter survival model (binomial distribution, logit-link) was run at the individual level, and thus included sex as a fixed effect. The model also included colony, breeding status, as well as the three-way and two-way interaction terms between sex, August mass, and breeding status as fixed effects. Non statistically significant interactions were removed from the model; only the August mass by breeding status interaction was retained in the final model. Breeding status was a two-level factor: non-breeders and breeders. Individual identity and year were included as random effects.

Parameters estimated from GLM(M)s are not selection gradient but are still informative about the shape of the fitness surface and can be interpreted directly. That said, we also estimated selection gradients from log-link model using methodology provided by Morrissey and Goudie (2022). However, one of the assumptions of their method is that the curvature is limited and that 2 times the quadratic slope is lower than 1 (Morrissey and Goudie 2022). Thus, we applied their method only to the clutch size model, for which assumptions were respected, and not the brood size at hatching and fledging models for which assumptions were violated. For logit-link models (weighted proportion of surviving fledglings and overwinter survival), we extended Morrisey and Goudie's (2022) approach with methodology from Janzen & Stern (1998) to approximate average selection gradients (see appendix for details of the method).

4.2.7. *Ethical note*

Adult swifts were caught at the nest between 8h00 and 20h00 (usually between 9h00 and 18h00) to avoid disturbing the adults during periods of intense social activity (dawn and dusk) (Meier et al. 2018). We minimized the number of captures and disturbances during severe weather events to avoid extra stress to the birds. To further limit stress to the birds, swifts were placed in cloth bags and handled quickly, typically 5-15 minutes depending on data collection. All individuals were released at the colony site. All handlers were trained by PB or senior members of the field team. All work was conducted in accordance with international standards on animal welfare and in compliance with Swiss local and national regulations (ringing permit 2235 & project 72 delivered to Pierre Bize by the Swiss Federal Office for the Environment).

4.3. Results

4.3.1. *Environmental variation in adult swift body mass*

There was an effect of meteorological factors on mass (Figure 4.1). For daily rainfall, the climatic window that best explained the variation in body mass included the 6 days just before mass measurement (window started 6 days before the mass measurement was taken and closed the day of the measurement; Figure C.1). For daily mean temperature, the best supported climatic window included the day before and the day of mass measurement (Figure C.1). In both cases, the best descriptive metric was mean, and the best function was quadratic, based on the delta AICc of each model. For temperature, the delta AICc of the quadratic function model was 109.17 units lower than that of the linear function model. For rainfall, the delta AICc of the quadratic function model was 66.73 units lower than that of the linear function model. Body mass decreased non-linearly with increasing average rainfall over the 6 days before the measurement, with an attenuation of this effect at high levels of rainfall. Body mass increased non-linearly with increasing average ambient temperature in the ~36 hours before the measurement, with an attenuation of this effect at high temperatures.

In addition, this population of Alpine swifts showed minor sexual dimorphism in body mass, with females being on average 1% heavier than males (Table 4.1). Average body mass was 98.9g (SD: 8.0g) for females and 98.0g (SD: 7.7g) for males based on the raw data. When including sternum length into the model to correct for skeletal size, females were on average 1.7% of higher body condition than males, and individuals of both sexes with longer sternums were heavier than those with shorter sternums (Table C.1). This sexual dimorphism was most apparent earlier in the season, as females lost more mass than males between the start and the end of the breeding period (significant sex by day of capture interaction, Table 4.1). Despite this steeper decline of mass in females than in males, mass decreased non-linearly with the day of capture in both sexes (Table 4.1, Figure C.2 a). Mass increased non-linearly with the hour of capture (Table 4.1, Figure C.2 b) and age in both sexes (Table 4.1, Figure C.2 c).

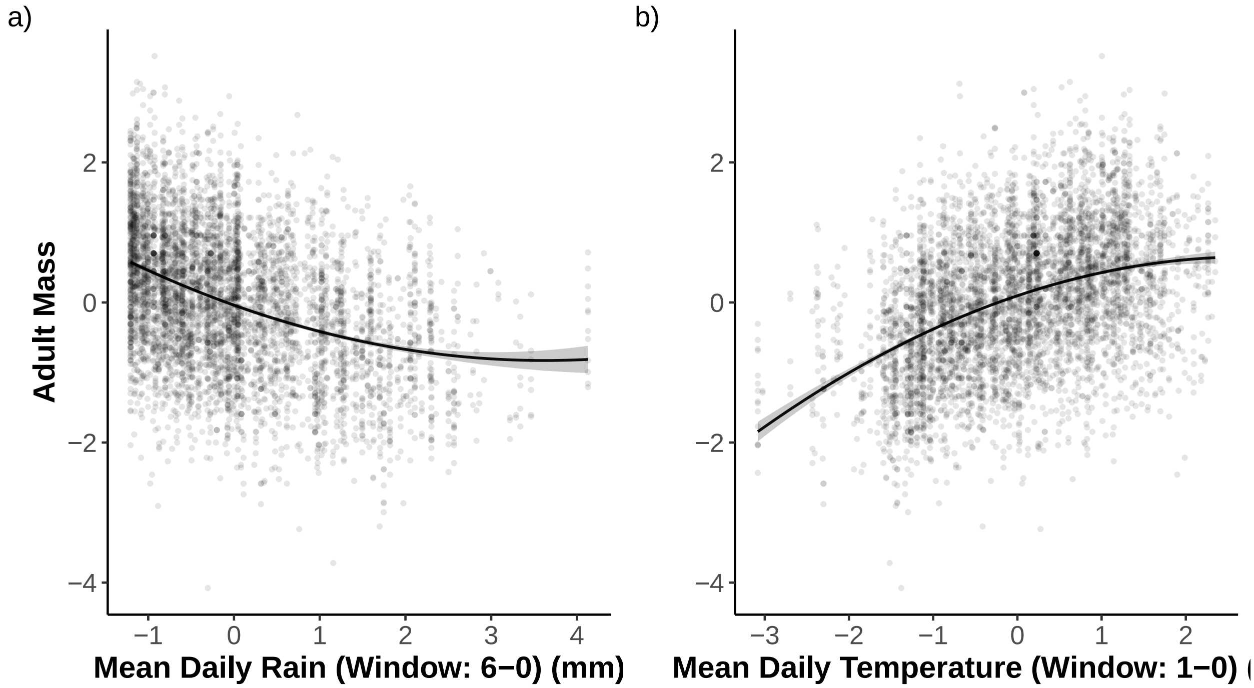

Figure 4.1.: Association between adult body mass in Alpine swifts and a) mean daily rainfall (mm) as well as b) mean daily temperature (°C)). Points are raw data and the line with the grey polygon represents the prediction from the models with 95% HPDI. The daily weather records were obtained by averaging observations from five Swiss Meteorological Stations (Bern-Zollikofen, Cressier, Grenchen, Koppigen, Wynau) to reflect regional weather. The data spans 1999-2021. The mean daily rainfall was estimated as the average rainfall in the period from 0 to 6 days before the measurement was taken, while for temperature the daily mean was estimated over the ~36 hours prior to measurement (Figure C.1). Number of individuals: 1079; number of observations: 5387.

Table 4.1.: Estimates (posterior mode) and 95% HDP intervals (Bayesian model fit using the R package MCMCglmm) for the relationships between body mass and fixed effects for male and female Alpine swifts measured over the May-August breeding period (1999-2021). Estimates with 95% HPD intervals that exclude 0 were deemed statistically significantly different from zero and bolded. Female is the reference level for sex. Biel is the reference level for colony.

	Estimate	**Lower 95% HDPI**	**Upper 95% HDPI**
Intercept	0.051	-0.034	0.14
Sex [M]	**-0.098**	**-0.18**	**-0.015**
Colony [Solothurn]	-0.027	-0.11	0.058
Age	**4.5**	**2.7**	**6.3**
Age ^2	**-5.7**	**-7.0**	**-4.4**

Rain Signal	**-9.0**	**-11**	**-7.4**
Rain Signal ^2	**3.1**	**1.8**	**4.4**
Temperature Signal	**39**	**37**	**41**
Temperature Signal ^2	**-7.8**	**-9.1**	**-6.6**
Hour of Capture	**11**	**9.3**	**12**
Hour of Capture ^2	**-1.9**	**-3.2**	**-0.63**
Day of Capture	**-31**	**-33**	**-29**
Day of Capture ^2	**7.5**	**5.7**	**9.2**
Sex [M] : Day of Capture	**5.6**	**3.4**	**8.2**
Sex [M] : Day of Capture ^2	**-3.1**	**-5.5**	**-0.59**

4.3.2. *Heritability and cross-sex genetic correlation of adult swift body mass*

We report additive genetic variance in both sexes, accounting for 15.4% [8.63, 21.8] (posterior mode [95% HPDI]) of the variance in females and 16.9% [10, 23.9] of the variance in males (Table 4.2). Heritability was of 0.265 [0.146-0.346] in females and 0.299 [0.168-0.377] in males, while evolvability was of 0.147% [0.0904-0.191] in females and 0.166% [0.111-0.206] in males. The permanent environment explained 18.3% [9.74, 27.1] of variance in female and 17.0% [9.28, 28.0] of variance in male body mass (Table 4.2). The year effect explained only a small proportion of variance in body mass (2.61% [1.28, 5.84] in females and 3.05% [1.79, 6.81] in males), and residual variance remained relatively high in both sexes. There was a positive cross-sex genetic correlation in body mass of 0.702 [0.264, 0.933], as well as a positive cross-sex yearly correlation in body mass of 0.914 [0.688; 0.996] (Table 4.2, Figure 4.2). Results were qualitatively similar when correcting for skeletal size (Table C.5).

Table 4.2.: Variance component and ratio estimates (posterior mode) along with their 95% HDP intervals for adult body mass in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, evolvability, permanent environment and year effects. Evolvability is expressed as a percentage. Given that variance components are bounded to zero, components for which the lower 95% HPDI was higher than 0.01 were deemed statistically significant and bolded. The cross-sex covariances and correlations are estimated as between the sexes and hence displayed in the table only once.

	Females	**Males**
Variance Components		
Additive Genetic Variance	0.15 [0.0884-0.222]	0.177 [0.0964-0.24]
Permanent Environment	0.0994 [0.0614-0.171]	0.114 [0.0597-0.171]
Year	0.0182 [0.00768-0.0369]	0.0184 [0.00955-0.0408]
Residual	0.314 [0.299-0.338]	0.297 [0.28-0.317]
Variance Ratios		
Heritability	0.265 [0.162-0.361]	0.294 [0.185-0.393]
Evolvability	0.147 [0.0904-0.191]	0.166 [0.111-0.206]
Permanent Environment	0.17 [0.0993-0.279]	0.182 [0.103-0.283]
Year	0.0279 [0.0125-0.0582]	0.0374 [0.015-0.0652]
Cross-Sex Covariances		
Genetic	0.0904 [0.0417-0.155]	-
Yearly	0.0147 [0.00721-0.0344]	-
Cross-Sex Correlations		
Genetic	0.604 [0.262-0.886]	-
Yearly	0.946 [0.69-0.995]	-

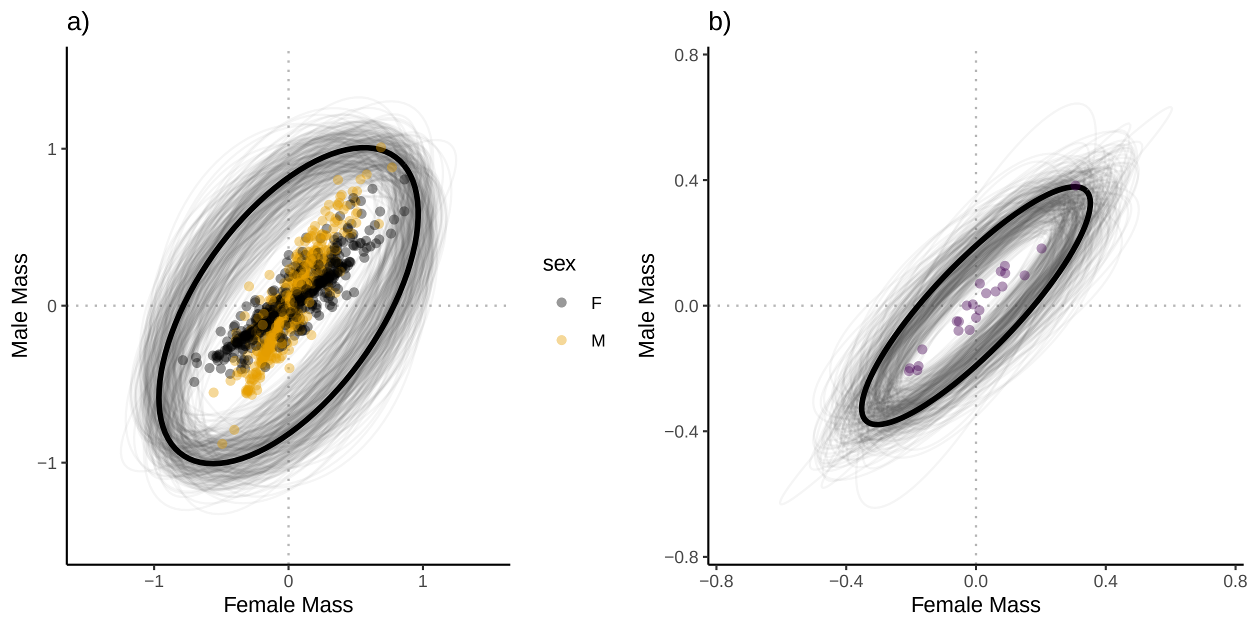

Figure 4.2.: The cross-sex a) genetic and b) yearly correlations in Alpine swift adult body mass. The points represent the posterior mode of the best linear unbiased predictors (BLUPs) from the MCMCglmm model. For the genetic correlation plot, points in black are females and yellow are males, while for the yearly correlation plot, points in purple correspond to each year (1999-2021). Ellipses represent the correlation estimate. The bold ellipses were estimated from the posterior mode while the grey ellipses represent the uncertainty (300 randomly selected estimates from the posterior distribution).

4.3.3. *Sex-specific selection over body mass in adult swifts*

There was a negative effect of female and male June mass on laying date, with heavier parents laying their clutches sooner than lighter ones (Table 4.3, Figure 4.4 a, Figure 4.4 b). The effects of maternal or paternal June mass on clutch size, brood size at hatching and brood size at fledgling were not significantly different from zero, but estimates suggest stabilizing selection on females and disruptive selection on males (Table 4.3). For the weighted proportion of surviving fledglings, there was evidence of stabilizing selection on female June mass, and diversifying selection on male June mass, with a negative and positive quadratic effect, respectively (Table 4.3, Figure 4.4 c, Figure 4.4 d). For females, threshold regression estimates showed that the weighted proportion of surviving fledglings increased with increasing June mass until a maximum was reached, followed by a decrease, though this decrease was not statistically different from zero (Table 4.4). For males, threshold regression estimates showed that the weighted proportion of surviving fledglings decreased with increasing June mass until a minimum was reached, followed by an increase, though this increase was not statistically different from zero (Table 4.4). The masses providing maximum fitness for females and minimum fitness for males were similar and close to the average mass of both sexes (females: 102.5g; males: 101.8g). Selection gradients estimated using the extended Morrissey & Goudie (2022) and Janzen & Stern (1998) approach for the weighted proportion of surviving fledglings model likewise reflects these trends with stabilizing selection for females and diversifying selection for males (Table 4.5). For all models except clutch size, we report a statistically significant effect of colony (Table 4.3). Laying dates were on average earlier in Solothurn than in Biel, and reproductive success (brood size at hatching and fledging, weighted proportion of surviving fledglings) and overwinter survival were higher in Solothurn than in Biel (Table 4.3). There were no sex differences in overwinter survival, and there was a two-way interaction between August mass and breeding status (Table 4.3, Figure 4.3). Non-breeding individuals that were heavier in August had higher overwinter survival than lighter non-breeding individuals, whereas August mass did not affect the survival probability of breeding individuals. Estimated average selection gradients likewise reflect these trends (Table 4.5), and similar conclusions were drawn when correcting for skeletal size (Table C.6).

Table 4.3.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between body mass and laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), the weighted proportion of surviving fledglings (binomial distribution), and overwinter survival (binomial distribution). Models were fitted on the 1000 sets of estimated mass from a Bayesian model. We report the posterior mode with 95% HPDI for each parameter. Post P-value is the posterior mode of the P-values. Statistically significant estimates (Post P-value < 0.05) were bolded. The reference levels are as follows: Biel for colony, females for sex, and non-breeders for breeding status. Data spans from 1999-2021.

	Estimate	**95% HPDI**	**Post. P-Value**
Laying Date[1]			
Intercept	0.20	[0.19; 0.21]	0.18
Female mass	**-3.9**	**[-5.4; -2.7]**	**< 0.001**
Female mass^2	0.12	[-0.85; 1.1]	0.77
Male mass	**-2.5**	**[-3.3; -1.4]**	**0.0045**
Male mass^2	-0.31	[-1.1; 0.50]	0.62
Colony	**-0.32**	**[-0.33; -0.31]**	**< 0.001**

Clutch Size[2]			
Intercept	**0.99**	**[0.98; 0.99]**	**< 0.001**
Female mass	-0.19	[-0.41; -0.021]	0.77
Female mass^2	-0.14	[-0.38; 0.046]	0.69
Male mass	0.15	[-0.044; 0.30]	0.81
Male mass^2	0.15	[-0.051; 0.29]	0.80
Colony	0.059	[0.058; 0.060]	0.076
Brood Size at Hatching[3]			
Intercept	**0.68**	**[0.68; 0.68]**	**< 0.001**
Female mass	0.078	[-0.39; 0.47]	0.92
Female mass^2	0.082	[-0.36; 0.61]	0.95
Male mass	-0.25	[-0.67; 0.22]	0.87
Male mass^2	0.62	[0.12; 1.1]	0.28
Colony	**0.16**	**[0.16; 0.17]**	**< 0.001**
Brood Size at Fledgling[4]			
Intercept	**0.45**	**[0.45; 0.45]**	**< 0.001**
Female mass	0.56	[0.11; 1.3]	0.32
Female mass^2	-0.32	[-1.0; 0.25]	0.68
Male mass	-0.43	[-1.1; 0.069]	0.44
Male mass^2	1.2	[0.56; 1.6]	0.090
Colony	**0.17**	**[0.17; 0.18]**	**< 0.001**
Weighted Proportion of Surviving Fledglings[5]			
Intercept	**0.42**	**[0.41; 0.44]**	**0.0099**
Female mass	2.1	[0.091; 4.3]	0.22
Female mass^2	**-3.2**	**[-5.5; -1.3]**	**0.0053**
Male mass	-3.9	[-5.3; -1.1]	0.12
Male mass^2	**5.3**	**[2.9; 7.2]**	**0.0011**
Colony	**0.34**	**[0.32; 0.35]**	**0.014**

Overwinter Survival[6]			
Intercept	**0.90**	**[0.89; 0.93]**	**0.0054**
Sex	0.063	[0.043; 0.075]	0.42
August Mass	0.15	[0.056; 0.28]	0.094
Colony	**0.52**	**[0.51; 0.52]**	**< 0.001**
Breeding Status	0.031	[0.0045; 0.054]	0.80
August Mass : Breeding Status	**-0.19**	**[-0.32; -0.091]**	**0.031**

[1] Number of observations: 1328; Number of females: 464; Number of males: 427; Number of years: 23 [2] Number of observations: 1334; Number of females: 470; Number of males: 432; Number of years: 23 [3] Number of observations: 1332; Number of females: 465; Number of males: 428; Number of years: 23 [4] Number of observations: 1330; Number of females: 465; Number of males: 428; Number of years: 23 [5] Number of observations: 1323; Number of females: 464; Number of males: 428; Number of years: 23 [6] Number of observations: 4111; Number of individuals: 1072; Number of years: 23

Table 4.4.: Threshold regression model assessing the association between body mass and the weighted proportion of surviving fledglings (binomial distribution). A single breakpoint was used at the stationary point (minimum or maximum). The model was run using the 1000 sets of mass estimates to obtain the posterior mode (estimate) with 95% HPDI and the posterior mode of p-values (Post. P-value). Posterior mode of p-values lower than 0.05 were deemed statistically significant and bolded. The reference level for colony is Biel. Data spans from 1999-2021.

	Estimate	Lower 95% HPDI	Upper 95% HPDI	P-Value
Intercept	0.376	0.227	0.475	0.054
Female mass (left)	**0.173**	**0.071**	**0.268**	**0.015**
Female mass (right)	-0.171	-0.294	0.018	0.114
Male mass (left)	**-0.274**	**-0.361**	**-0.151**	**0.001**
Male mass (right)	0.211	0.048	0.312	0.101
Colony	**0.332**	**0.316**	**0.351**	**0.015**

Table 4.5.: Selection gradients calculated using the Morrissey & Goudie (2022) method for log-link models (clutch size) as well as the extended Morrisey and Goudie (2022) and Janzen & Stern (1998) approach for logit-link models (weighted proportion of surviving fledglings and overwinter survival).

	Mass	**Mass²**
Clutch size		
Females	-0.00273	-0.209
Males	0.00159	0.319
Weighted Proportion of Surviving Fledglings		
Females	0.01430	-0.0404
Males	-0.02330	0.0506
Overwinter Survival		
Non-Breeders	0.03300	-
Breeders	-0.00810	-

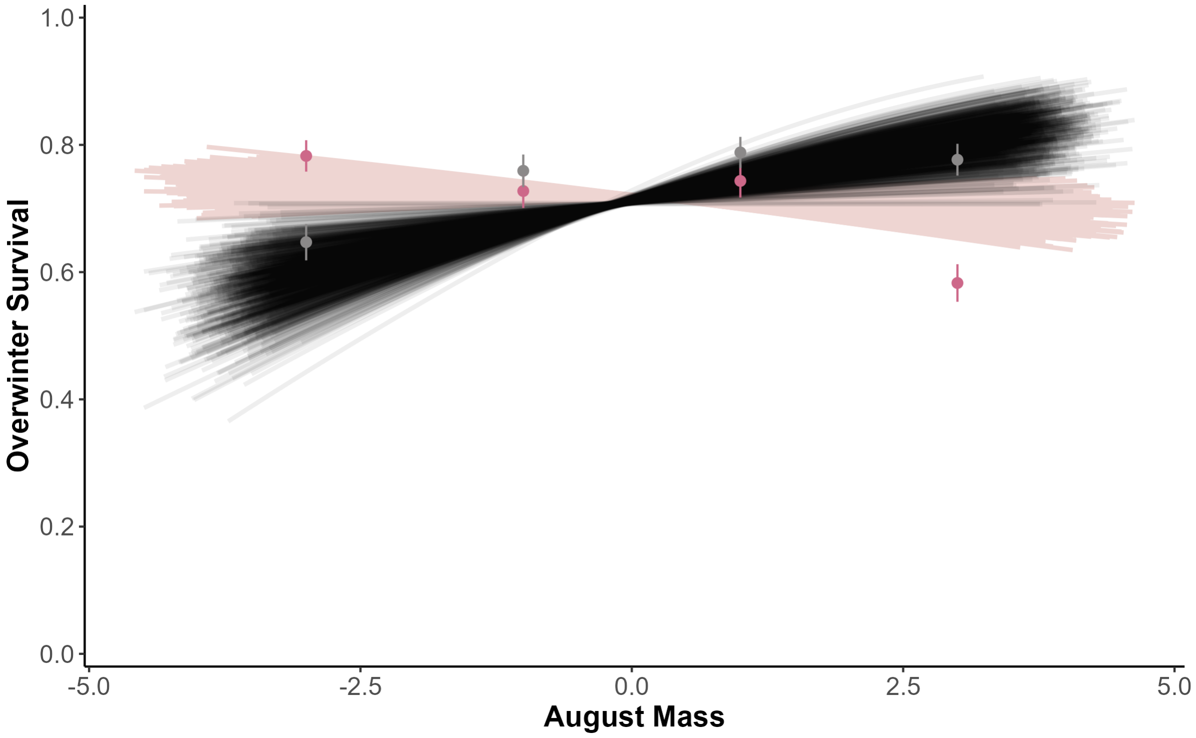

Figure 4.3.: Association between August mass and survival of non-breeders (black) and breeders (pink) of Alpine swifts monitored in Switzerland between 1999-2021. Mean and confidence intervals per adjusted August mass interval are displayed (non-breeders: black; breeders: pink).

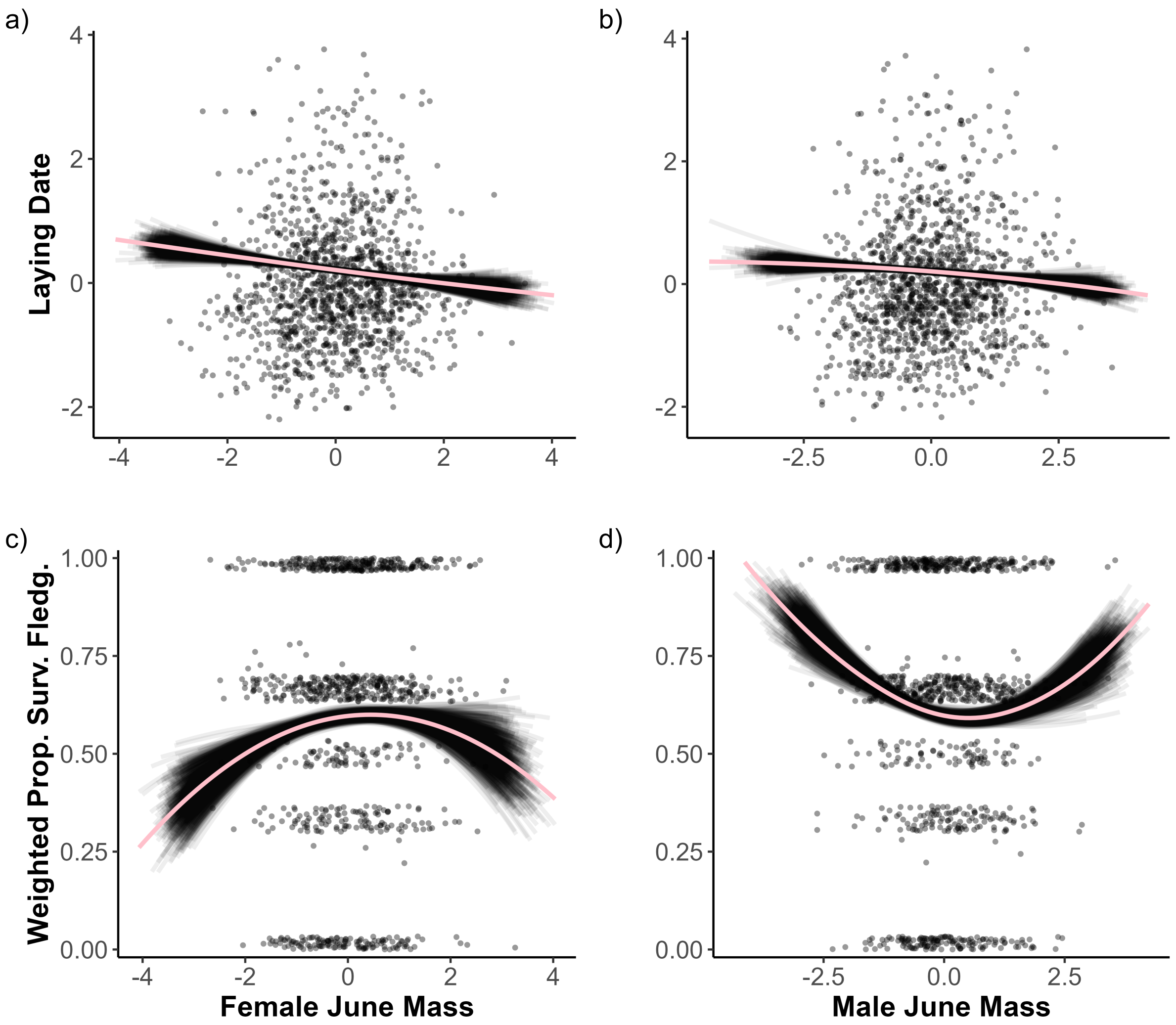

Figure 4.4.: Association between female (left) and male (right) June mass and laying date (panels a and b) as well as the weighted proportion of surviving fledglings (panels c and d) in a Swiss population of Alpine swifts (data spans 1999-2021). The pink lines are the mean response across all Bayesian models while the black lines are associated with each individual model and hence reflect the error around adjusted June mass. The data points correspond to the raw data.

4.4. Discussion

In this study, we aimed to understand the evolution of sexual dimorphism and sexual conflicts over adult body mass using 20+ years of data from a wild population of Alpine swifts, a weakly dimorphic bird. We investigated the relative contributions of environmental and genetic effects and whether these effects and their fitness consequences were sex-specific. In line with our predictions, we report that body mass was a moderately heritable trait in both sexes and was positively genetically correlated between the sexes. We also found that the shape of selection in relation to the weighted proportion of surviving fledglings differed between the sexes, suggesting the potential for intra-locus sexual conflict. Finally, we report that short-term environmental variations play a role in explaining variations in adult body mass in the Alpine swift.

Body mass presented comparable and non-zero additive genetic variance and heritability in both sexes. This suggests that body mass has the potential to evolve in response to selection at the same rate in both sexes. Evolvability was nonetheless low, suggesting that the magnitude of any change would be small even with strong selection. However, as the Alpine swift is a highly aerial avian species which can fly non-stop for up to 200 days (Liechti et al. 2013) even a small change in mass would be biologically relevant. Further, we found a moderately positive cross-sex genetic correlation indicating that the sexes would be positively correlated in any evolutionary response. Positive cross-sex genetic correlations in body mass have been found in many other species (see review by Kruuk et al. 2008), as have positive correlations between mass and fitness (e.g., snow voles *Chionomys nivalis* Bonnet et al. 2017).

When evaluating sex-specific selection for body mass in relation to the weighted proportion of surviving fledglings, we found indications of stabilizing selection for female, but diversifying selection for male June mass based on statistically significant negative and positive quadratic effects, respectively. This difference in the shape of selection between the sexes could potentially result in a difference in the variance but not the mean value of the trait. Thus, we would not expect the evolution of more pronounced sexual dimorphism. However, this would help to maintain genetic diversity in the population. Coefficient of variations for males and females were similar, suggesting that either the differences in the shape of selection are weak or that the shape of selection are not truly stabilizing and disruptive. Follow up analyses using threshold regression models revealed that female reproductive success increased linearly with June mass until a maximum was reached close to the average female mass, while for males, reproductive success decreased linearly with June mass until the minimum was reached close to the average male mass. This suggests the possibility of sexually antagonistic selection with heavy mass favoured in females and light mass favoured in males. Taken together, the positive cross-sex genetic correlation coupled with this sexually antagonistic selection would suggest the possible presence of an intra-locus sexual conflict over body mass in the Alpine swift. Intra-locus sexual conflict has been shown in other species (e.g., conflict over tarsus length in the collared flycatcher *Ficedula albicollis,* Merilä et al. 1998).

The differing shape of selection between the sexes for June body mass in relation to the weighted proportion of surviving fledglings could be associated with sex-specific reproductive tactics. For females, fecundity selection may play a role: the costs of laying eggs may set a minimum viable mass, while the costs of being too heavy may likewise set an upper limit. In birds, the costs of being too large can stem from increased predation risk (e.g., increased exposure to predators due to increased foraging times, Lima 1986) and physiological limitations (e.g., higher cost of flight, Pennycuick 1978). In addition, heavier females may not only be able to produce more eggs than lighter females, but their eggs are also larger, allowing them to fledge more offspring (Bize et al. 2002). Indeed, larger eggs will typically lead to larger offspring, which are more likely to survive until fledgling and to be recruited into the population (Dawson and Clark 2000). For males, intra-sexual competition potentially causing niche specialization may play a role. Light and heavy males may be specializing on different prey items, with both classes of male able to provide more resources to their young than average weight males. Light males may be more agile than average or heavy males and therefore able to catch faster prey. Heavy males may be targeting larger and slower flying insects than the light or average weight males and may monopolize access to these resources as a result of their greater mass. These results could potentially also arise as a result of size disassortative pairing, with light and heavy females pairing with average weight males and average weight females pairing with light and heavy males. Under size assortative mating, it is expected that the fitness function for body mass would be similar for males and females since within a pair both sexes share the exact same fitness value. The contrasted selection pattern for male and female mass thus suggests at least an absence of assortative mating and potentially disassortative mating. Further research on assortative or disassortative pairings will be required to better understand this result. Differences in the strength or shape of selection between the sexes for body mass is uncommon in wild populations, though numerous examples of sexually concordant selection for body mass can be found. For instance, while selection for larger body mass in the greater white-toothed shrew *Crocidura russula* may be sexually concordant, the magnitude of this selection is much larger in males than in females, resulting in heavier body mass in males than in females (Bouteiller-Reuter and Perrin 2005).

We found that females were heavier than males on average, with a 1% difference in mass between sexes. This sexual size dimorphism is most apparent early in the season, when females are at their heaviest in preparation for egg laying. Females then decreased in mass more sharply than males over the course of the season, likely reflecting their higher initial reproductive investment.

Body mass further fluctuates in response to the time of capture, likely reflecting daily foraging patterns in both sexes. During the breeding season, foraging is typically restricted to daylight hours, with swifts returning to the colony at dusk and fasting overnight. Body mass increases throughout the day as swifts resume foraging, with a maximum daily weight reached in the afternoon. Since foraging success may depend on individual experience, we also considered the effect of age on body mass. We report a non-linear increase of mass with age in both sexes, suggesting improvement in foraging abilities as an individual ages. This effect has been observed in many species including the Alpine swift (Moullec et al. 2023) and Adélie penguins *Pygoscelis adeliae* (Lescroël et al. 2019, 2021).

Heavier individuals tend to lay their eggs sooner than lighter ones, which may be explained through one of two mechanisms. First, migration to the breeding grounds may only occur after a certain weight has been reached. Consequently, heavier individuals may arrive to the breeding grounds earlier than lighter ones. This appears to be the case for the semipalmated sandpipers *Calidris pusilla,* which must weigh at least 25g before migrating (Fedrizzi et al. 2004). However, this seems unlikely to explain our result as swifts arrive at the breeding ground several weeks before the breeding season begins, and hence arrival dates should not be strictly related to laying dates, though additional research is required. Second and more likely, larger energetic reserves may potentially allow heavier individuals to begin reproducing sooner after arriving at the breeding grounds than lighter ones. Indeed, there is strong selection on egg laying date in the Alpine swift in relation to annual reproductive success (de Villemereuil et al. 2020). Alternatively, this result may be due to experience as older individuals tend to be heavier than lighter ones. More experienced individuals may be able to reproduce right away as opposed to less experienced individuals that must spend more time preparing for reproduction (e.g., finding a partner and building their nest). For example, Australian magpie-larks *Grallina cyanoleuca* that had mated together previously were able to reproduce earlier than those pairs which had not (Hall 1999).

Furthermore, we report directional selection on adult August mass in both sexes in relation to overwinter survival. However, this result was only apparent for non-breeding individuals, with heavier non-breeders having better chances of survival than lighter ones. Breeders had the same chances of survival regardless of their weight. This may point to breeders having larger energy reserves than non-breeders, enabling them to both survive and reproduce. Non-breeders may not have enough initial energy reserves to produce a clutch and may prioritize their own survival and weight gain over reproducing. This has been seen in great cormorants *Phalacrocorax carbo carbo* where breeding individuals will not lose body mass over the course of the breeding season, sometimes at the expense of their brood (Grémillet 1997). However, our estimates of overwinter survival are associated with very large confidence intervals and should be interpreted with caution.

Adult body mass was strongly impacted by meteorological conditions. This was expected as previous studies showed that cold temperatures and high precipitations strongly affected the mass of nestling swifts (Alpine swift: Bize et al. 2007; common swift: Sicurella et al. 2015). In our study, adult body mass increased non-linearly with ambient temperature, possibly stemming from increased insect availability during periods of warmer than colder temperatures. However, as temperatures continue to rise, swifts may be incurring higher metabolic costs, decelerating mass gain. Insect activity may also plateau with increasing temperatures, providing no additional mass gain. Ambrosini et al. (2006) report similar results in nestling barn swallows *Hirundo rustica* with a positive relationship between mass and temperature. Conversely, adult body mass in our study decreased non-linearly with increasing rainfall, potentially stemming from decreased insect availability. In conditions of very high rainfall, adult swifts may be able to offset continuous mass loss by waiting out the rain or foraging elsewhere. In the first case, they may conserve their energy by not flying in poor conditions, while in the second case they may be reaching new foraging opportunities in areas with better weather. These results are also supported by Cox et al. (2019), who found a negative relationship between body mass and precipitation in nestling tree swallows *Tachycineta bicolor*.

The permanent environment and year effects further accentuate the importance of short-term weather effects on adult body mass. The permanent environment effect suggests that environmental conditions encountered in early life will have some carryover effects at adulthood, accounting for 17% and 18% of the variance in males and females, respectively. The small year effect suggests little inter-annual variation in body mass, explaining only 3% of the variance in both sexes. The strong cross-sex yearly correlation however indicates that the impact of year on body mass would be similar for both sexes. Such strong cross-sex yearly correlations have been reported in several species across a wide range of traits, such as for reproductive success in yellow-bellied marmots where in good years, individuals of both sexes will perform well (St Lawrence et al. 2022). Body mass was also higher in Biel than in Solothurn, reflecting microenvironmental differences between these two colonies.

In conclusion, body mass variation in the Alpine swift was largely due to short term environmental effects and genetic variance. Temperature and precipitation greatly impacted body mass and the trait was heritable in both sexes. There were differences in the strength and shape of selection acting on body mass depending on the fitness component used. The limited evidence for sexually antagonistic selection in relation to the weighted proportion of surviving fledglings coupled with a moderately positive cross-sex genetic correlation suggests the possible presence of intra-locus sexual conflict over body mass. Alternatively, the weak sexual dimorphism in body mass (1%) we report may simply reflect the fact that both sexes are already at their fitness optimum, and that these optimums are similar for males and females.

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Chapter 5

Chapter 5: Who keeps the house after divorcing? Partner and nest (in)fidelity in the long-lived Alpine swift

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Preamble

This chapter is probably my personal favourite, at least partially because of how easy it was to write. By the time I finished the previous chapter, I was quite familiar with the analyses needed to tackle these questions, which also made the process smoother. Aside from the general topic—which by virtue of involving animal behaviour is near and dear to my heart—a big part of what I found fun about this chapter was that its more straightforward to talk about whenever people outside the field ask about what it is that I do. After watching people's eyes glaze over from hearing about genetic correlations and sex-specific selection, telling them that birds also go through relationship drama is a sure way to get a laugh!

Abstract

Despite the advantages of lasting pair bonds and the prevalence of monogamy, at least in avian species, some individuals switch mates (divorce). Divorce is generally considered to be adaptive (i.e., conferring net fitness benefits) though its causes and consequences often remain unclear, most notably regarding the genetic basis of this behaviour. Using over 30 years of data in a long-lived bird with obligate bi-parental care, the Alpine swift, we first described the overall patterns of mate and nest site fidelity and investigated the predictors of between-year divorce. We show that 16.6% of pairings ended in divorce, with low reproductive success and young age as predictors of divorce, and that males retained the nest site more often than females. By then studying individual repeatability and heritability of divorce, we show moderate repeatability in females and low repeatability in males, and little additive genetic variance in either sex. Finally, we assessed the fitness consequences of divorce and report that an active decision to modify the pair bond (divorce) may be more beneficial than reactionary re-pairing following a partner's death. Overall, divorce may provide some reproductive benefits for Alpine swifts, but no microevolutionary potential of this behaviour is evident in this population.

5.1. Introduction

Monogamy refers to the formation of exclusive pair bonds between a male and female of the same species, either at the social or genetic level (*herein* 'monogamy' refers to either social or genetic monogamy, unless specified otherwise). These bonds may be limited to a single breeding attempt or persist over several breeding attempts and occur in varying frequencies throughout the animal kingdom. Monogamy is relatively rare in fish, amphibians and reptiles (e.g., Whiteman and Côté 2004), and only slightly more common in mammals, with an estimated 9% of mammalian species displaying a socially monogamous mating system (Lukas and Clutton-Brock 2013). Though the determining factors of monogamy remain debated, life history traits such as parental care are often cited as a key driver (i.e., bi-parental investment in dependent offspring is expected to favour monogamy over promiscuity, Orians 1969). In line with this hypothesis, monogamy occurs much more frequently in avian species, most of which exhibit bi-parental care, with an estimated 80-90% of birds displaying a socially monogamous mating system (Bennett and Owens 2002; Black 1996).

Maintaining a pair bond between reproductive events allows individuals to minimize the costs associated with finding and securing a new partner (e.g., time and energy, increased risks of infections or parasites), and to potentially increase lifetime reproductive success as a result of improved coordination and cooperation between partners with each shared reproductive attempt (Black 1996; Griffith 2019). Indeed, a positive relationship between the duration of the pair bond and lifetime reproductive success has been noted in numerous species (Charmantier et al. 2006; Pyle et al. 2001). For instance, barnacle geese *Branta leucopsis* who maintained pair bonds over longer periods of time produced more offspring than those who did not (Black 2001). Despite the advantages of lasting pair bonds and the prevalence of social monogamy (at least in avian species), some individuals seek additional mating opportunities in the form of extra-pair copulations or abandon a current partner entirely in a favour of a new partner.

Mate switching or ‘divorce’ is broadly defined as the dissolution of pair bonds while both partners are still alive, with one or both partners re-pairing with a new mate (Choudhury 1995). Instances of divorce have been recorded as occurring between seasons (i.e., mate switching from one year to the next) and within a season (i.e., rapid mate switching within a single breeding season). Divorce is often reported in monogamous species, whether they are mammals (e.g., Azara’s owl monkey *Aotus azarai,* Fernandez-Duque and Huck 2013), fish (e.g., convict cichlid *Archocentrus nigrofasciatus,* van Breukelen and Draud 2005), or birds (e.g., black-legged kittiwake *Rissa tridactyla,* Mercier et al. 2021). In birds forming breeding pairs, instances of divorce between breeding events have been reported in as many as 92% of species (Choudhury 1995), and may range from 0-100% of pairs (Chen et al. 2023; Jeschke and Kokko 2008). These modifications of the initial mating decision are generally considered to be adaptive, in the sense that they confer net fitness benefits, as low reproductive success is often a precursor of divorce (Culina et al. 2015; Dubois and Cézilly 2002). And yet, the rate and predictors of divorce are often unclear and vary within and between species (e.g., *successful* rather than unsuccessful breeding predicted divorce in plovers *Charadrius spp.;* Halimubieke et al. 2020).

Several non-mutually exclusive hypotheses have been proposed to explain within- and between-season divorce in birds (reviewed by Choudhury 1995). On one hand, divorce may provide fitness benefits if it allows individuals to pair with a potentially more compatible partner (“incompatibility hypothesis” Coulson 1966), or with a ‘higher quality’ partner (“better option hypothesis” Ens et al. 1993), or to gain access to a higher quality territory (“better territory hypothesis” Desrochers and Magrath 1996). One or both former partners would then be expected to benefit and see an increase in their reproductive success in the following breeding event(s). The benefits of a more compatible or 'higher quality' mate or territory should outweigh the costs of having to form a new pair bond via genetic or social compatibility, offspring with better genes, or access to more and/or better resources (e.g., food, nesting sites). Consistent with this prediction, Culina et al. (2015) report that female birds gain fitness benefits from 'trading up' by divorcing a partner with whom reproductive success was relatively low in the previous year, based on a meta-analysis of 64 species. Specific to within-season divorce with multiple reproductions per season, it has also been suggested that divorce may be a male strategy to gain additional reproductive success by forming a new pair and starting a second reproduction event while the previous partner is still providing parental care to the first clutch (Birkhead and Møller 1992; Choudhury 1995). On the other hand, divorce may rather be a side effect of external events and provide no fitness benefits, as may be the case following the asynchronous arrival of both partners at their breeding site ("musical chairs hypothesis" Dhondt and Adriaensen 1994). Divorce could also result from a partner being usurped by a more aggressive individual, in which case only the usurper would be expected to benefit ("usurper hypothesis" Ens et al. 1996; e.g., Fernandez-Duque and Huck 2013), or even stochastic environmental disturbances such as climate change ("habitat-mediated" hypothesis Desrochers and Magrath 1993; e.g., Ventura et al. 2021). In these cases, neither partner of the original pair would, on average, be expected to increase their reproductive success following the divorce. In any case, the costs and benefits of divorce are likely to differ between the sexes and between individuals of different ages (Culina et al. 2015), with individual experience expected to modulate reproductive decisions (Pitera et al. 2021).

In addition, mate fidelity is often highly correlated with breeding site fidelity. In some species, mate fidelity has been identified as a by-product of breeding site fidelity (Choudhury 1995; but see Fairweather and Coulson 1995). Indeed, breeding site fidelity may facilitate the reunion of partners which have overwintered separately (Aebischer et al. 1995) as well as provide other benefits (e.g., lower aggression towards known rather than new neighbours, better knowledge of the surrounding territory, Bried and Jouventin 2001). Crucially, nests can be costly to build in both time and energy (e.g., female blue tits *Cyanistes caeruleus* who build larger nest have reduced immunocompetence as compared to females who build smaller nests, Tomás et al. 2006). Reusing these costly structures can therefore allow individuals to reallocate limited energetic resources (e.g., Pied Flycatcher *Ficedula hypoleuca* females fed their offspring more frequently when nest construction costs were experimentally reduced, Moreno et al. 2010) and potentially increase their reproductive success. For instance, white storks *Ciconia ciconia* reuse nests from year to year and compete for access to the largest (and hence oldest) nests, which are associated with increased fledgling success (Vergara et al. 2010). The consequences of divorce may therefore extend to nest site retention, with both former partners competing for continued access to the nest as the dissolution of the pair bond implies that one or both of the former partners must disperse (either simply from the nest site or to a new breeding ground entirely in species with breeding dispersal). The relationship between mate and breeding site fidelity therefore requires further study, especially so in cases where the territory is limited to the nest site as with most cliff- and burrow-nesting species.

Finally, for divorce to evolve, the variation underlying this trait must have a genetic basis. Despite much of the literature focusing on the adaptive nature of mate switching, only two studies have previously examined the heritability of divorce in wild birds. Wheelwright & Teplitsky (2017) reported no additive genetic variance of divorce in either sex of Savannah sparrows *Passerculus sandwichensis* based on 18 years of data (repeatability (posterior mode [lower, upper 95% confidence interval]): 0.002 [0, 0.45] for males, 0.66 [0.22, 0.83] for females; additive genetic variance: not estimated for males, 0.035 [0, 5.68] for females). Germain et al. (2018) reported low heritability of divorce in both sexes of the song sparrows *Melospiza melodia* based on 39 years of data (repeatability: 0.001 [3×10^{-8}, 0.15] for males, 0.16 [3×10^{-6}, 0.30] for females; heritability: 0.001 [2×10^{-8}, 0.12] for males, 0.001 [2×10^{-9}, 0.14] for females; R_{fm} -0.0002 [-0.08, 0.06]). These two sparrow species have a maximum longevity of 7 and 11 years respectively and are not representative of the diversity of lifespan and mating systems in birds. Therefore, there is currently a lack of studies on the genetic basis of divorce, and the little information that does exist suggests that divorce has very low evolutionary potential in natural populations.

In this study, we examined mate and nest site infidelity in a long-lived bird with bi-parental care, the Alpine swift *Tachymarptis melba.* As Alpine swifts have only one reproductive attempt per year and are considered genetically monogamous, divorce was estimated between years. Using three decades of data (1991-2021) collected from three Alpine swift colonies in Switzerland, we first described the overall patterns of partner and nest fidelity and infidelity in both sexes and investigated the predictors of divorce from one year to the next. We then used animal models to estimate the sex-specific genetic basis of divorce and its cross-sex genetic correlation to gain knowledge on the heritability and possibility of sexual conflict over this behaviour. Finally, we characterized the fitness consequences of divorce by comparing measures of annual reproductive success as well as possible improvements in reproductive success between individuals that formed new pair-bonds following divorce ('divorced') or the original partner's death ('widowed'), or that retained the same mate ('faithful') from one year to the next. Per Culina et al. (2015), explicitly contrasting reproductive success between these subgroups enables us to disentangle fitness costs of divorce from that of mate change itself. We expected individuals who retained the same mate from one year to the next to have the highest reproductive success out of all three groups, and for divorced individuals to have higher reproductive success and greater improvements in reproductive success than widowed individuals.

5.2. Materials & Methods

5.2.1. *Study Species & Site*

The Alpine swift is a long-lived (median lifespan of approx. 7 years & maximum of 26 years, Bize et al. 2006a) and colonially nesting bird. Swifts live an impressively aerial lifestyle, remaining in flight for the majority of the year and only landing during the breeding season (Liechti et al. 2013). Up to a hundred pairs will nest on cliffs, or in the roof spaces of tall buildings when breeding in urban settings. Swifts construct their nests entirely with dry (or even fresh) materials (e.g., feathers, plant matter, and nowadays even plastics) collected in flight that they then glue together using saliva (Lack 1956). Swifts typically build upon nest structures from previous years, as nest building is a time consuming and energetically costly behaviour. These behaviours are rarely documented in swifts, though nest structures are similarly described in the literature on pallid swifts *Apus pallidus* (Paesani 2012) and white-throated swifts *Aeronautes saxatalis* (Collins 2010). Both parents care for their single yearly clutch of 1-4 eggs (incubation: approx. 18 days and fledging: 50-70 days after hatching, Bize et al. 2004). Both parents build and maintain the nest, incubate the eggs and feed their offspring until fledging. Consequently, both sexes are expected to have approximately the same allocation into reproduction, with the exception of egg laying which only involves costs for females. Swifts begin breeding on average (mean ± SE) at 2.9 ± 0.03 years of age for females and 3.1 ± 0.04 years of age for males (raw data) and breed each year until their death (Tettamanti et al. 2012). Although Alpine swifts are genetically monogamous (no detected extra-pair paternity

EPP; C. M. Meier & P. Bize, unpublished), new pairings can and do occur following divorce or widowing.

Three Swiss urban-nesting colonies have been followed at the individual level since 1991, 1999 and 2000 respectively. Each year, there are approximately 30-40 breeding pairs in the colony located in the building *Landvogteischloss* in Baden, 60-100 breeding pairs in the colony located in the building *Stadtkiche* in Biel, and 40-55 breeding pairs in the colony located in the building *Bieltor* in Solothurn. Birds are permanently identified by ringing them as nestlings, or at their first capture at adulthood if not already ringed as nestlings, and molecularly sexed using DNA taken from blood or feathers (Griffiths et al. 1998). As with other species of swifts, Alpine swifts may leave their natal colony to reproduce in a neighbouring colony (i.e., natal dispersal), but they then return each year to their breeding colony (i.e., no breeding dispersal). Individuals who changed colonies between their birth and their first breeding attempt are considered to be natal dispersers, with 10% natal dispersal having been recorded between Biel and Solothurn (Bize et al. 2017). Throughout the breeding season, parents are caught by hand at the nest while brooding the eggs or chicks and later feeding the chicks, and their yearly reproductive success (clutch size, brood size at hatching and fledgling) is determined by regularly monitoring the nest. As no EPP has been recorded in this population, these behavioural observations are sufficient for pair-bond identification and to assign breeding pairs to a nest, as well as to construct a detailed social pedigree. Indeed, a molecular analysis of the colony nesting in Baden's *Landvogteischloss* (50 breeding pairs) showed no evidence of EPP (C. M. Meier and P. Bize, manuscript in preparation). Likewise, low (4.5%) incidences of EPP have been reported for the common swift *Apus apus* (Martins et al. 2003), which has similar ecology to the Alpine swift. Note also that Charmantier and Réale (2005) showed that misassigned paternities have a negligeable impact on heritability estimates in cases were EPP rates are under 20%. While subtle sexual dimorphisms have been recorded (e.g., females are 1% heavier than males, Dumas et al. 2024c), these differences are not apparent to observers during field data collection. As such, fieldwork is done blind to the sex of the individual.

To identify the fitness consequences and predictors of divorce, we categorized each breeding event of females and males as being 'divorced' (i.e., paired with a different mate while the previous mate was still alive), 'widowed' (i.e., paired with a different mate following the death of the previous mate) or 'faithful' (i.e., retained the same mate) when comparing one year to the next. Although varied terminology can be found in the literature, we use the categorizations of 'divorced', 'widowed' and 'faithful' in accordance Choudhury (1995) and Culina et al. (2015). The probability of recapturing breeding adult Alpine swifts approaches 1 (Bize et al. 2006a), allowing us to accurately estimate adult survival through yearly capture records (Robinson et al. 2020) and hence accurately disentangle divorced from widowed individuals. We likewise categorized nest site fidelity for each breeding event for females and males (0: changed nest site; 1: same nest site) from one year to the next. There were few instances of replacement clutches in the same year in our 30-year-dataset (46 replacement clutches out of 3524 total clutches; 1.3%). Hence, replacement clutches were excluded from the data set, so that only between year mate and nest site fidelity is considered. It is also important to note that we currently lack the necessary data to identify which partner initiated the divorce, which is generally challenging and near unfeasible in wild populations. As such, we modelled the probability of divorcing for both original partners. This approach assumes that the divorce was a mutual decision with equal likelihood to be beneficial for both former partners.

5.2.2. *Statistical analyses*

All statistical analyses were conducted in R version 4.3.1 "Beagle Scouts" (R Core Team 2023), using the R packages *lmerTest* (Kuznetsova et al. 2017) and *MCMCglmm* (Hadfield 2010). Only breeding individuals were retained for the analyses, and only pairs for which the identity of both partners as well as their pair bond status from one year to the next were known were considered.

5.2.3. *Patterns of Partner & Nest Fidelity*

In a first part, we characterized the overall trends in partner and nest fidelity of Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) throughout the years of the study (1991-2021) to better understand the extent of these behaviours. We quantified the overall proportions of pairs which ended in divorce or widowing, or for which partners retained the same mate from one year to the next, as well as the yearly and between colony fluctuations in pair bond status. We also investigated repeat occurrences of divorce throughout an individual's lifetime. We did so for both males and females as some individuals repeatedly divorced and re-paired throughout their lifetime, and this distribution of events need not necessarily be the same between the sexes.

We further quantified the overall proportions of nest site fidelity (i.e., using the same nest) in relation to partner fidelity (i.e., remaining with the same mate) from one year to the next for each breeding event for both females and males: FF (same mate and same nest); FU (same mate but different nest); UF (different mate but same nest: following divorce or widowing, the focal member of the original pair remained in the same nest); and UU (different mate and different nest: following divorce or widowing, the focal member of the original pair was observed in a new nest). By definition, FF and FU are at the pair level, while UF and UU are sex specific. Although re-pairing after the loss of the original partner does not constitute partner infidelity in the same sense as divorce, we did not seek to differentiate between widowed or divorced individuals here. We also categorized individuals as 'unknown' when the pair bond status or the nest site usage for one of the partners was not known from one year to the next, as these partial data are still informative.

5.2.4. *Predictors of Partner & Nest Fidelity*

Next, we assessed the causes of partner and nest fidelity to better understand the factors influencing the probability of divorcing between years as well as the link between mate and nest site retention. As divorce is an emergent property of social interactions involving more than one individual, our models incorporated both female and male characteristics.

We first considered the effects of individual (i.e., age, native dispersal status) and reproductive (i.e., brood size at fledging) traits, as these are expected to influence the probability of divorcing. Indeed, we expected divorce to be more common in younger rather than older birds and occur more frequently in the year following poor reproductive success. As natal dispersal is a costly behaviour (i.e., increased risk of mortality during dispersal), behaviours which facilitate integration into the new social environment should be favoured; we therefore expected natal dispersers to be less likely to divorce than those who remained in their natal colony. We first fit a generalized linear mixed effects model (Model I) with divorce as a function of female and male age, female and male native dispersal status (native or immigrant), brood size at fledging in the year preceding the divorce, as well as the colony as fixed effects. Female and male age (pooled across the sexes) were mean centred and scaled to a variance of 1. Native dispersal status was a two-level factor, native (non-dispersers) and immigrants (natal dispersers). We included female and male identity as random effects to assess the sex-specific repeatability of divorce and included year as a random effect to estimate year-to-year variation in this behaviour.

With the same model structure, we fit a second generalized linear mixed effects model (Model II) which additionally included pedigree data to estimate quantitative genetic parameters of divorce (an 'animal model,' Kruuk et al. 2008). Animal models allow users to decompose total phenotypic variance between environmental and genetic sources, and hence make inferences about the evolutionary potential of a trait (Kruuk et al. 2008; Wilson et al. 2009). To estimate the heritability of divorce in both sexes (and hence its evolutionary potential), as well as estimate the cross-sex genetic correlation of this trait (and hence the presence of genetic constraints on its evolutionary potential), we included female and male individual identity linked to a pedigree as random effects. As divorce had repeated measures across an individual's lifetime, a permanent environment (i.e., individual identity not linked to the pedigree) effect was included. As with model I, model II also included year as a random effect.

Following Pick et al. (2023), variance parameters and ratios for both models were reported as the mode, median and mean of the posterior distribution and reported with their 95% highest posterior density intervals (HPDI) (the mode and mean are reported in the supplemental only). Variance ratio estimates were calculated as the proportion of total phenotypic variation explained by the given variance parameter, i.e., heritability on the latent scale conditioned on the fixed effects was estimated as the sex-specific additive genetic variance divided by the (conditional) total phenotypic variance. The pruned social pedigree used in this study was 5 generations deep and included data on 1596 individuals, with 653 maternities and 640 paternities (Table D.1). The pedigree statistics were determined using the R package *pedantics* (Morrissey 2023).

We used weakly informative priors suggested by de Villemereuil (2018) with V = 1, nu = 1000, alpha.mu = 0, alpha.V = 1 for the permanent environment and year effects (Models I & II). We used an expanded prior suitable for estimating cross-sex correlations with V = diag(2), nu = 2, alpha.mu = rep(0, 2), alpha.V = diag(2) for the additive genetic variance and cross-sex genetic correlation (Model II). All models had a burn-in period of 75000 iterations and were sampled every 5000 iterations for a total effective sample size of 2000. In the case of Model II, two chains were run and then merged together, resulting in a posterior distribution of 1000 points. Since divorce was modelled as a binomial trait, residual variance was fixed to 1 for both sexes, and we added a constant of $\pi^2/3$ when calculating repeatability and variance ratio estimates (Nakagawa and Schielzeth 2010). Plot traces were visually assessed, and absolute autocorrelation values were verified to be <0.1. We verified chain convergence for each parameter using the Heidelberger and Welch's convergence diagnostic (heidel.diag function) as recommended by Hadfield (2010); all converged well except for the cross-sex genetic correlation.

We then investigated the link between partner and nest fidelity to better understand their co-occurrences as well as which individuals divorce. We fit a generalized linear mixed effects model with the probability of nest fidelity (i.e., retaining the same nest from one year to the next) as a function of sex, pair bond status (divorced, widowed or faithful) and the colony (Baden, Biel or Solothurn). We included an interaction term between sex and pair bond status to assess whether the sexes differed in their nest use patterns according to their pair bond status. Individual identity and year were included as random effects to account for repeated measures at the individual level and between years, respectively. The model also included pair identity as a random effect to account for repeated measures at the pair level. Sex-specific models with nest fidelity as a function of the pair bond status and the colony yielded qualitatively similar results (Table D.4). The sex-specific models had female and male identity as well as year as random effects to account for repeated measures at the individual level and between years, respectively.

5.2.5. *Fitness Consequences of Partner Fidelity*

Finally, we investigated the fitness consequences of divorce in both females and males as the various hypotheses seeking to explain divorce entail improved reproductive success for one, both or neither partner of the original pair. Reproductive success traits considered were clutch size, brood size at hatching and at fledgling, and the weighted proportion of surviving fledglings. The weighted proportion of surviving fledglings was modelled as brood size at fledging over clutch size. Surviving fledglings are defined as those that successfully leave the colony at the end of a giving breeding season. Though not a fitness component per se, egg laying date is strongly related to fitness in the Alpine swift (de Villemereuil et al. 2020). As such, we also fitted a model with laying date to detect potential indirect effects of mate switching on fitness. Laying date was modeled as day of the year and mean-centered and scaled to a variance of 1 (pooled across all years). Laying date data was not available for Baden, and hence only data from Biel and Solothurn are considered for the laying date models.

We ran two sets of analyses to evaluate the potential benefits (and costs) of divorce for female and male Alpine swifts. First, we compared the reproductive success of individuals in newly formed pairs after a divorce (‘divorced’) with that of individuals in newly formed pairs due to the death of a partner (‘widowed’) and with that of individuals in pairs that retained the same mate (‘faithful’) from one year to the next. We expected faithful individuals to have the highest reproductive success, as well as differences between the reproductive success of male and female divorced individuals in accordance with the various hypotheses seeking to explain divorce. For instance, in the case of the incompatibility hypothesis, both original partners of a divorced pair would be expected to have higher reproductive success following the divorce. We also expected divorced individuals to perform better than widowed individuals, should divorce provide fitness benefits outweighing the costs of re-pairing itself.

Second, we compared the changes in reproductive success from one year to the next between divorced, widowed and faithful individuals, defined as reproductive success in the year X+1 (i.e., after divorce or partner death) minus reproductive success in the year X. A negative value would suggest deterioration while a positive value would suggest an improvement in reproductive success from year one year to the next, with 0 indicating no change. Individuals retaining the same mate from one year to the next should improve in reproductive success over their lifetime, but not necessarily from one year to the next as they may already be performing well. Should divorce provide fitness benefits outweighing the costs of re-pairing, we would expect divorced individuals to perform better than widowed individuals. However, as divorce is expected to occur more frequently following poor reproductive success, it is possible for an apparent increase in reproductive success from one year to the next to reflect a regression to the mean effect. To test this effect, we compared the changes in reproductive success between divorced, widowed and faithful individuals who had failed in the year preceding the divorce, where failure was defined as no surviving fledglings (Table D.7).

For each measure of reproductive success in both sets of analyses, we fit a model with reproductive success as a function of the pair bond status (divorced, widowed, faithful), with sex and the colony as fixed effects. Individual identity as well as year were included as random effects to account for repeated measures at the individual and year levels, respectively. We also included a nest ID specific to a given nest in each year as well as pair ID to account for repeated measures at the nest and pair levels, respectively, as reproductive success is shared between the male and female of each pair in a given year. An interaction term between status and sex was also included for all models, but dropped from the final models as this term was not statistically significant or showed only negligeable effects (Table D.5). In addition, we ran these sets of analyses with the inclusion of age (linear and quadratic terms calculated as orthogonal polynomials) and prior performance (modelled as the brood size at fledging in the year X) as fixed effects in order to account for these possible biases (i.e., divorced birds may be younger and have lower prior performance than birds who were widowed or retained the same mate from one year to the next). Results were qualitative similar, albeit with reduced power due to the lower sample size of birds with known ages, and hence are presented only in the supplemental (Table D.8; Table D.9).

5.2.6. *Ethical Note*

Swifts were caught at the nest by hand and handled for 5-15 minutes before being released at the colony site. To minimize stress, we avoided capturing swifts during sever weather events, and the bulk of captures took place between 9h00 and 18h00 so as to avoid disturbances during periods of intense social activity at dusk and dawn (Meier et al. 2018). All handlers were trained by PB or senior members of the field team. All work was conducted in accordance with international standards on animal welfare and in compliance with Swiss local and national regulations (ringing permits 2235 & 3672 and projects 72 & 54 delivered by the Swiss Federal Office for the Environment to PB and CMM, respectively).

5.3. Results

5.3.1. *Patterns of Partner & Nest Fidelity*

There were a total of 2260 pair-years including 1267 unique pairs from a total of 914 females and 820 males. Overall, 268 females and 258 males accounting for 16.6% of pairs (n=372) divorced across all three colonies from 1991 to 2021 (Figure D.1).

Divorce ranged from 8.2% to 35.7% of pairs each year throughout the study period (Figure D.2). The proportion of divorced vs widowed vs faithful pairs from one year to the next was comparable between colonies (13.3%-18.8%), though Biel had the highest proportion of divorced pairs and Baden the lowest (Figure D.3). Individuals of both sexes who divorced did so between 1 and 5 times throughout their lives (Figure 5.1 A). There were four instances in which a pair divorced only to re-pair after both original pair members had paired and divorced from other partners (described in the supplemental). Widowed individuals of both sexes re-paired following the loss of their original partner between 1 and 5 times throughout their lives, with a single male outlier re-pairing 8 times (Figure 5.1 A). These patterns of lifetime divorce and widowing were comparable between the sexes (Figure 5.1 A).

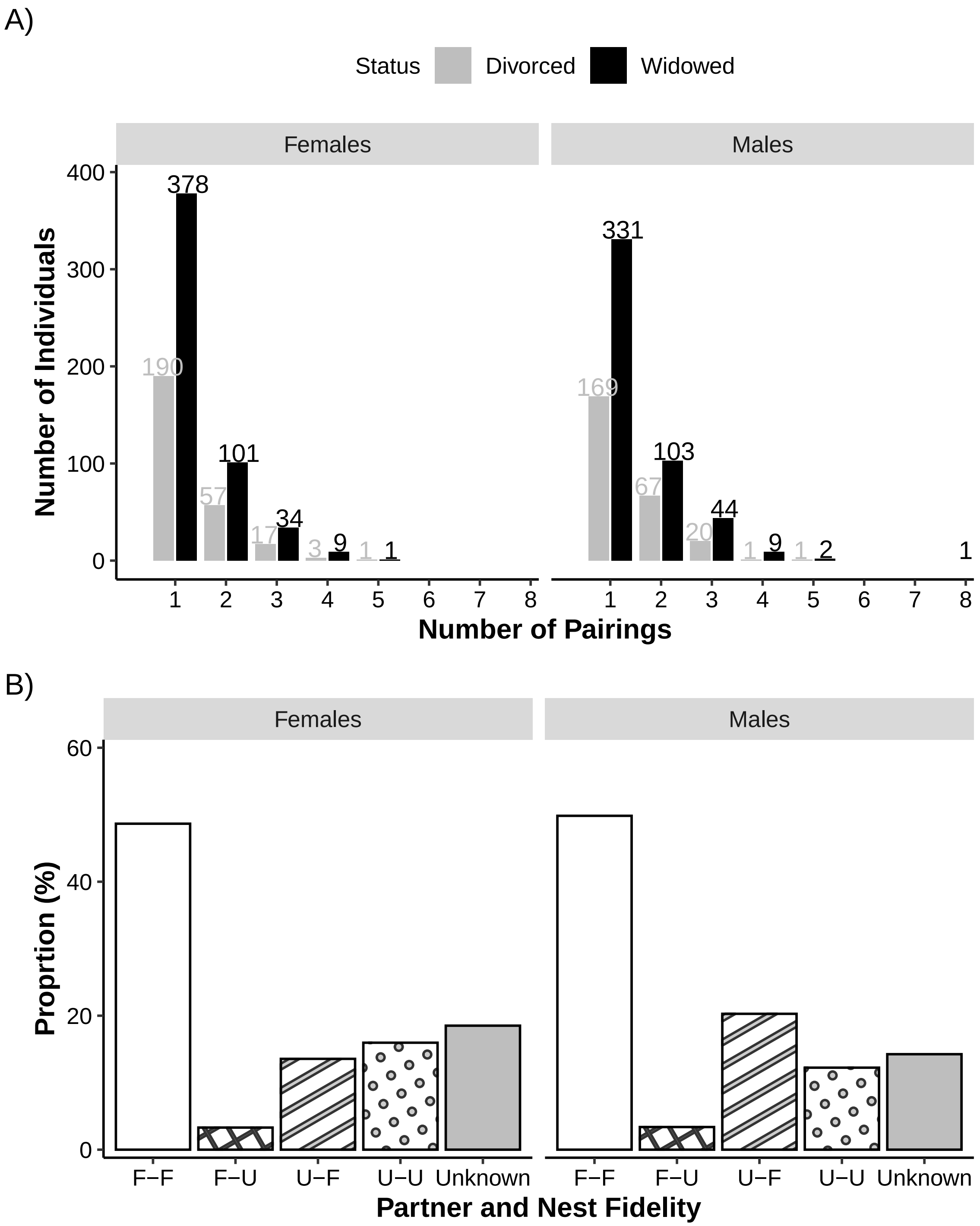

Figure 5.1.: A) Number of individuals who re-paired following divorce (grey) or widowing (black) in relation to the number of lifetime pairings (1-8) for female and male Alpine swifts. B) Observed proportion of female and male swifts which retained the same partner and/or nest from one year to the next. FF: same mate and same nest; FU: same mate but different nest; UF: different partner but same nest; UU: different mate and different nest. By definition, FF and FU are at the pair level, while UF and UU are sex-specific. Data is from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

Over all individuals and pairing events for which the pair bond status and nest use patterns were known for both partners, 49% of pairs were retained the same partner and nest site, while 3% retained the same partner but changed nests from one year to the next (Figure 5.1 B). When individuals re-paired between years (following divorce or widowing), males retained the nest site more often than females (20% and 14% of males and females retained the same nest site, respectively) (Figure 5.1 B UF). 12% of males changed both mates and nests, as compared to 16% of females (Figure 5.1 B UU). For 14% of males and 18% of females, either the pair bond status or the nest usage patterns were unknown (Figure 5.1 B unknown), out of a total of 2242 female-focal pairs and 2189 male-focal pairs.

5.3.2. *Predictors of Partner & Nest Fidelity*

Divorce from one year to the next was more likely in pairs that produced fewer fledglings, and when females and males were young rather than old (Table 5.1). The mean age of individuals who divorced at least once (mean ± standard error, raw data) was 5.3 ± 0.2 years for females and 5.6 ± 0.2 years for males. The mean age of individuals who retained the same mate from one year to the next (raw data) was 6.3 ± 0.2 years for females and 6.8 ± 0.2 years for males. Individuals were more likely to divorce in Solothurn than in Baden or Biel (Table 5.1). There were no statistically significant differences in the probability of divorce between natal dispersers and non-natal dispersers of either sex (Table 5.1).

Divorce was moderately repeatable in females (median: 0.108; 95% HPDI: [0.0166; 0.195]), and weakly repeatable in males (0.0233 [6.43e-08; 0.0901]) (Table 5.2). Divorce was weakly heritable in both sexes (females: 0.0458 [7.79e-09; 0.139]); males: 0.0169 [1.54e-09; 0.0818]), with low additive genetic variance (females: 0.232 [3.85e-08; 0.742]); males: 0.0789 [7.22e-09; 0.402]) and a somewhat positive cross-sex genetic correlation (0.128 [-0.821; 0.943]) (Table 5.2). Though the credible intervals were large and should therefore be interpreted with caution (Table 5.2), estimates for females in a female-only model were qualitatively similar (Table D.3). In the case of the cross-sex genetic correlation specifically, the credible interval spanned nearly the entire range of possible values, and the posterior distribution contained a majority of very small values approaching zero (Table 5.2, Figure D.4).

On average, males were more likely to retain the same nest site from one year to the next than females (Table 5.3, Figure D.5). Divorced individuals of both sexes were less likely to retain their nest sites than widowed or faithful individuals, with divorced males being more likely than divorced females to retain the nest (Table 5.3, Figure D.5). Individuals of both sexes were more likely to retain their nest sites in Baden than in either Solothurn or Biel (Table 5.3). In addition, widowed individuals of both sexes were more likely to retain their nest site than divorced individuals, but less likely to retain their nest site than faithful individuals (with widowed as the reference level (estimate ± standard error) contrasts for: [divorced] 1.984 ± 0.243; [faithful] -2.684 ± 0.231), with males being more likely than females to retain their nest sites ([divorced] 0.074 ± 0.303; [faithful] 0.971 ± 0.299).

Table 5.1.: Estimates (posterior mode) and 95% credible intervals (Bayesian model in R package MCMCglmm) for the relationships between divorce from the one year to the next and fixed effects for male and female swifts. Estimates with 95% HPDIs that exclude 0 were deemed statistically significant and bolded. Non-native disperser (vs native disperser) is the reference level for female and male dispersal status. Baden is the reference level for colony (Biel, Solothurn). Data is from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Lower 95% HPDI**	**Upper 95% HPDI**
Intercept	**-2.3**	**-2.9**	**-1.7**
Female Age	**-0.33**	**-0.55**	**-0.15**
Female Dispersal Status	-0.14	-0.50	0.22
Male Age	**-0.33**	**-0.52**	**-0.16**
Male Dispersal Status	0.094	-0.24	0.42
Brood Size at Fledging (Year X)	**-0.23**	**-0.38**	**-0.087**
Colony : Biel	0.18	-0.27	0.65
Colony : Solothurn	**0.57**	**0.079**	**1.0**

Table 5.2.: Repeatability (model I), variance component as well as variance ratio estimates (model II) (median) along with their 95% HPD intervals for divorce in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year. Residual variance was fixed to 1 for both sexes. Variance ratios: heritability, permanent environment and year effects. The cross-sex covariances and correlations are estimated as between the sexes and hence displayed in the table only once. Data is from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Females	**Males**	***Rfm***
Model I			
Repeatability	0.11 [0.017; 0.19]	0.023 [6.4e-08; 0.09]	
Model II: Variance Components			
Additive Genetic Variance	0.23 [3.8e-08; 0.74]	0.079 [7.2e-09; 0.4]	0.13 [-0.82; 0.94]
Permanent Environment	0.31 [4.3e-08; 0.85]	0.069 [3.8e-09; 0.4]	
Year	0.16 [0.017; 0.41]	0.16 [0.017; 0.41]	
Model II: Variance Ratios			
Heritability	0.046 [7.8e-09; 0.14]	0.017 [1.5e-09; 0.082]	
Permanent Environment	0.061 [8.9e-09; 0.16]	0.015 [8.9e-09; 0.08]	
Year	0.032 [0.0033; 0.077]	0.034 [0.0037; 0.082]	

Table 5.3.: Nest site tenacity (0: different nest; 1: same nest) in both sexes in relation to pair bond status (divorced, widowed, or faithful) from one year to the next. The chi-squared value is displayed for status, colony and the sex by status interaction estimated from a type III Anova, while z-values are displayed for the intercept and sex estimates. Reference levels are: females for sex, divorced for status, and Baden for colony. Statistically significant ($P < 0.05$) estimates are bolded (P-values from the Anova are reported for status, colony, and the sex by status interaction). Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**Z-Value/chi-squared**	**P-Value**
Intercept	**-0.696**	**0.211**	**-3.3**	**< 0.001**
Sex [M]	**0.917**	**0.212**	**4.32**	**< 0.001**
Status			**287.32**	**< 0.001**
Widowed	**1.98**	**0.243**		
Faithful	**4.67**	**0.279**		
Colony			**18.87**	**< 0.001**
Biel	**-0.808**	**0.189**		
Solothurn	**-0.62**	**0.197**		
Sex [M] : Status			**14.1**	**< 0.001**
Sex [M] : Widowed	**0.0745**	**0.303**		
Sex [M] : Faithful	**-0.896**	**0.283**		

5.3.3. *Fitness Consequences of Partner Fidelity*

Divorced individuals had lower subsequent reproductive success than widowed or faithful individuals (Table 5.4, Figure D.6). Divorced individuals laid their clutches later in the season, had fewer chicks hatch and fledge, as well as smaller weighted proportions of surviving fledglings than either widowed or faithful individuals (Table 5.4, Figure D.6). There were no differences in clutch sizes between divorced, widowed or faithful individuals, or between colonies (Table 5.4). There were no sex differences in reproductive success between divorced, widowed or faithful individuals (Table 5.4). Clutches were laid sooner in Solothurn as compared to Biel, and brood sizes at hatching and fledging as well as the weighted proportions of surviving fledglings were smaller in Baden as compared to Biel or Solothurn (Table 5.4). In addition, faithful individuals laid their clutches sooner in the season as compared to divorced or widowed individuals (with faithful individuals as the reference level (estimate ± standard error) contrasts for: [divorced] 0.333 ± 0.035; [widowed] 0.266 ± 0.029), and had higher reproductive success than either divorced or widowed individuals (brood size at hatching: [divorced] -0.081 ± 0.031, [widowed] -0.076 ± 0.029; brood size at fledging: [divorced] -0.132 ± 0.035, [widowed] -0.119 ± 0.032; weighted proportion of surviving fledglings: [divorced] -0.512 ± 0.139, [widowed] -0.429 ± 0.118).

Divorced individuals had greater improvement in reproductive success from one year to the next than either widowed or faithful individuals. Divorced and widowed individuals had a delay in their egg laying dates as compared to faithful individuals (i.e., clutches were laid later in the season in year X+1 as compared to year X), and this delay was greater for widowed than divorced individuals. Divorced individuals had a larger increase in brood size and number of chicks that hatched than widowed or faithful individuals (Table 5.5, Figure D.6). Though the differences were not statistically significant for the brood size at fledging and weighted proportion of surviving fledgling models, the direction of the effects are the same (marginal statistical significance $P < 0.07$). There were no sex or colony differences in the changes in reproductive success between divorced, widowed or faithful individuals (Table 5.5, Figure D.6). In addition, widowed individuals had a greater delay in their egg laying dates than divorced or faithful individuals (with widowed individuals as the reference level contrasts for: [divorced] -0.121 ± 0.058, [faithful] -0.222 ± 0.046), and had lower reproductive success than either divorced or faithful individuals (clutch size: [divorced] 0.124 ± 0.041, [faithful] 0.067 ± 0.031; brood size at hatching: [divorced] 0.188 ± 0.079, [faithful] 0.125 ± 0.059; brood size at fledging: [divorced] 0.178 ± 0.083, [faithful] 0.122 ± 0.063; weighted proportion of surviving fledglings: [divorced] 0.173 ± 0.083, [faithful] 0.118 ± 0.063).

Table 5.4.: Subseuqent reproductive success (year X+1) in relation to pair bond status (divorced, widowed, or faithful). The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant (P < 0.05) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**T-Value or Chisq**	**P-Value**
Laying Date[1]				
Intercept	0.11	0.13	0.79	0.44
Sex [M]	0.0070	0.013	0.53	0.60

Status			**130**	**< 0.001**
Widowed	**-0.068**	**0.038**		
Faithful	**-0.33**	**0.035**		
Colony [Solothurn]	**-0.27**	**0.030**	**-9.0**	**< 0.001**
Clutch Size[2]				
Intercept	**1.0**	**0.031**	**33**	**< 0.001**
Sex [M]	-0.0043	0.020	-0.22	0.83
Status			2.8	0.25
Widowed	0.0073	0.033		
Faithful	0.038	0.027		
Colony			3.1	0.22
Biel	-0.016	0.025		
Solothurn	0.025	0.025		
Brood Size at Hatching[3]				
Intercept	**0.86**	**0.038**	**23**	**< 0.001**
Sex [M]	-0.011	0.022	-0.50	0.62
Status			**11**	**0.0039**
Widowed	**0.0048**	**0.038**		
Faithful	**0.081**	**0.031**		
Colony			**40**	**< 0.001**
Biel	**-0.17**	**0.028**		
Solothurn	**-0.047**	**0.028**		
Brood Size at Fledging[4]				
Intercept	**0.74**	**0.048**	**15**	**< 0.001**
Sex [M]	-0.014	0.024	-0.60	0.55
Status			**23**	**< 0.001**
Widowed	**0.013**	**0.042**		
Faithful	**0.13**	**0.035**		
Colony			**130**	**< 0.001**

Biel	**-0.35**	**0.031**		
Solothurn	**-0.18**	**0.030**		
Weighted Proportion of Surviving Fledglings[5]				
Intercept	**2.0**	**0.20**	**10**	**< 0.001**
Sex [M]	-0.040	0.059	-0.68	0.50
Status			**21**	**< 0.001**
Widowed	**0.090**	**0.15**		
Faithful	**0.52**	**0.14**		
Colony			**170**	**< 0.001**
Biel	**-1.9**	**0.15**		
Solothurn	**-1.3**	**0.14**		

[1] Number of: Observations: 2546; Nests: 1566; Pairs: 930; Individuals: 790; Years: 23

[2] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31

[3] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31

[4] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31

[5] Number of: Observations: 3586; Nests: 2197; Pairs: 1251; Individuals: 1075; Years: 31

Table 5.5.: Changes in reproductive success (year X+1 - year X) in relation to pair bond status (divorced, widowed, or faithful). The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant ($P < 0.05$) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**T-Value or Chisq**	**P-Value**
Laying Date[1]				
Intercept	0.11	0.13	0.79	0.44
Sex [M]	0.0070	0.013	0.53	0.60
Status			**130**	**< 0.001**
Widowed	**-0.068**	**0.038**		

Faithful	**-0.33**	**0.035**		
Colony [Solothurn]	**-0.27**	**0.030**	**-9.0**	**< 0.001**
Clutch Size[2]				
Intercept	**1.0**	**0.031**	**33**	**< 0.001**
Sex [M]	-0.0043	0.020	-0.22	0.83
Status			2.8	0.25
Widowed	0.0073	0.033		
Faithful	0.038	0.027		
Colony			3.1	0.22
Biel	-0.016	0.025		
Solothurn	0.025	0.025		
Brood Size at Hatching[3]				
Intercept	**0.86**	**0.038**	**23**	**< 0.001**
Sex [M]	-0.011	0.022	-0.50	0.62
Status			**11**	**0.0039**
Widowed	**0.0048**	**0.038**		
Faithful	**0.081**	**0.031**		
Colony			**40**	**< 0.001**
Biel	**-0.17**	**0.028**		
Solothurn	**-0.047**	**0.028**		
Brood Size at Fledging[4]				
Intercept	**0.74**	**0.048**	**15**	**< 0.001**
Sex [M]	-0.014	0.024	-0.60	0.55
Status			**23**	**< 0.001**
Widowed	**0.013**	**0.042**		
Faithful	**0.13**	**0.035**		
Colony			**130**	**< 0.001**
Biel	**-0.35**	**0.031**		

Solothurn	**-0.18**	**0.030**		
Weighted Proportion of Surviving Fledglings[5]				
Intercept	**2.0**	**0.20**	**10**	**< 0.001**
Sex [M]	-0.040	0.059	-0.68	0.50
Status			**21**	**< 0.001**
Widowed	**0.090**	**0.15**		
Faithful	**0.52**	**0.14**		
Colony			**170**	**< 0.001**
Biel	**-1.9**	**0.15**		
Solothurn	**-1.3**	**0.14**		

[1] Number of: Observations: 2546; Nests: 1566; Pairs: 930; Individuals: 790; Years: 23

[2] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31

[3] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31

[4] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31

[5] Number of: Observations: 3586; Nests: 2197; Pairs: 1251; Individuals: 1075; Years: 31

5.4. Discussion

In this study, we investigated the patterns, predictors and fitness consequences of mate and nest site fidelity in a Swiss population of Alpine swifts. As expected, and in line with the general trend reported in socially monogamous birds, low reproductive success was a key predictor of divorce, as was young age. Contrary to our expectations, divorce was not, on average, associated with higher reproductive success for either females or males. However, divorced individuals had a greater improvement in reproductive success from one year to the next than those who were widowed, suggesting some benefits or at least fewer costs of actively dissolving a pair bond (divorce) as compared to passive re-pairing following the death of the original partner. Furthermore, the heritability of divorce was estimated to be low in both sexes, suggesting little evolutionary potential of this behaviour in the Alpine swift.

Overall, 16.6% of all Alpine swift pairings ended in divorce, which is comparable to the median divorce rate of 13.4% reported by Jeschke and Kokko (2008) across 158 species. As with the general trend observed in birds, low reproductive success was an important predictor of divorce. This suggests a possible adaptive function of divorce (Culina et al. 2015; Dubois and Cézilly 2002), in that divorce may provide individuals with an opportunity to increase their reproductive success by modifying the initial mating decision. However, reproductive success is determined by various environmental and genetic factors, such as parental age, genetic and phenotypic compatibility, and annual fluctuation in weather and food availability, all of which could play a direct or indirect role in predicting the dissolution of pair bonds.

We found that the probability of divorce was higher for younger rather than older individuals of both sexes. This may be due to the relative inexperience of younger birds, who may be engaging in trial-and-error mate selection. Younger birds may also face challenges associated with completing migration in a timely manner, acquiring a nest site, or synchronising their reproductive behaviours (including nest building) with those of their partner for the first time. Indeed, younger birds tend to have lower reproductive success than older birds (Choudhury 1995), and have a greater potential for improvement with a new partner than older birds (Ens et al. 1993). By contrast, older birds may have gained the experience required for more enduring pair bonds, as they may have already found a compatible mate, and hence may be more likely to remain paired to that compatible partner from one year to the next in order to maximize their reproductive success. This result is consistent with that reported by other studies on long-lived avian species, such as thick-billed murres *Uria lomvia,* for which younger, inexperienced birds are more likely to divorce than older, more experienced birds (Gousy-Leblanc et al. 2023). Although not apparent in our analyses (Figure D.6), Wheelwright & Teplitsky (2017) identified age-specific consequences of divorce, with older females alone benefiting from divorce suggesting that these females may have learned to make more appropriate mate choices.

Although the question of who initiated divorce remains of central importance, such behavioural data are difficult, if not impossible, to obtain and remain beyond the scope of this study. We found that birds who remained with the same partner from one year to the next were also those who were more likely to retain the same nesting site from one year to the next. Interestingly, following divorce or re-pairing after being widowed, males were more likely to retain the same nest site than females. This suggests that male Alpine swifts may be expelling their mates from the nest or that females initiate divorce by leaving the nest site. Indeed, females appear to be the sex initiating divorce in many other monogamous birds (Cézilly et al. 2000; Culina et al. 2015) and are expected to benefit the most from a new mate (Flodin and Blomqvist 2012). For instance, García-Vavas & Sanz (2011) report that divorce in a Mediterranean blue tit *Cyanistes caeruleus* population was initiated by the female's decision to disperse to a higher quality breeding site. It is at present unclear what Alpine swifts compete for regarding specific nesting sites within each colony, but the incentive may be comparable for both sexes (*i.e,* lower parasite load, better thermoregulatory properties).

Many of the hypotheses seeking to explain the frequent occurrences of divorce in animal populations predict fitness benefits for one (i.e., better options or territory hypotheses) or both (i.e., incompatibility hypothesis) members of the former pair. Contrary to our expectations, we found that divorce did not, on average, result in increased subsequent reproductive success for either members of the former pair, with divorced birds performing poorly in the year following the divorce as compared to widowed or faithful birds. This suggests that divorce may be a poor strategy in the Alpine swift. However, our data does not make it possible to accurately identity which partner initiated the divorce, and our approach therefore assumes a mutual decision with equal possible benefits for males and females. Hence, this could mask an effect if only the partner initiating divorce (either the male or the female, depending on the pair) were to benefit from the divorce. The assumption that both members of the pair stand to gain from the divorce is only compatible with the incompatibility hypothesis, making it difficult to rule out the better options or better territories hypotheses entirely. In addition, other studies have shown that newly formed pairs bear higher reproductive costs (i.e., delayed breeding, lower breeding success, and reduced clutch mass) during their first breeding attempt as compared to pairs which remained with the same partner (e.g., blue-footed boobies *Sula nebouxii,* Sánchez-Macouzet et al. 2014). However, in species that produce few high-quality rather than many low-quality offspring, reproductive success is expected to increase with higher coordination between partners that can be achieved only after repeated experience (e.g., oystercatchers *Haematopus ostralegus,* van de Pol et al. 2006). This trend is therefore likely to be driven, at least in part, by the increase reproductive success of pairs with greater familiarity and hence coordination. The low reproductive success of divorced birds in the year following the divorce we identified may therefore also point towards the need to consider the consequences of divorce over multiple years. Indeed, divorce may provide these birds with lifetime fitness benefits not apparent immediately following the divorce. Further studies will be needing to begin disentangling these potential drivers of divorce in long-lived species by considering lifetime rather than single year fitness consequences.

Furthermore, we found that individuals from divorced pairs had greater improvement in reproductive success than widowed individuals, suggesting some benefits or at least fewer costs of divorce than of re-pairing itself. Indeed, the active choice to modify the pairing decision via divorce may enable those individuals to resume breeding earlier and more efficiently than widowed individuals, who may have delayed breeding to seek out the previous (dead) partner. This result could alternatively be due to a regression to the mean effect where individuals with really low reproductive success one year (and who divorce) simply return toward the mean the next year. However, that appears unlikely as restricting the analyses to individuals with null reproductive success in the year X showed no marked differences in reproductive success between divorced, widowed or faithful individuals (Table D.7). Therefore, divorce may be a 'best of a bad job' strategy in this population, with the optimal strategy being to pair with the same partner in good years, when offspring are successfully fledged, and to divorce and pair with a new partner after bad years, when no or few offspring are successfully fledged.

We also report relatively high inter-annual variation in divorce, which is likely driven at least in part by high brood failure in some years due to poor environmental conditions. Indeed, stochastic environmental disturbances are a likely contributor of divorce in this population ("habitat-mediated" hypothesis, Desrochers and Magrath 1993) as has been described in other studies (e.g., warming sea conditions were associated with an increased probability of divorce for pairs with poor reproductive success but also females in successful partnerships in the black-browed albatross *Thalassarche melamophris,* Ventura et al. 2021). Specifically, average temperatures in our study site have been steadily increasing (1.28°C warmer than the 100-year average, Masoero et al., in prep) and have become more variable as a result of climate change, with weather conditions presenting direct consequences on chick fledgling success (Masoero et al. 2024). In recent years, this population of Alpine swifts has also been subject to increased chick mortality due to the hemoparasite *Trypanosoma* spp., resulting in lower-than-expected fledgling success (Cigler et al. 2024). As such, these environmental perturbations are likely to be a contributing factor of divorce in the Alpine swift and warrant additional environmental-focused studies.

Although our data does not make it possible to rule out alternative hypotheses entirely (i.e., one partner being usurped by another individual, Ens et al. 1996), it appears unlikely for divorce in the Alpine swift to be primarily driven by a failure of partners to reconnect after migration (i.e., the musical chairs hypothesis, Dhondt and Adriaensen 1994; Heg et al. 2003). Though relatively little is known about swift social associations during and outside the breeding season, swifts typically arrive to the breeding grounds a month before reproduction begins (Meier et al. 2020), with no expected differences between male and female arrival dates. It is thus unlikely (but not impossible) that partners are failing to synchronise their arrival, though this period may be critical to reestablish pair bonds. In the event of delays, initiating breeding with a new mate rather than waiting for a former mate to arrive, and potentially fail to return, would protect individuals against the possibility of failing to reproduce entirely. Preliminary results have identified one pair which divorced after failing to return from migration in the same time period. Further studies contrasting the arrival dates of partners as well as social interactions in the period following arrival to the breeding grounds would provide much needed information on the speed with which partnerships are (re)established with a same or new partner, and in the event that a former mate does not promptly return. If EPP rates in this population are higher than expected, another open question remains whether or not divorced individuals were engaged in EPP before divorce and then establish a new pair-bond with the secondary partner the following year.

Finally, the heritability of divorce was estimated near-zero in both sexes, with little additive genetic variance in males and only moderate additive genetic variance in females, suggesting little potential for evolution of divorce in this population. Repeatability of divorce was likewise low in males and moderate in females, possibly indicating that females with low reproductive success tend to switch mates to potentially improve their fitness. Our animal model was unable to accurately detect a cross-sex genetic correlation signal, likely due to male additive genetic variance being so small, and due to an overall lack of power. Should EPP prove to be higher than expected in the Alpine swift, this could also have reduced our power to detect heritability of this behaviour. In any case, and as both Wheelwright & Teplitsky (2017) and Germain et al. (2018) highlighted, the heritability of binary traits is challenging to estimate, even with long-term studies (de Villemereuil et al. 2013). As such, and although these results suggest limited scope for an evolutionary response, it is not possible to rule out a genetic basis of divorce in either sex of the Alpine swift.

To conclude, our study suggests that Alpine swift pairs are more likely to end in divorce when individuals are young and when reproductive success is low, and hence when there is greater scope for improvement in reproductive success. Overall, this suggests that these birds may be operating under a win-stay lose-switch decision making paradigm with the intent of divorce being to restore individual reproductive success. Although divorced individuals had lower subsequent reproductive success than widowed or faithful individuals, they also had greater improvements in their reproductive success than widowed individuals. Hence, an active decision to modify the pair bond provided these wild birds with some fitness benefits. Future studies considering the lifetime fitness consequences of divorce will be needed. Finally, our study corroborates previous findings suggesting a limited scope for micro-evolutionary responses of divorce in wild birds.

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Chapter 6

General Discussion

The central aims of my thesis were to investigate how sexual selection operates in both sexes of a species with little apparent sexual dimorphism, the Alpine swift *Tachymarptis melba*, and to evaluate how shared genetic architecture may drive sex-specific trait evolution and responses to selection. Given that the evolution of sexual dimorphism is seen as a potential resolution of sexual conflict, such conflicts have the potential to be especially strong in species with weak or subtle sexual dimorphisms. Hence, I first characterised the sexual dimorphism in morphometric traits, and showed that the Alpine swift is subtly dimorphic with males having 7% longer forks than females and females being 1% heavier than males. I then studied the genetic architecture as well as the evolutionary trajectories of fork length and body mass. I showed that sexual dimorphism in these traits changed over the course of the study such that fork length became more similar between the sexes while body mass diverged. The cross-sex genetic correlation, indicating genetic constraints, was strong for fork length but weak for body mass, suggesting that sex-specific genetic variance may have played a role in this changing sexual dimorphism. Finally, I investigated changes in pairing dynamics shaped by mate switching (divorce) and showed that divorce provides some reproductive benefits for both sexes but shows little microevolutionary potential, with low additive genetic variance in both sexes. Hence, divorce has the potential to generate additional opportunities for sexual selection in both sexes. The results presented in this thesis are however limited by our incomplete knowledge of the biology and ecology of Alpine swifts, owing to their highly aerial lifestyle. Indeed, changes in air density and wind patterns, in the availability and distribution of food resources, as well as in the timing of migration and social assemblages in the overwintering grounds, with many of these changes being nowadays accelerated by global warming, are all likely to play a role in explaining these results by shaping sex-specific selection, requiring further study beyond the scope of this thesis.

6.1. *Evolution of Sexual Dimorphism*

Sexual dimorphism varies widely across the animal kingdom, with incredible variation in its extent and form within bird species specifically. Indeed, in some species the sexes are so similar as to be nearly indistinguishable, whereas in others, the sexes appear so dissimilar as to seem from different species. The widespread occurrence of sexual dimorphism suggests that divergence towards sex-specific adaptive phenotypic optima is often possible (Arnqvist and Rowe 2005; Fairbairn 2007), although the independent evolution of the sexes may be constrained by cross-sex genetic correlations

(r_{fm} Lande 1980). Hence, sexual dimorphism, when selected for, is expected to evolve more readily when r_{fm} is small. However, it remains unclear if such an r_{fm} presents a transient constraint on the evolution of sexual dimorphism, given that the evolution of sexual dimorphism and an r_{fm} approaching zero is seen as a potential resolution of intra-locus sexual conflict. Species with little apparent sexual dimorphism provide an especially interesting avenue to answer such questions, as sexual conflict in these cases should be especially strong and un-resolved.

To begin with, in *Chapter 2* I described the patterns of sexual dimorphism and allometric scaling occurring in morphometric traits in the Alpine swift, a species previously characterized as monomorphic. Counter to this classification, my work identified subtle sexual dimorphisms in morphological traits, such that the Alpine swift may instead by considered a cryptically or weakly dimorphic species. I found that some traits, namely fork length and body mass, have the potential to be shaped by sexual selection: both traits are cryptically dimorphic, are over-expressed in breeding individuals, and fork length displayed negative allometric scaling. Negative allometric scaling is not unexpected in traits serving a courtship signaling function (Rodríguez and Eberhard 2019), as is likely to be the case in the Alpine swift, as courtship traits are not generally selected to emphasize body size. Interestingly, the sex-specific allometric scaling of fork length may have changed over the course of the study, suggesting shifts in the benefits or costs of relatively long forks in males and females. For a highly aerial species such as the Alpine swift, these costs and benefits are likely to be tightly linked to aerodynamic capacities and may point to shifting resource usage between the sexes. Although allometric slopes are generally considered to evolve very slowly (Voje et al. 2014), artificial selection experiments have demonstrated that they can be modified within the span of a few generations in laboratory settings (Houle et al. 2019). My results suggest that allometric scaling can be modified in response to shifting selection in the wild. Further, the sexual dimorphism in fork length and body mass changed over the course of the study: decreasing in fork length and increasing in body mass.

Hence, I more closely investigated fork length in *Chapter 3*. I found that fork length was under directional selection in both sexes, suggesting that this trait may signal aspects of individual condition in both sexes. Indeed, the overall shape of selection appears to be similar and largely positive in both sexes. However, fork length correlated positively with different aspects of fitness for both sexes, reflecting primary investment into reproductive in females (egg volume) and secondary investment in males (weighted proportion of surviving fledglings for males). I therefore suggest that the costs of bearing more deeply forked tails likely differ between the sexes. Indeed, females may be selecting long-forked males that can best deal with costs relating to parental care. However, as there was a trend towards a positive correlation with fitness for females past the egg volume stage, it is also possible that females bear higher (hidden) parental care costs during offspring provisioning than males. Regardless, the size and shape of birds' tails are key to their overall aerodynamic abilities (Fitzpatrick 1999), with fork length in particular having been shown to be under strong selection in many species (Fitzpatrick 1999; Hasegawa and Arai 2020). Hence, fork length in Alpine swifts is certainly shaped by both sexual and natural selection for both sexes. Furthermore, I found that males and females largely share the same genetic architecture for fork length, and that fork length is essentially the same trait in both sexes. This suggests that the sexes should share the same evolutionary trajectory. As selection was positive in both sexes (albeit in relation to different fitness components), we would expect the existing sexual dimorphism in this trait to be maintained, with fork length increasing in both sexes. Contrary to this expectation, sexual dimorphism in fork length has decreased over the course of the study such that female fork length has increased, reflected by the changes in allometric scaling identified in *Chapter 2*, which poses an interesting evolutionary puzzle to be addressed in follow-up studies.

Likewise, I scrutinized mass in *Chapter 4*. I showed that body mass in both sexes was highly weather dependent, with cold and rainy conditions predicting lower body mass at the time of measurement. The highly labial nature of body mass in swifts reflects their dependence on insect prey abundance and availability, which is itself tightly linked to weather conditions, and required the implementation of statistical methods to adjust mass for selection analyses. In addition, I found that males and females do not entirely share the same genetic architecture for body mass. Coupled with selection that differs in shape between the sexes, I suggest that mass therefore has the potential to evolve to sex-specific fitness optima in the Alpine swift, albeit slowly and limited by relatively similar fitness peaks. In line with this expectation, sexual dimorphism in body mass has increased over the course of the study, as shown in *Chapter 2*. Body mass is a trait of key importance in species spending the majority of their time aloft, such as Alpine swifts, and is therefore expected to be under strong selection. Indeed, both natural and sexual selection often favour individuals of larger size and heavier mass (Ronget et al. 2018). Hence, it is especially interesting to have identified this possible difference in selection on mass between the sexes as well as its sex-specific genetic architecture. Although studies estimating sex-specific heritability, selection, and cross-sex genetic correlations are still relatively scarce in wild population, r_{fm} tends to be strongly positive

(Kruuk et al. 2008). To my knowledge, this is the first study to identify possible intra-locus sexual conflict in a weakly dimorphic species.

Taken together, the results from *Chapters 2*, *3* and *4* suggest that sex-specific genetic variance and a weak cross-sex genetic correlation may be important in the evolution of sexual dimorphism, in that the changes in sexual dimorphism in fork length and mass match this prediction. Indeed, Poissant et al. (2010) identified a negative correlation between r_{fm} and sexual dimorphism in a meta-analysis on 488 estimates of r_{fm}. That said, sexual dimorphism in the Alpine swift remains strongest in the trait with the strongest cross-sex genetic correlation, fork length, suggesting rather that cross-sex genetic correlations do not necessarily hamper the evolution of sexual dimorphism. Hence, and while the erosion of cross-sex genetic correlations may facilitate the evolution of sexual dimorphism, as seen for body mass, they may, in some cases, present only transient or negligeable genetic constraints.

6.2. *Mate Choice and the Opportunity for Sexual Selection*

It is necessary to consider the impact of pairing decisions to fully understand sex-specific reproductive success. Indeed, sex-specific investment in competition, mate choice, parental care, and sexual dimorphism vary dramatically across the animal kingdom (Janicke et al. 2016), and this variation deserves our attention and interest. Variations in sexual dimorphism in particular have been linked with the social mating system (Owens and Hartley 1998), such that monogamous species tend to express less sexual dimorphism in plumage coloration and body size than polygamous species (Andersson 1994). Hence, the cryptic sexual dimorphism identified in *Chapter 2* appears unsurprising. However, when both sexes vary in their quality as mates, selection can generate mating competition and selective mate choice in either sex (Parker 1983). Importantly, mate choice need not be a static event occurring only once in an individual's lifetime, even in species with social or genetically monogamous pairings.

As such, in *Chapter 5*, I considered the consequences of mate switching ('divorce') as an emergent property of both sexes and the only way for these otherwise monogamous birds to modify pairing decisions, and hence potentially increase their individual reproductive success. Such lifetime patterns of paring dynamics can inform us as to the mating patterns occurring and generating opportunities for sexual selection. Indeed, high divorce rates have been associated with strong sexual selection (Jeschke and Kokko 2008). I found that approximately 16% of pairings end in divorce, which is only slightly above the median of 13% reported by Jeschke and Kokko (2008). Hence, divorce rate is not especially high in Alpine swifts when compared to other birds in general, but still presents an opportunity for variation in mating success between individuals over the course of their lifetime. In addition, I found that previous reproductive success informed an individual's decision to remate with their old partner or find a new one following a win-stay lose-switch paradigm. Although the heritability of divorce was estimated to be near zero in both sexes, suggesting little scope for microevolutionary potential of this behaviour, the fitness benefits of divorce did outweigh the costs of mate replacement. Hence, and although only capturing one dimension of mate choice, the propensity of individuals to divorce may be generating additional opportunities for sexual selection in the Alpine swift.

6.3. *Environmental Influences*

The results presented throughout this thesis are limited by our incomplete knowledge of the biology and ecology of Alpine swifts, owing to their highly aerial lifestyle. Indeed, we have very limited understanding of what occurs outside the breeding period, including but not limited to migration patterns and timing, social interactions throughout the year, as well as foraging ecology both during and outside the breeding period. Changes in wind patterns as well as in the timing of migration and in the availability and distribution of food resources are all likely to play a role in driving sex-specific selection. For instance, changes in the availability and distribution of food resources have clearly shaped the evolution of body mass in the Alpine swift and may also be shaping the evolution of tail length via niche segregation, although this remains to be clarified. Indeed, global warming has been found to drive changes in body size and shape in numerous species (Ryding et al. 2021; Weeks et al. 2020), such as increased wing length in birds in response to changing wind patterns and air density (Youngflesh et al. 2022), as well as decreases in body mass in response to changing food quantity and availability (Gardner et al. 2011). Importantly, these can also have sex-specific consequences (e.g., greater wing loading in male than female wandering albatrosses *Diomedea exulans* results in differential usage of strong winds, suggesting different foraging strategies, Clay et al. 2020).

In particular, the observed change only in female fork length could be attributed to evolution for both sexes but cryptic evolution on males only due to counteracting environmental effects on males only, or to environmental changes acting more strongly on females with or without microevolution in both sexes. Though the sources of such environmental effects are difficult to elucidate, several examples can be found in the literature. For instance, collisions with cars appear to have generated strong selection for shorter wings in cliff swallows *Petrochelidon pyrrhonota* (Brown and Brown 2013), and trophy hunting has generated intense artificial selection for shorter horns in bighorn sheep *Ovis canadensis* (Pigeon et al. 2016).

6.4. *Limitations & Next Steps*

We have only just begun scratching the surface when it comes to sexual selection and mate choice in Alpine swifts, paving the way to delve more deeply into evolutionary questions which can only readily be investigated with long-term field studies. For instance, the benefits of divorce may only become apparent when considering lifetime fitness rather than yearly reproductive success, especially so in long-lived species. Indeed, the limited fitness benefits of divorce we demonstrated may reflect costs immediately following the divorce, without capturing overall lifetime fitness benefits. Having now established that divorce does occur in the Alpine swift, this species presents an interesting model with which to answer such questions. Divorce could also explain the differing patterns of selection I identified acting on sex-specific body mass in *Chapter 4*, as this pattern could arise as a result of divorce if older males paired with younger females following a divorce. Several other questions based on the results of this thesis remain to be explored, some of which I briefly outline here.

First, colour is a fundamental component of visual communication, and can signal an individual's age (Cline et al. 2016), dominance status (Santos et al. 2011), or correlate with aspects of fitness (Doucet et al. 2004). Such sexually selected phenotypic variations can be especially noticeable in bird plumage (e.g., male birds of paradise are notoriously colourful). Despite receiving less attention than brightly coloured plumage, achromatic feathers (i.e., pigment-free white plumage) may also serve a signalling function used in mate choice. For example, male black-capped chickadees *Poecile atricapilla* have brighter white plumage than females (Mennill et al. 2003), and males with the brightest white feathers where preferred as mates and sired the most offspring within a clutch (Doucet et al. 2004). Because birds perceive colours differently than humans, including perception into the ultraviolet (UV) spectrum (300-400 nm: Cuthill et al. 2000), it is plausible for this dimension of dimorphism and mate choice to have been previously overlooked. For instance, in the blue tit *Parus caeruleus*, reflectance spectrometry has revealed that females and males differ in plumage colour in the UV range (Hunt et al. 1998). This avenue of research is especially interesting in the Alpine swift, as they have an achromatic throat breast patch, varying levels of melanization of the rachis of the feathers of the breast patch and are likely to rely on UV signaling (e.g., nestling skin UV reflectance has been shown to reflect body condition, and parents utilize this cue to determine food allocation, Bize et al. 2006a). Although I did not explore this avenue of research due to lack of time, data collection on the size and UV reflectance of the throat patch using photography has been undertaken. Preliminary results suggest that females have 4% larger throat patches than males, although this difference was not statistically significant. As another possibly female-biased trait, the signling value, sex-specifc selection and cross-sex genetic correlation of throat and breast patch colouration as well as UV reflectance would be especially interesting to investigate.

Second, one prediction of the mutual sexual selection hypothesis is that it should result in assortative mating (Trivers 1972). As results from *Chapter 3* suggest potential mutual sexual selection on the basis of fork length, and results from *Chapter 4* suggest possibly size-disassortative pairing on the basis of body mass, investigating assortative paring will be a logical follow-up to the present studies. Assortative mating occurs when similar individuals pair with each other and can be determined by a positive correlation between the trait in both partners of a pair (Class et al. 2017). Further, divorce rates have been found to correlate positively with mutual ornamentation in sexually monomorphic birds (Jeschke and Kokko 2008; Kraaijeveld 2003). Hence, it will be interesting to investigate the link between fork length and divorce (as well as other secondary sexual traits such as coloration) in a future study. This would provide additional support for the better options hypothesis of divorce, which at present we cannot rule out in the Alpine swift.

Third, more research will be needed to disentangle nest site fidelity from partner fidelity. Indeed, because divorce is often companied by a change in nest site, and since divorced birds tend to initiate their clutches later in the season, they may have fewer choices of nest sites and hence be confined to less desirable ('poorer-quality') sites, explaining why divorced birds had lower reproductive success than widowed or faithful birds. In order to investigate this further in the Alpine swift we must first categorize nest site quality and identify the conditions which make a nest site more desirable, which I began doing by collecting data on nest shape and nesting material composition. These preliminary results suggest that older nests, as measured by the height of the nest, given that swifts reuse and add to their nests over the course of several years, is associated with increased fledgling success. Hence, a research question which emerges in this area is, *does divorce occur in an attempt to secure an older, higher quality nest?* Additional studies will be needed to further investigate the effects of environmental (i.e., climate change) and social (i.e., sex-specific arrival dates to the breeding grounds, intra-sexual competition for nesting sites) effects in driving divorce in the Alpine swift.

It should also be noted that the results presented in this thesis are correlative, and hence can be strengthened by a follow-up experimental approach. For instance, the results presented in *Chapter 3* suggest that fork length may be a mutually sexually selected trait, as it correlates positively with aspect of reproductive success in both sexes. By performing experimental manipulations of fork length in both sexes and investigating pairing decisions as well as reproductive investment in response to this manipulation in both sexes, we may be able to demonstrate that fork length is under sexual selection in one or both sexes (i.e., demonstrate a preference for mates with longer forks, as well as costs of longer forks in terms of reproductive investment which are expected to differ between the sexes). Hence, it will be necessary to establish more conclusively the role that these traits may play in mate choice.

6.5. *Conclusion*

To conclude, my thesis has highlighted subtle sexual dimorphism in a bird previously categorized as monomorphic. My results suggest small yet rapid changes of fork length and body mass under sexual selection, with implications for the future impacts of sexual selection on population dynamics and pairing decisions. Overall, my thesis highlights the need to consider both sexes in studies of sexual selection and sexual conflict and to broaden our current scope of model organisms to explicitly include species with cryptic dimorphisms, as only then can we reach a more complete understanding of these complex evolutionary processes.

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Appendix A

Supplementary for Chapter 2 ‘Temporal changes in sex-specific cryptic sexual dimorphism and allometric scaling in the long-lived Alpine swift *Tachymarptis melba*’

A.1. Sexual Dimorphism

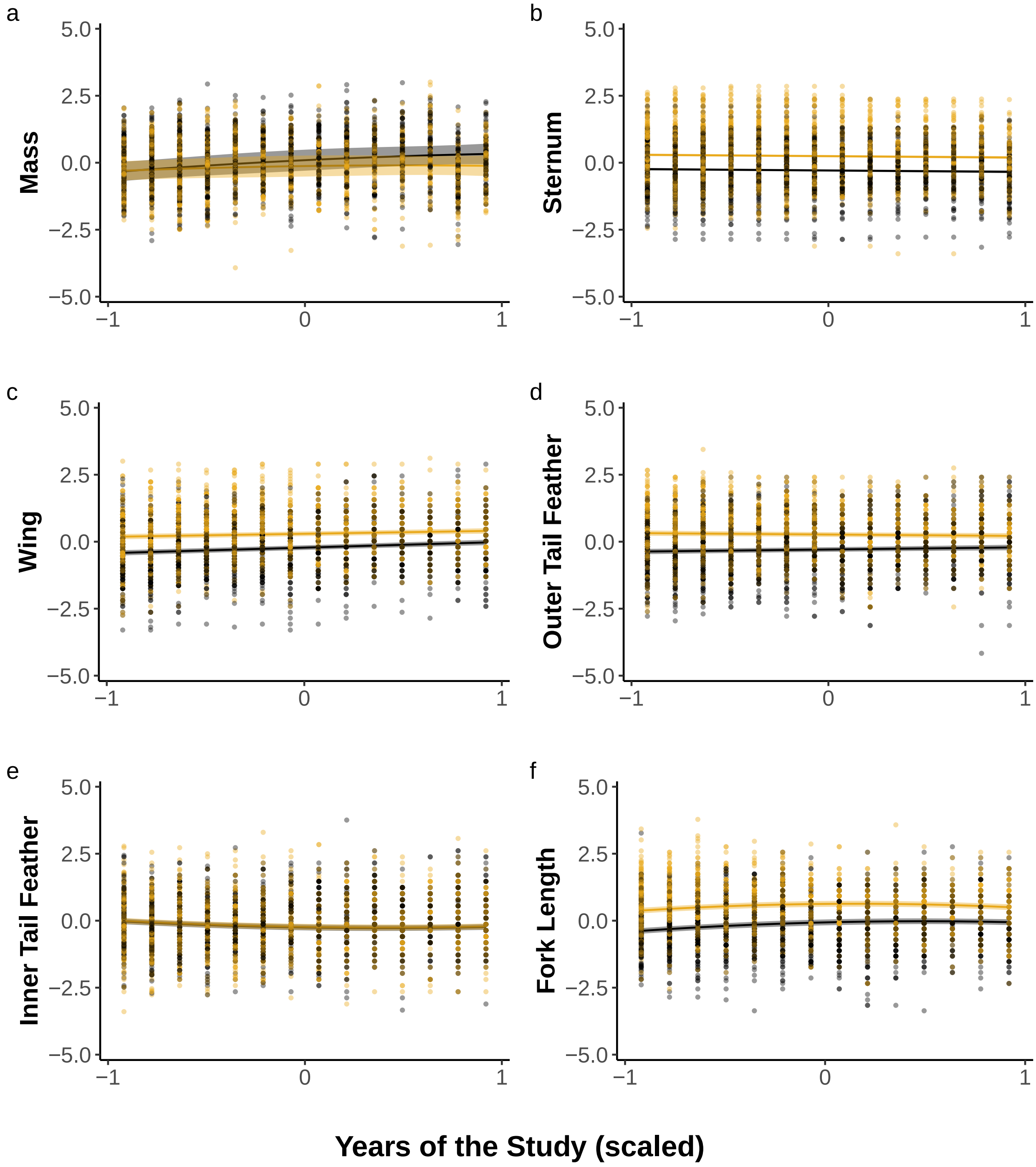


Figure A.1.: Changes in sexual dimorphism over the course of the study in morphometric traits: adjusted body mass, sternum length, wing length, outer and inner tail feather length, and fork length. Females in black, males in gold. The data points correspond to the raw data.

Table A.1.: Simplified linear (LMM) mixed-effects models assessing the sexual dimorphism in morphometric traits between periods of the study (1999-2010 & 2011-2021): adjusted body mass, sternum length, wing length, outer and inner tail feather length, and fork length. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, first period (1999-2010) for period, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	Standard Error	T-Value	P-Value
Mass[1]				
Intercept	**-0.46**	**0.19**	**-2.4**	**0.025**
Sex	0.099	0.053	1.9	0.061
Period	**0.61**	**0.27**	**2.2**	**0.036**
Breeding Status	**0.24**	**0.015**	**16**	**< 0.001**
Colony	-0.066	0.039	-1.7	0.095
Sex : Period	**-0.49**	**0.045**	**-11**	**< 0.001**
Sex : Breeding Status	**-0.15**	**0.021**	**-7.1**	**< 0.001**
Period : Breeding Status	**-0.17**	**0.032**	**-5.4**	**< 0.001**
Sex : Period : Breeding Status	**0.15**	**0.045**	**3.3**	**< 0.001**
Sternum Length[2]				
Intercept	**-0.35**	**0.044**	**-7.9**	**< 0.001**
Sex	**0.53**	**0.026**	**21**	**< 0.001**
Period	0.049	0.066	0.75	0.46
Breeding Status	**0.12**	**0.044**	**2.7**	**0.0061**
Colony	**0.18**	**0.026**	**6.9**	**< 0.001**
Period : Breeding Status	**-0.17**	**0.072**	**-2.4**	**0.015**
Wing Length[3]				
Intercept	**-0.70**	**0.055**	**-13**	**< 0.001**
Sex	**0.68**	**0.056**	**12**	**< 0.001**
Period	**0.45**	**0.063**	**7.1**	**< 0.001**
Breeding Status	**0.36**	**0.025**	**14**	**< 0.001**
Colony	0.015	0.047	0.32	0.75

Sex : Period	**-0.12**	**0.034**	**-3.4**	**< 0.001**
Sex : Breeding Status	**-0.12**	**0.032**	**-3.7**	**< 0.001**
Period : Breeding Status	**-0.13**	**0.037**	**-3.6**	**< 0.001**
Outer Tail Feather Length[4]				
Intercept	**-0.64**	**0.055**	**-12**	**< 0.001**
Sex	**0.73**	**0.059**	**12**	**< 0.001**
Period	**0.15**	**0.065**	**2.3**	**0.023**
Breeding Status	**0.38**	**0.031**	**12**	**< 0.001**
Colony	0.074	0.048	1.5	0.12
Sex : Period	**-0.15**	**0.041**	**-3.7**	**< 0.001**
Sex : Breeding Status	**-0.11**	**0.040**	**-2.7**	**0.0063**
Period : Breeding Status	**-0.11**	**0.045**	**-2.4**	**0.015**
Inner Tail Feather Length[5]				
Intercept	**-0.16**	**0.071**	**-2.3**	**0.027**
Sex	0.057	0.052	1.1	0.27
Period	-0.10	0.087	-1.2	0.25
Breeding Status	**0.12**	**0.026**	**4.5**	**< 0.001**
Colony	**0.29**	**0.048**	**6.1**	**< 0.001**
Sex : Period	-0.089	0.050	-1.8	0.078
Fork Length[6]				
Intercept	**-0.57**	**0.081**	**-7.1**	**< 0.001**
Sex	**0.79**	**0.059**	**13**	**< 0.001**
Period	0.17	0.10	1.7	0.11
Breeding Status	**0.29**	**0.032**	**9.1**	**< 0.001**
Colony	**-0.18**	**0.045**	**-4.1**	**< 0.001**
Sex : Period	**-0.093**	**0.046**	**-2.0**	**0.042**
Sex : Breeding Status	**-0.11**	**0.045**	**-2.4**	**0.018**

*1*Number of: Observations: 4195; Individuals: 1079; Years: 23 *2*Number of: Observations: 5355; Years: 24 *3*Number of: Observations: 5333; Individuals: 1450; Years: 24 *4*Number of: Oservations: 5284; Individuals: 1447; Years: 24 *5*Number of: Observations: 5263; Individuals: 1445; Years: 24 *6*Number of: Observations: 5282; Individuals: 1445; Years: 24

Table A.2.: Sexual dimorphism in morphometric traits over both periods (1999-2010 & 2011-2021): adjusted body mass, sternum length, wing length, outer tail feather length, inner tail feather length, fork length. Calculated using the formula (mean male trait – female meal trait) / mean female trait * 100 such that a positive value denotes male-biased expression and a negative value denotes female-biased expression. Bolded estimates denoted a statistically significant change in dimorphism over the course of the study.

	Adjusted Mass	**Sternum**	**Wing**	**Outer Tail**	**Inner Tail**	**Fork**
Overall						
Sexual Dimorphism	**-0.72**	1.6	**1.1**	**1.9**	0.033	**7.3**
Period 1: 1999-2009						
Sexual Dimorphism	**-0.34**	1.6	**1.2**	**2.1**	-0.015	**8.2**
Period 2: 2010-2021						
Sexual Dimorphism	**-1.5**	1.6	**1.1**	**1.7**	-0.076	**6.7**

Table A.3.: Full linear (LMM) mixed-effects models assessing the sexual dimorphism in morphometric traits: adjusted body mass, sternum length, wing length, outer and inner tail feather length, and fork length. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T-Value**	**P-Value**
Mass*1*				
Intercept	-0.14	0.14	-1.0	0.31
Breeding Status	**-0.19**	**0.064**	**-3.0**	**0.0031**
Sex [M]	**0.13**	**0.019**	**6.8**	**< 0.001**
Year	**32**	**10**	**3.1**	**0.0048**

Year^2	-3.2	9.7	-0.33	0.74
Colony [Solothurn]	-0.086	0.049	-1.8	0.079
Sex [M] : Breeding Status	-0.013	0.025	-0.52	0.61
Sex [M] : Year	**-26**	**2.4**	**-10**	**< 0.001**
Sex [M] : Year^2	**-5.8**	**2.0**	**-2.8**	**0.0044**
Breeding Status : Year	**-9.2**	**1.8**	**-5.2**	**< 0.001**
Breeding Status : Year^2	**-3.4**	**1.5**	**-2.3**	**0.020**
Sex [M] : Colony [Solothurn]	0.042	0.084	0.50	0.62
Sex [M] : Breeding Status : Year	**9.1**	**2.3**	**3.9**	**< 0.001**
Sex [M] : Breeding Status : Year^2	**7.3**	**2.0**	**3.6**	**< 0.001**
Sternum Length[2]				
Intercept	**-0.32**	**0.049**	**-6.7**	**< 0.001**
Breeding Status	**0.53**	**0.068**	**7.8**	**< 0.001**
Sex [M]	0.035	0.050	0.70	0.48
Year	-2.8	3.4	-0.82	0.41
Year^2	4.1	3.6	1.1	0.25
Colony [Solothurn]	**0.20**	**0.037**	**5.5**	**< 0.001**
Sex [M] : Breeding Status	0.032	0.070	0.46	0.64
Sex [M] : Year	4.9	4.8	1.0	0.31
Sex [M] : Year^2	-3.6	5.1	-0.71	0.48
Breeding Status : Year	-1.5	3.7	-0.40	0.69
Breeding Status : Year^2	-4.4	3.9	-1.1	0.25
Sex [M] : Colony [Solothurn]	-0.048	0.053	-0.91	0.36
Sex [M] : Breeding Status : Year	-5.4	5.3	-1.0	0.31
Sex [M] : Breeding Status : Year^2	4.2	5.5	0.75	0.45
Wing Length[3]				
Intercept	**-0.46**	**0.052**	**-8.9**	**< 0.001**
Breeding Status	**0.58**	**0.069**	**8.4**	**< 0.001**
Sex [M]	**0.26**	**0.025**	**10**	**< 0.001**

Year	**25**	**2.8**	**9.0**	**< 0.001**
Year^2	3.8	2.3	1.7	0.097
Colony [Solothurn]	0.0045	0.063	0.072	0.94
Sex [M] : Breeding Status	**-0.074**	**0.035**	**-2.1**	**0.034**
Sex [M] : Year	**-12**	**3.2**	**-3.9**	**< 0.001**
Sex [M] : Year^2	**-5.9**	**2.5**	**-2.4**	**0.018**
Breeding Status : Year	**-12**	**2.1**	**-5.5**	**< 0.001**
Breeding Status : Year^2	-2.8	1.8	-1.6	0.12
Sex [M] : Colony [Solothurn]	0.022	0.095	0.23	0.82
Sex [M] : Breeding Status : Year	**6.1**	**2.9**	**2.1**	**0.034**
Sex [M] : Breeding Status : Year^2	**5.0**	**2.5**	**2.0**	**0.045**
Outer Tail Feather Length[4]				
Intercept	**-0.56**	**0.054**	**-10**	**< 0.001**
Breeding Status	**0.64**	**0.072**	**9.0**	**< 0.001**
Sex [M]	**0.32**	**0.031**	**10**	**< 0.001**
Year	**8.6**	**3.1**	**2.7**	**0.0066**
Year^2	-1.1	2.6	-0.44	0.66
Colony [Solothurn]	0.073	0.065	1.1	0.26
Sex [M] : Breeding Status	**-0.084**	**0.043**	**-2.0**	**0.050**
Sex [M] : Year	**-9.7**	**3.8**	**-2.5**	**0.011**
Sex [M] : Year^2	-2.7	3.1	-0.86	0.39
Breeding Status : Year	-3.4	2.6	-1.3	0.19
Breeding Status : Year^2	-1.6	2.3	-0.72	0.47
Sex [M] : Colony [Solothurn]	0.0015	0.096	0.016	0.99
Sex [M] : Breeding Status : Year	0.048	3.5	0.014	0.99
Sex [M] : Breeding Status : Year^2	2.0	3.1	0.64	0.52
Inner Tail Feather Length[5]				
Intercept	**-0.22**	**0.061**	**-3.7**	**< 0.001**
Breeding Status	0.054	0.077	0.70	0.49

Sex [M]	**0.13**	**0.040**	**3.3**	**< 0.001**
Year	-4.6	4.0	-1.2	0.25
Year^2	5.5	3.4	1.6	0.11
Colony [Solothurn]	**0.29**	**0.065**	**4.4**	**< 0.001**
Sex [M] : Breeding Status	-0.048	0.055	-0.87	0.39
Sex [M] : Year	4.5	4.7	0.95	0.34
Sex [M] : Year^2	0.75	4.0	0.19	0.85
Breeding Status : Year	-1.2	3.4	-0.36	0.72
Breeding Status : Year^2	1.9	2.9	0.67	0.50
Sex [M] : Colony [Solothurn]	0.0094	0.096	0.098	0.92
Sex [M] : Breeding Status : Year	-8.3	4.5	-1.8	0.069
Sex [M] : Breeding Status : Year^2	2.2	4.1	0.54	0.59
Fork Length[6]				
Intercept	**-0.46**	**0.057**	**-8.1**	**< 0.001**
Breeding Status	**0.71**	**0.071**	**10**	**< 0.001**
Sex [M]	**0.26**	**0.035**	**7.5**	**< 0.001**
Year	**14**	**3.6**	**4.0**	**< 0.001**
Year^2	**-6.8**	**3.1**	**-2.2**	**0.027**
Colony [Solothurn]	**-0.18**	**0.061**	**-3.0**	**0.0026**
Sex [M] : Breeding Status	-0.062	0.048	-1.3	0.20
Sex [M] : Year	**-14**	**4.2**	**-3.3**	**0.0011**
Sex [M] : Year^2	-4.8	3.5	-1.4	0.17
Breeding Status : Year	-3.9	3.0	-1.3	0.19
Breeding Status : Year^2	-3.8	2.5	-1.5	0.13
Sex [M] : Colony [Solothurn]	0.0011	0.090	0.013	0.99
Sex [M] : Breeding Status : Year	7.6	4.0	1.9	0.055
Sex [M] : Breeding Status : Year^2	2.4	3.5	0.68	0.50

[1] Number of: Observations: 4195; Individuals: 1079; Years: 23 [2] Number of: Observations: 5355; Years: 24 [3] Number of: Observations: 5333; Individuals: 1450; Years: 24 [4] Number of: Observations: 5284; Individuals: 1447; Years: 24 [5] Number of: Observations: 5263; Individuals: 1445; Years: 24 [6] Number of: Observations: 5282; Individuals: 1445; Years: 24

A.2. Allometry

A.2.1. Scalling to Sternum Length

Table A.4.: Linear (LMM) mixed-effects models assessing the allometric scaling of morphometric traits in relation to sternum length on a log-log scale: wing length, outer and inner tail feather length, and fork length. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T-Value**	**P-Value**
Wing Length[1]				
Intercept	**-0.17**	**0.05**	**-3.59**	**< 0.001**
Sex [M]	**0.48**	**0.05**	**8.78**	**< 0.001**
Sternum	**0.06**	**0.02**	**3.16**	**0.002**
Year	**0.20**	**0.03**	**6.16**	**< 0.001**
Colony [Solothurn]	0.01	0.05	0.14	0.887
Sex [M] : Year	**-0.11**	**0.03**	**-3.84**	**< 0.001**
Outer Tail Feather Length[2]				
Intercept	**-0.19**	**0.05**	**-4.04**	**< 0.001**
Sex [M]	**0.49**	**0.05**	**9.22**	**< 0.001**
Sternum	**0.09**	**0.02**	**4.38**	**< 0.001**
Year	0.04	0.03	1.27	0.208
Colony [Solothurn]	0.07	0.05	1.31	0.191
Sex [M] : Year	**-0.14**	**0.03**	**-4.13**	**< 0.001**
Inner Tail Feather Length[3]				

Intercept	-0.04	0.05	-0.73	0.466
Sex [M]	-0.05	0.05	-0.90	0.371
Sternum	**0.09**	**0.02**	**3.85**	**< 0.001**
Year	**-8.05**	**2.58**	**-3.12**	**0.004**
Year ^2	**7.84**	**2.45**	**3.20**	**0.004**
Colony [Solothurn]	**0.29**	**0.05**	**5.44**	**< 0.001**
Fork Length[4]				
Intercept	**-0.19**	**0.05**	**-3.83**	**< 0.001**
Sex [M]	**0.62**	**0.05**	**12.25**	**< 0.001**
Sternum	0.04	0.02	1.80	0.071
Year	**9.74**	**2.64**	**3.70**	**< 0.001**
Year ^2	**-8.91**	**2.43**	**-3.67**	**< 0.001**
Colony [Solothurn]	**-0.18**	**0.05**	**-3.54**	**< 0.001**
Sex [M] : Year	**-5.48**	**2.21**	**-2.48**	**0.013**
Sex [M] : Year ^2	-1.76	1.74	-1.01	0.311

[1]Number of observations: 3714; Number of individuals: 1192; Number of years: 24 [2]Number of observations: 4534; Number of individuals: 1302; Number of years: 24 [3]Number of observations: 4520; Number of individuals: 1300; Number of years: 24 [4]Number of observations: 4527; Number of individuals: 1300; Number of years: 24

Table A.5.: Linear (LMM) mixed-effects models assessing the allometric scaling of morphometric traits in relation to sternum length and correcting for body mass on a log-log scale: wing length, outer and inner tail feather length, and fork length. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T-Value**	**P-Value**
Wing Length[1]				
Intercept	**-0.22**	**0.05**	**-4.68**	**< 0.001**
Sex [M]	**0.49**	**0.05**	**9.27**	**< 0.001**
Sternum	**0.09**	**0.02**	**4.30**	**< 0.001**

Mass	**0.05**	**0.01**	**7.43**	**< 0.001**
Colony [Solothurn]	**0.28**	**0.03**	**8.36**	**< 0.001**
Year	-0.02	0.05	-0.37	0.714
Sex [M] : Year	**-0.13**	**0.03**	**-4.44**	**< 0.001**
Sternum : Year	**-0.03**	**0.01**	**-2.34**	**0.019**
Outer Tail Feather Length[2]				
Intercept	**-0.24**	**0.05**	**-5.08**	**< 0.001**
Sex [M]	**0.52**	**0.05**	**9.94**	**< 0.001**
Sternum	**0.10**	**0.02**	**4.72**	**< 0.001**
Mass	**0.04**	**0.01**	**4.62**	**< 0.001**
Colony [Solothurn]	0.03	0.05	0.58	0.562
Year	**0.13**	**0.03**	**3.78**	**< 0.001**
Sex [M] : Year	**-0.16**	**0.03**	**-5.00**	**< 0.001**
Inner Tail Feather Length[3]				
Intercept	-0.09	0.05	-1.75	0.083
Sex [M]	-0.04	0.05	-0.84	0.398
Sternum	**0.10**	**0.02**	**4.19**	**< 0.001**
Mass	**0.03**	**0.01**	**2.49**	**0.013**
Colony [Solothurn]	**0.27**	**0.05**	**5.26**	**< 0.001**
Year	-0.06	0.04	-1.30	0.205
Fork Length[4]				
Intercept	**-0.19**	**0.06**	**-3.26**	**0.002**
Sex [M]	**0.64**	**0.05**	**13.21**	**< 0.001**
Sternum	0.04	0.02	1.65	0.099
Mass	**0.03**	**0.01**	**3.49**	**< 0.001**
Colony [Solothurn]	**-0.21**	**0.05**	**-4.40**	**< 0.001**
Year	**0.18**	**0.05**	**3.24**	**0.003**
Sex [M] : Year	**-0.12**	**0.03**	**-3.53**	**< 0.001**

[1] Number of observations: 4180; Number of individuals: 1304; Number of years: 22 [2] Number of observations: 4164; Number of individuals: 1302; Number of years: 22 [3] Number of observations: 4149; Number of individuals: 1301; Number of years: 22 [4] Number of observations: 4152; Number of individuals: 1301; Number of years: 22

A.2.2. Scalling to Wing Length

Table A.6.: Simplified allometric scaling for each trait in relation to wing length in both sexes on a log-log scale contrasting both periods of the study (1999-2010 & 2011-2021). Females are the reference level for sex and Biel is the reference level for colony. Effects deemed statistically significant are bolded.

	Estimate	**Standard Error**	**T-Value**	**P-Value**
Outer Tail Feather Length				
Intercept	**-0.09**	**0.04**	**-2.09**	**0.039**
Sex [M]	**0.35**	**0.04**	**8.36**	**< 0.001**
Wing	**0.44**	**0.02**	**21.33**	**< 0.001**
Colony [solothurn]	0.08	0.04	1.88	0.060
Period [2]	**-0.15**	**0.05**	**-3.29**	**0.003**
Sex [M] : Wing	-0.06	0.03	-1.93	0.054
Inner Tail Feather Length				
Intercept	0.08	0.07	1.17	0.249
Sex [M]	**-0.14**	**0.04**	**-3.08**	**0.002**
Wing	**0.33**	**0.02**	**17.35**	**< 0.001**
Colony [solothurn]	**0.30**	**0.05**	**6.59**	**< 0.001**
Period [2]	**-0.22**	**0.09**	**-2.57**	**0.017**
Fork Length				
Intercept	**-0.18**	**0.08**	**-2.29**	**0.029**
Sex [M]	**0.50**	**0.05**	**11.07**	**< 0.001**
Wing	**0.28**	**0.03**	**10.03**	**< 0.001**

Colony [solothurn]	**-0.17**	**0.05**	**-3.87**	**< 0.001**
Period [2]	0.04	0.10	0.37	0.711
Sex [M] : Wing	**-0.08**	**0.04**	**-2.10**	**0.036**
Wing : Period [2]	-0.05	0.03	-1.64	0.101
Sex [M] : Wing : Period [2]	**0.11**	**0.05**	**2.52**	**0.012**

Table A.7.: Allometric scaling (full models) for each trait in relation to wing length in both sexes on a log-log scale, modeling year as a continuous variable. Females are the reference level for sex and Biel is the reference level for colony. Effects deemed statistically significant are bolded. Data spans 1999-2021.

	Estimate	Standard Error	T-Value	P-Value
Outer Tail Feather Length[1]				
Intercept	**-0.16**	**0.04**	**-3.74**	**< 0.001**
Sex [M]	**0.34**	**0.05**	**6.55**	**< 0.001**
Wing	**0.43**	**0.02**	**20.34**	**< 0.001**
Year	-0.84	1.86	-0.45	0.655
Year^2	-2.65	1.60	-1.65	0.106
Colony [solothurn]	0.07	0.06	1.15	0.251
Sex [M] : Wing	-0.04	0.03	-1.42	0.155
Sex [M] : Year	**-5.88**	**1.80**	**-3.27**	**0.001**
Sex [M] : Year^2	-0.24	1.35	-0.18	0.857
Wing : Year	0.89	1.12	0.79	0.430
Wing : Year^2	**2.37**	**0.91**	**2.62**	**0.009**
Sex [M] : Colony [solothurn]	0.01	0.08	0.15	0.879
Sex [M] : Wing : Year	0.22	1.60	0.14	0.889
Sex [M] : Wing : Year^2	-1.80	1.32	-1.37	0.172
Inner Tail Feather Length[2]				
Intercept	-0.01	0.05	-0.27	0.789
Sex [M]	**-0.15**	**0.06**	**-2.66**	**0.008**

Wing	**0.35**	**0.03**	**13.63**	**< 0.001**
Year	**-8.05**	**2.26**	**-3.57**	**< 0.001**
Year^2	**6.03**	**1.99**	**3.03**	**0.004**
Colony [solothurn]	**0.27**	**0.06**	**4.35**	**< 0.001**
Sex [M] : Wing	-0.05	0.04	-1.33	0.185
Sex [M] : Year	-2.19	2.20	-1.00	0.320
Sex [M] : Year^2	3.15	1.74	1.81	0.070
Wing : Year	1.84	1.40	1.31	0.189
Wing : Year^2	1.35	1.18	1.15	0.251
Sex [M] : Colony [solothurn]	0.04	0.09	0.46	0.649
Sex [M] : Wing : Year	-2.92	2.01	-1.45	0.146
Sex [M] : Wing : Year^2	0.35	1.71	0.21	0.836
Fork Length[3]				
Intercept	**-0.16**	**0.05**	**-3.19**	**0.002**
Sex [M]	**0.51**	**0.06**	**8.91**	**< 0.001**
Wing	**0.24**	**0.02**	**10.35**	**< 0.001**
Year	**6.85**	**2.31**	**2.96**	**0.005**
Year^2	**-9.50**	**2.04**	**-4.66**	**< 0.001**
Colony [solothurn]	**-0.17**	**0.06**	**-2.74**	**0.006**
Sex [M] : Wing	-0.02	0.03	-0.55	0.580
Sex [M] : Year	**-4.29**	**2.00**	**-2.15**	**0.032**
Sex [M] : Year^2	-1.79	1.51	-1.18	0.237
Wing : Year	-1.27	1.25	-1.02	0.310
Wing : Year^2	1.67	1.02	1.64	0.101
Sex [M] : Colony [solothurn]	-0.01	0.09	-0.11	0.912
Sex [M] : Wing : Year	2.88	1.79	1.61	0.107
Sex [M] : Wing : Year^2	-2.60	1.48	-1.76	0.078

[1] Number of: Observations: 4534; Individuals: 1302; Years: 24 [2] Number of: Observations: 4520; Individuals: 1300; Years: 24 [3] Number of: Observations: 4527; Individuals: 1300; Years: 24

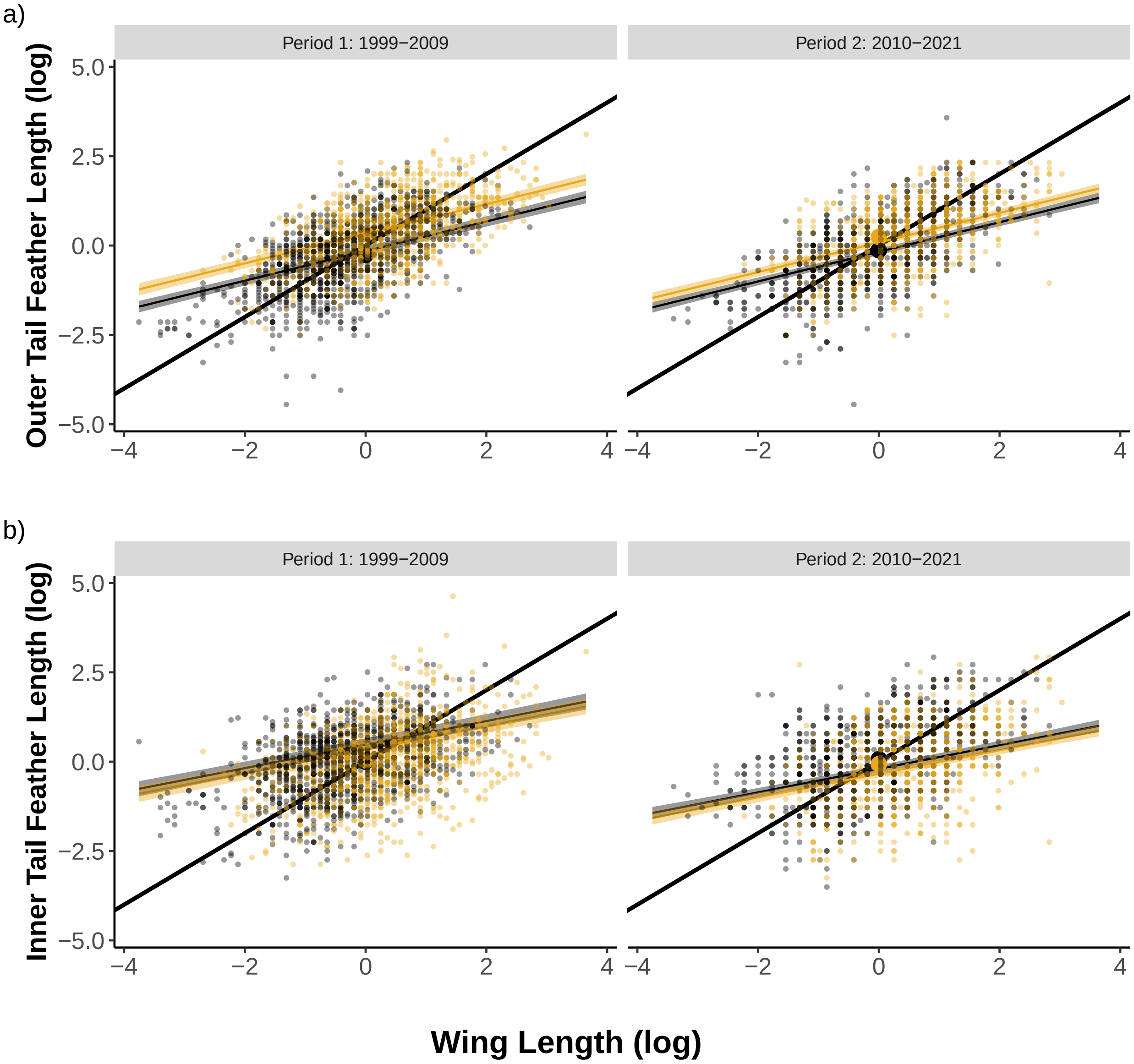


Figure A.2.: Sex-specific changes in allometric scalling of outer and inner tail feather in relation to wing length. Females in black, males in gold. The mean outer and inner tail feather length per sex per period are displayed. The data points correspond to the raw data. The solid black lines denote isometry.

Appendix B

Supplementary for Chapter 3 'Shared genetic architecture and sex-specific fitness consequences of forked tails in the Alpine swift *Tachymarptis melba*'

B.1. Selection Analyses

Table B.1.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between fork depth and breeding status (binomial distribution), laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), the weighted proportion of surviving fledglings (binomial distribution) and overwinter survival (binomial distribution), with the inclusion of non statisticaly significant interations terms and quadratic effects. The T-Value is reported for the laying date model, while the Z-Value is reported for all other models. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T- or Z-Value**	**P-Value**
Breeding Status[1]				
Intercept	**2.65**	**0.21**	**12.59**	**< 0.001**
Sex [M]	**-0.47**	**0.14**	**-3.40**	**< 0.001**
Fork	**22.94**	**5.61**	**4.09**	**< 0.001**
Fork^2	**-12.11**	**3.24**	**-3.73**	**< 0.001**
Colony [Solothurn]	**-0.32**	**0.15**	**-2.22**	**0.027**
Sex [M] : Fork	0.05	0.11	0.45	0.656
Sex [M] : Colony [Solothurn]	0.20	0.20	0.97	0.332
Laying Date[2]				
Intercept	0.17	0.12	1.36	0.187
Fork [Female]	-1.25	1.04	-1.20	0.232
Fork^2 [Female]	-0.09	1.00	-0.09	0.932
Fork [Male]	-1.42	0.92	-1.55	0.122
Fork^2 [Male]	-0.21	0.98	-0.21	0.831
Wing [Female]	-1.53	1.07	-1.43	0.154
Wing^2 [Female]	0.45	1.09	0.42	0.676
Wing [Male]	0.85	0.93	0.92	0.361
Wing^2 [Male]	-0.88	0.94	-0.94	0.348
Colony [Solothurn]	**-0.34**	**0.05**	**-6.58**	**< 0.001**

Fork [Female] : Wing [Female]	0.00	0.03	-0.07	0.943
Fork [Male] : Wing [Male]	0.03	0.02	1.31	0.192
Egg Volume[3]				
Intercept	**5.77**	**0.03**	**210.97**	**< 0.001**
Fork [Female]	**3.47**	**0.85**	**4.10**	**< 0.001**
Fork^2 [Female]	0.72	0.73	0.98	0.327
Fork [Male]	0.91	0.62	1.46	0.144
Fork^2 [Male]	-0.32	0.59	-0.54	0.591
Wing [Female]	**2.53**	**0.96**	**2.62**	**0.009**
Wing^2 [Female]	0.02	0.88	0.02	0.986
Wing [Male]	0.86	0.68	1.27	0.206
Wing^2 [Male]	-0.44	0.67	-0.65	0.516
Colony [Solothurn]	**0.07**	**0.04**	**2.07**	**0.039**
Fork [Female] : Wing [Female]	0.00	0.01	-0.28	0.776
Fork [Male] : Wing [Male]	-0.01	0.01	-0.90	0.369
Clutch Size[4]				
Intercept	**0.99**	**0.02**	**48.16**	**< 0.001**
Fork [Female]	0.33	0.66	0.49	0.621
Fork^2 [Female]	-0.67	0.71	-0.95	0.342
Fork [Male]	0.16	0.64	0.26	0.796
Fork^2 [Male]	0.16	0.71	0.23	0.820
Wing [Female]	0.18	0.65	0.28	0.777
Wing^2 [Female]	-0.19	0.71	-0.27	0.786
Wing [Male]	0.20	0.63	0.31	0.755
Wing^2 [Male]	-0.08	0.66	-0.12	0.906
Colony [Solothurn]	0.05	0.03	1.72	0.085
Fork [Female] : Wing [Female]	0.01	0.02	0.48	0.633
Fork [Male] : Wing [Male]	0.00	0.02	-0.10	0.924

Brood Size at Hatching[5]

Intercept	**0.63**	**0.04**	**14.77**	**< 0.001**
Fork [Female]	0.67	0.80	0.84	0.403
Fork^2 [Female]	-0.73	0.84	-0.87	0.383
Fork [Male]	**2.13**	**0.78**	**2.75**	**0.006**
Fork^2 [Male]	0.52	0.79	0.66	0.509
Wing [Female]	0.10	0.80	0.12	0.902
Wing^2 [Female]	-0.45	0.86	-0.52	0.603
Wing [Male]	**-1.74**	**0.76**	**-2.28**	**0.022**
Wing^2 [Male]	1.28	0.77	1.66	0.097
Colony [Solothurn]	**0.18**	**0.04**	**5.06**	**< 0.001**
Fork [Female] : Wing [Female]	0.02	0.02	1.05	0.292
Fork [Male] : Wing [Male]	-0.03	0.02	-1.37	0.170

Brood Size at Fledgling[6]

Intercept	**0.34**	**0.06**	**5.36**	**< 0.001**
Fork [Female]	1.18	0.94	1.26	0.206
Fork^2 [Female]	-0.98	0.97	-1.01	0.314
Fork [Male]	**1.89**	**0.91**	**2.08**	**0.038**
Fork^2 [Male]	0.64	0.98	0.65	0.517
Wing [Female]	0.52	0.92	0.57	0.570
Wing^2 [Female]	-0.16	0.98	-0.16	0.870
Wing [Male]	-1.29	0.90	-1.43	0.152
Wing^2 [Male]	1.54	0.90	1.71	0.086
Colony [Solothurn]	**0.22**	**0.04**	**5.19**	**< 0.001**
Fork [Female] : Wing [Female]	0.03	0.03	1.24	0.214
Fork [Male] : Wing [Male]	-0.02	0.02	-1.01	0.312

Weighted Proportion of Surviving Fledglings[7]

Intercept	0.21	0.17	1.27	0.204
Fork [Female]	3.48	2.46	1.42	0.157

Fork^2 [Female]	-1.20	2.37	-0.51	0.613
Fork [Male]	**7.05**	**2.36**	**2.99**	**0.003**
Fork^2 [Male]	3.00	2.16	1.39	0.165
Wing [Female]	1.10	2.54	0.43	0.666
Wing^2 [Female]	0.69	2.56	0.27	0.786
Wing [Male]	-3.87	2.53	-1.53	0.126
Wing^2 [Male]	3.85	2.47	1.56	0.118
Colony [Solothurn]	**0.58**	**0.14**	**4.24**	**< 0.001**
Fork [Female] : Wing [Female]	0.08	0.06	1.26	0.209
Fork [Male] : Wing [Male]	-0.06	0.06	-0.98	0.329
Overwinter Survival[8]				
Intercept	**0.71**	**0.22**	**3.17**	**0.002**
Sex [M]	0.05	0.07	0.65	0.513
Fork	-0.64	3.79	-0.17	0.866
Fork^2	-1.46	2.44	-0.60	0.549
Colony [Solothurn]	**0.33**	**0.07**	**4.54**	**< 0.001**
Sex [M] : Fork	-0.02	0.08	-0.29	0.775

[1]Number of; Observations: 5220; Individuals: 1364; Years: 24 [2]Number of; Observations: 1880; Females: 575; Males: 540; Years: 24 [3]Number of; Observations: 4894; Nests: 1599; Females: 558; Males: 518; Years: 23 [4]Number of; Observations: 1875; Females: 575; Males: 541; Years: 24 [5]Number of; Observations: 1885; Females: 576; Males: 541; Years: 24 [6]Number of; Observations: 1882; Females: 576; Males: 540; Years: 24 [7]Number of; Observations: 1872; Females: 576; Males: 540; Years: 24 [8]Number of; Observations: 4481; Individuals: 1224; Years: 24

Table B.2.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between fork depth relative to inner (left) and outer (right) tail feather length as well as breeding status (binomial distribution), laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), the weighted proportion of surviving fledglings (binomial distribution) and overwinter survival (binomial distribution). The T-Value is reported for the laying date model, while the Z-Value is reported for all other models. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Inner Tail Feather				**Outer Tail Feather**			
	Estimate	**SE**	**T-/Z-Value**	**P-Value**	**Estimate**	**SE**	**T-/Z-Value**	**P-Value**
Breeding Status								
Intercept	**2.55**	**0.21**	**12.28**	**< 0.001**	**2.56**	**0.21**	**12.30**	**< 0.001**
Sex [M]	**-0.30**	**0.11**	**-2.84**	**0.004**	**-0.30**	**0.11**	**-2.84**	**0.005**
Relative Fork Depth	**18.40**	**3.68**	**4.99**	**< 0.001**	**18.50**	**3.67**	**5.05**	**< 0.001**
Relative Fork Depth ^2	**-9.26**	**2.62**	**-3.53**	**< 0.001**	**-10.59**	**2.76**	**-3.83**	**< 0.001**
Colony [Solothurn]	-0.19	0.10	-1.79	0.074	-0.19	0.11	-1.80	0.071
Laying Date								
Intercept	0.18	0.12	1.46	0.155	0.18	0.12	1.47	0.155
Relative Fork Depth [Female]	-0.03	0.02	-1.24	0.214	-0.03	0.02	-1.24	0.216
Relative Fork Depth [Male]	-0.03	0.02	-1.63	0.103	-0.03	0.02	-1.72	0.086

Wing [Female]	-0.04	0.02	-1.68	0.093	-0.04	0.02	-1.67	0.095
Wing [Male]	0.02	0.02	0.96	0.336	0.02	0.02	0.97	0.332
Colony [Solothurn]	**-0.34**	**0.05**	**-6.76**	**< 0.001**	**-0.34**	**0.05**	**-6.78**	**< 0.001**
Egg Volume								
Intercept	**5.76**	**0.03**	**213.98**	**< 0.001**	**5.76**	**0.03**	**214.01**	**< 0.001**
Relative Fork Depth [Female]	**0.04**	**0.01**	**3.69**	**< 0.001**	**0.04**	**0.01**	**3.65**	**< 0.001**
Relative Fork Depth [Male]	0.01	0.01	0.67	0.506	0.01	0.01	0.84	0.401
Wing [Female]	**0.05**	**0.01**	**3.38**	**< 0.001**	**0.05**	**0.01**	**3.38**	**< 0.001**
Wing [Male]	0.01	0.01	1.57	0.116	0.01	0.01	1.55	0.123
Colony [Solothurn]	**0.07**	**0.04**	**2.04**	**0.042**	**0.07**	**0.04**	**2.05**	**0.041**
Clutch Size								
Intercept	**0.99**	**0.02**	**51.87**	**< 0.001**	**0.99**	**0.02**	**51.85**	**< 0.001**
Relative Fork Depth [Female]	0.01	0.01	0.67	0.506	0.01	0.01	0.70	0.483
Relative Fork Depth [Male]	0.00	0.01	0.32	0.753	0.00	0.01	0.30	0.763
Wing [Female]	0.00	0.01	0.32	0.747	0.00	0.01	0.31	0.753
Wing [Male]	0.00	0.01	0.36	0.718	0.01	0.01	0.36	0.717
Colony [Solothurn]	0.05	0.03	1.79	0.074	0.05	0.03	1.79	0.074

Brood Size at Hatching								
Intercept	**0.63**	**0.04**	**15.04**	**< 0.001**	**0.63**	**0.04**	**15.00**	**< 0.001**
Relative Fork Depth [Female]	0.01	0.02	0.80	0.425	0.01	0.02	0.81	0.415
Relative Fork Depth [Male]	**0.04**	**0.02**	**2.43**	**0.015**	**0.04**	**0.02**	**2.44**	**0.015**
Wing [Female]	0.00	0.02	0.27	0.787	0.00	0.02	0.25	0.801
Wing [Male]	**-0.04**	**0.02**	**-2.12**	**0.034**	**-0.04**	**0.02**	**-2.12**	**0.034**
Colony [Solothurn]	**0.19**	**0.04**	**5.23**	**< 0.001**	**0.19**	**0.04**	**5.25**	**< 0.001**
Brood Size at Fledgling								
Intercept	**0.34**	**0.06**	**5.40**	**< 0.001**	**0.34**	**0.06**	**5.40**	**< 0.001**
Relative Fork Depth [Female]	0.02	0.02	1.01	0.310	0.02	0.02	1.03	0.303
Relative Fork Depth [Male]	0.04	0.02	1.80	0.073	0.04	0.02	1.77	0.076
Wing [Female]	0.02	0.02	0.88	0.378	0.02	0.02	0.87	0.384
Wing [Male]	-0.03	0.02	-1.29	0.196	-0.03	0.02	-1.29	0.197
Colony [Solothurn]	**0.23**	**0.04**	**5.32**	**< 0.001**	**0.23**	**0.04**	**5.32**	**< 0.001**
Weighted Proportion of Surviving Fledglings								
Intercept	0.22	0.17	1.28	0.201	0.21	0.17	1.28	0.201
Relative Fork Depth [Female]	0.05	0.05	0.93	0.354	0.05	0.05	0.92	0.356
Relative Fork Depth [Male]	**0.14**	**0.05**	**2.87**	**0.004**	**0.14**	**0.05**	**2.79**	**0.005**

Wing [Female]	0.04	0.06	0.77	0.442	0.04	0.06	0.76	0.448
Wing [Male]	-0.07	0.06	-1.33	0.184	-0.07	0.06	-1.32	0.187
Colony [Solothurn]	**0.60**	**0.14**	**4.32**	**< 0.001**	**0.60**	**0.14**	**4.33**	**< 0.001**
Overwinter Survival								
Intercept	**0.71**	**0.22**	**3.19**	**0.001**	**0.71**	**0.22**	**3.19**	**0.001**
Sex [M]	0.05	0.07	0.64	0.521	0.05	0.07	0.65	0.516
Relative Fork Depth1	-0.01	0.04	-0.21	0.837	-0.01	0.04	-0.23	0.821
Colony [Solothurn]	**0.33**	**0.07**	**4.52**	**< 0.001**	**0.33**	**0.07**	**4.52**	**< 0.001**

Table B.3.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between fork depth and breeding status (binomial distribution), laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), the weighted proportion of surviving fledglings (binomial distribution) and overwinter survival (binomial distribution), without wing length as a fixed effect. The T-Value is reported for the laying date model, while the Z-Value is reported for all other models. Statistically significant estimates ($P < 0.05$) were bolded. The reference levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-2021.

	Estimate	**Standard Error**	**T- or Z-Value**	**P-Value**
Breeding Status				
Intercept	**2.60**	**0.21**	**12.66**	**< 0.001**
Sex [M]	**-0.38**	**0.11**	**-3.55**	**< 0.001**
Fork Length	**24.80**	**3.78**	**6.56**	**< 0.001**
Fork Length ^2	**-12.96**	**2.85**	**-4.54**	**< 0.001**
Colony [Solothurn]	**-0.22**	**0.10**	**-2.15**	**0.032**
Laying Date				
Intercept	0.18	0.12	1.44	0.161
Fork Depth [Female]	-0.04	0.02	-1.63	0.105
Fork Depth [Male]	-0.02	0.02	-1.22	0.222
Colony [Solothurn]	**-0.34**	**0.05**	**-6.68**	**< 0.001**
Egg Volume				
Intercept	**5.76**	**0.03**	**209.61**	**< 0.001**
Fork Depth [Female]	**0.05**	**0.01**	**4.64**	**< 0.001**
Fork Depth [Male]	0.01	0.01	1.58	0.114
Colony [Solothurn]	**0.08**	**0.04**	**2.12**	**0.034**
Clutch Size				
Intercept	**0.99**	**0.02**	**52.16**	**< 0.001**
Fork Depth [Female]	0.01	0.01	0.63	0.529
Fork Depth [Male]	0.00	0.01	0.36	0.720

Colony [Solothurn]	0.05	0.03	1.77	0.076
Brood Size at Hatching				
Intercept	**0.63**	**0.04**	**15.17**	**< 0.001**
Fork Depth [Female]	0.02	0.02	0.90	0.368
Fork Depth [Male]	**0.04**	**0.02**	**2.08**	**0.037**
Colony [Solothurn]	**0.18**	**0.04**	**5.00**	**< 0.001**
Brood Size at Fledgling				
Intercept	**0.34**	**0.06**	**5.43**	**< 0.001**
Fork Depth [Female]	0.03	0.02	1.55	0.121
Fork Depth [Male]	0.03	0.02	1.70	0.090
Colony [Solothurn]	**0.22**	**0.04**	**5.21**	**< 0.001**
Weighted Proportion of Surviving Fledglings				
Intercept	0.22	0.17	1.31	0.191
Fork Depth [Female]	0.09	0.05	1.62	0.106
Fork Depth [Male]	**0.14**	**0.05**	**2.74**	**0.006**
Colony [Solothurn]	**0.58**	**0.14**	**4.23**	**< 0.001**
Overwinter Survival				
Intercept	**0.71**	**0.22**	**3.19**	**0.001**
Sex [M]	0.05	0.07	0.70	0.485
Fork Length	-0.02	0.04	-0.60	0.546
Colony [Solothurn]	**0.33**	**0.07**	**4.53**	**< 0.001**

B.2. Quantitative Genetic Analyses

B.2.1. Pedigree

Table B.4.: Summary statistics of the pruned social pedigree used in the quantitative genetic analyses. The pedigree was generated using the R package *pedantics*. The pedigree was built using data collected between 1999 and 2021 in a Swiss population of Alpine swifts from two colonies, Biel and Solothurn.

	Sample Size
Total Sample Size	1396
Total Maternities	590
Total Paternities	571
Total Full Siblings	280
Total Maternal Siblings	580
Total Paternal Siblings	577
Total Pedigree Depth	5

B.2.2. Main model modifications

Table B.5.: Estimates (median) and 95% credible intervals (Bayesian model in R package MCMCglmm) for the relationships between fork depth and fixed effects for male and female swifts with the inclusion of age effects. Estimates with 95% CIs that exclude 0 are deemed significant and bolded. Female is the reference level for sex, and Biel is the reference level for Colony.

	Estimate	**Lower 95% HDPI**	**Lower 95% HDPI**
Intercept	**-0.23**	**-0.34**	**-0.11**
Sex [M]	**0.64**	**0.51**	**0.75**
Year	**7.35**	**2.07**	**11.97**
Year^2	**-10.69**	**-14.35**	**-6.91**
Age	**6.40**	**3.82**	**9.29**
Age^2	**-8.23**	**-9.68**	**-6.64**

Colony [Solothurn]	-0.14	-0.29	0.01
Sex [M] : Year	**-5.77**	**-11.31**	**-0.01**
Sex [M] : Year^2	-1.56	-4.55	1.97
Sex [M] : Age	-1.66	-5.32	2.28
Sex [M] : Age^2	**4.10**	**1.91**	**6.24**
Sex [M] : Colony [Solothurn]	-0.05	-0.22	0.13

Table B.6.: Variance component as well as variance ratio estimates (median) along with their 95% HDP intervals of fork depth in Alpine swifts after conditioning on individual age. Results are pooled across the sexes. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment and year effects.

	Females	**Males**	R_{fm}
Variance Components			
Additive Genetic Variance	0.53 [0.4; 0.65]	0.41 [0.29; 0.53]	0.88 [0.74; 0.99]
Permanent Environment	0.14 [0.074; 0.22]	0.15 [0.071; 0.24]	
Year	0.014 [0.0064; 0.027]	0.013 [0.006; 0.026]	0.89 [0.67; 1]
Residual	0.2 [0.18; 0.21]	0.2 [0.18; 0.21]	
Variance Ratios			
Heritability	0.6 [0.49; 0.69]	0.53 [0.4; 0.64]	
Permanent Environment	0.15 [0.081; 0.26]	0.2 [0.081; 0.31]	
Year	0.016 [0.0068; 0.031]	0.017 [0.0074; 0.033]	

Table B.7.: Variance component and 95% HDP intervals of fork depth in female and male Alpine swifts estimated using the R package *asreml*. Base model: model with a single estimate pooled across the sexes. Full model: model estimating sex-specific effects as well as the cross-sex genetic correlation. Fixed model: model estimating sex-specific effects with the cross-sex genetic correlation fixed to 1. Log-likelihood ratio test (LRT): Full - Base LRT = 0.135; Fixed - Base LRT = 1.

	Estimate	**Standard Error**	**Z-Ratio**
Base Model			
Year	0.04	0.01	3.17
Permanent Environment	0.11	0.03	3.67
Additive Genetic Variance	0.56	0.05	11.48
Residual [F]	0.21	0.01	31.15
Residual [M]	0.20	0.01	30.88
Full Model			
Year	0.04	0.01	3.18
Permanent Environment [F]	0.08	0.05	1.42
Permanent Environment [M]	0.09	0.06	1.69
Cross-sex Genetic Correlation	0.92	0.09	10.75
Additive Genetic Variance [F]	0.64	0.08	8.24
Additive Genetic Variance [M]	0.51	0.07	6.83
Residual [F]	0.20	0.01	31.13
Residual [M]	0.20	0.01	30.80
Fixed Model			
Year	0.04	0.01	3.18
Permanent Environment [F]	0.09	0.05	1.86
Permanent Environment [M]	0.13	0.05	2.55
Cross-sex Genetic Correlation	1.00	NA	NA
Additive Genetic Variance [F]	0.63	0.07	8.44
Additive Genetic Variance [M]	0.47	0.07	7.10

Residual [F]	0.20	0.01	31.13
Residual [M]	0.20	0.01	30.80

Table B.8.: Variance component as well as variance ratio estimates (median, mean and mode of the posterior distribution) along with their 95% HDP intervals of fork depth in female and male Alpine swifts.Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment and year effects.

	Females	**Males**	$\boldsymbol{R_{fm}}$
Median - Variance Components			
Additive Genetic Variance	0.58 [0.45; 0.68]	0.46 [0.34; 0.56]	0.89 [0.76; 0.99]
Permanent Environemnt	0.13 [0.059; 0.21]	0.14 [0.064; 0.21]	
Year	0.014 [0.0061; 0.027]	0.014 [0.0053; 0.026]	0.89 [0.65; 1]
Residual	0.2 [0.19; 0.22]	0.2 [0.19; 0.21]	
Median - Variance Ratios			
Heritability	0.62 [0.53; 0.71]	0.57 [0.45; 0.66]	
Permanent Environment	0.14 [0.067; 0.23]	0.17 [0.067; 0.27]	
Year	0.015 [0.0063; 0.028]	0.017 [0.0065; 0.031]	
Mean - Variance Components			
Additive Genetic Variance	0.58 [0.45; 0.68]	0.46 [0.34; 0.56]	0.88 [0.76; 0.99]
Permanent Environemnt	0.13 [0.059; 0.21]	0.14 [0.064; 0.21]	
Year	0.015 [0.0061; 0.027]	0.015 [0.0053; 0.026]	0.86 [0.65; 1]
Residual	0.2 [0.19; 0.22]	0.2 [0.19; 0.21]	
Mean - Variance Ratios			
Heritability	0.62 [0.53; 0.71]	0.57 [0.45; 0.66]	
Permanent Environment	0.14 [0.067; 0.23]	0.17 [0.067; 0.27]	
Year	0.015 [0.0063; 0.028]	0.017 [0.0065; 0.031]	
Mode - Variance Components			

Additive Genetic Variance	0.57 [0.45; 0.68]	0.44 [0.34; 0.56]	0.94 [0.76; 0.99]
Permanent Environemnt	0.12 [0.059; 0.21]	0.11 [0.064; 0.21]	
Year	0.013 [0.0061; 0.027]	0.014 [0.0053; 0.026]	0.9 [0.65; 1]
Residual	0.21 [0.19; 0.22]	0.2 [0.19; 0.21]	
Mode - Variance Ratios			
Heritability	0.62 [0.53; 0.71]	0.57 [0.45; 0.66]	
Permanent Environment	0.14 [0.067; 0.23]	0.17 [0.067; 0.27]	
Year	0.015 [0.0063; 0.028]	0.017 [0.0065; 0.031]	

Table B.9.: Variance component as well as variance ratio estimates (median) along with their 95% HDP intervals of fork depth in Alpine swifts. Results are pooled across the sexes. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment and year effects.

	Estimate	**95% HPDI**
Variance Components		
Additive Genetic Variance	0.53	[0.44; 0.62]
Permanent Environment	0.13	[0.08; 0.18]
Year	0.062	[0.032; 0.11]
Residual	0.2	[0.19; 0.21]
Variance Ratios		
Heritability	0.57	[0.5; 0.64]
Permanent Environment	0.14	[0.086; 0.2]
Year	0.068	[0.036; 0.11]

B.2.3. Relative fork depth models

Table B.10.: Variance component and ratio estimates (median) along with their 95% HDP intervals of relative fork depth (ratio of fork length to inner tail feather length) in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment and year effects.

	Females	**Males**	$\boldsymbol{R_{fm}}$
Variance Components			
Additive Genetic Variance	0.5 [0.39; 0.61]	0.42 [0.32; 0.53]	0.89 [0.76; 0.99]
Permanent Environment	0.14 [0.066; 0.21]	0.14 [0.072; 0.22]	
Year	0.04 [0.016; 0.072]	0.054 [0.024; 0.094]	0.96 [0.87; 1]
Residual	0.23 [0.22; 0.25]	0.24 [0.23; 0.26]	
Variance Ratios			
Heritability	0.55 [0.45; 0.64]	0.49 [0.39; 0.59]	
Permanent Environment	0.15 [0.075; 0.24]	0.16 [0.075; 0.25]	
Year	0.044 [0.018; 0.076]	0.062 [0.032; 0.11]	

Table B.11.: Variance component and ratio estimates (median) along with their 95% HDP intervals of relative fork depth (ratio of fork length to outer tail feather length) in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment and year effects.

	Females	**Males**	$\boldsymbol{R_{fm}}$
Variance Components			
Additive Genetic Variance	0.54 [0.4; 0.65]	0.42 [0.31; 0.52]	0.9 [0.76; 1]
Permanent Environment	0.14 [0.07; 0.22]	0.13 [0.07; 0.21]	
Year	0.042 [0.02; 0.078]	0.054 [0.025; 0.094]	0.96 [0.88; 1]
Residual	0.24 [0.23; 0.26]	0.24 [0.22; 0.25]	
Variance Ratios			

Heritability	0.55 [0.45; 0.64]	0.5 [0.39; 0.6]
Permanent Environment	0.15 [0.07; 0.23]	0.16 [0.07; 0.25]
Year	0.044 [0.021; 0.077]	0.064 [0.032; 0.11]

B.2.4. Microevolution

Table B.12.: Percentage of the estimated slopes for female-trait and male-trait fork length which is less than or greater than that simulated under genetic drift alone, when considering all available data (left) or only birth years after 1999 (right).

	All birth years		**Birth years after 1999 (inclusive)**	
	Female-trait	**Male-trait**	**Female-trait**	**Male-trait**
Less than drift	3.47	7.47	24.40	35.60
Greater than drift	96.53	92.53	75.60	64.40

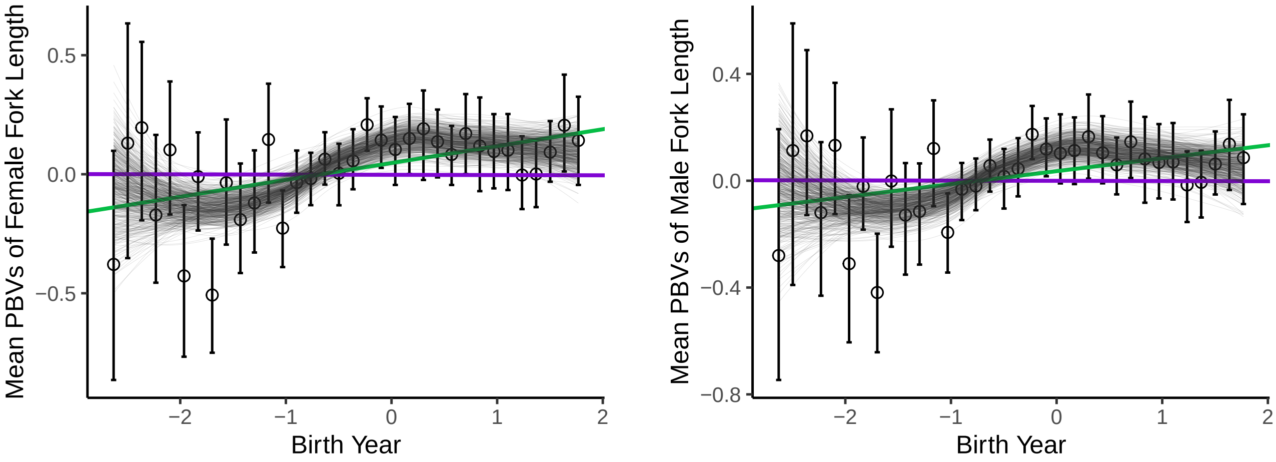


Figure B.1.: Changes in mean predicted breeding values for Alpine swifts in relation to their birth year from 1985 to 2018. The green line represent the median of predicted changes from linear regressions, while the purple line represents the predict changes under genetic drift alone from simulated random breeding values. Circles with bars are the median of PBV per birth year with their associated 95% HPD intervals. Thin grey lines are a loess fit on the random draw of 500 iterations (out of 1500) from the posterior distribution of average PBV per birth year.

The slope is more positive than expected under drift for both female-trait and male-trait, when looking both at the complete data set and when considering only birth years after 1999.

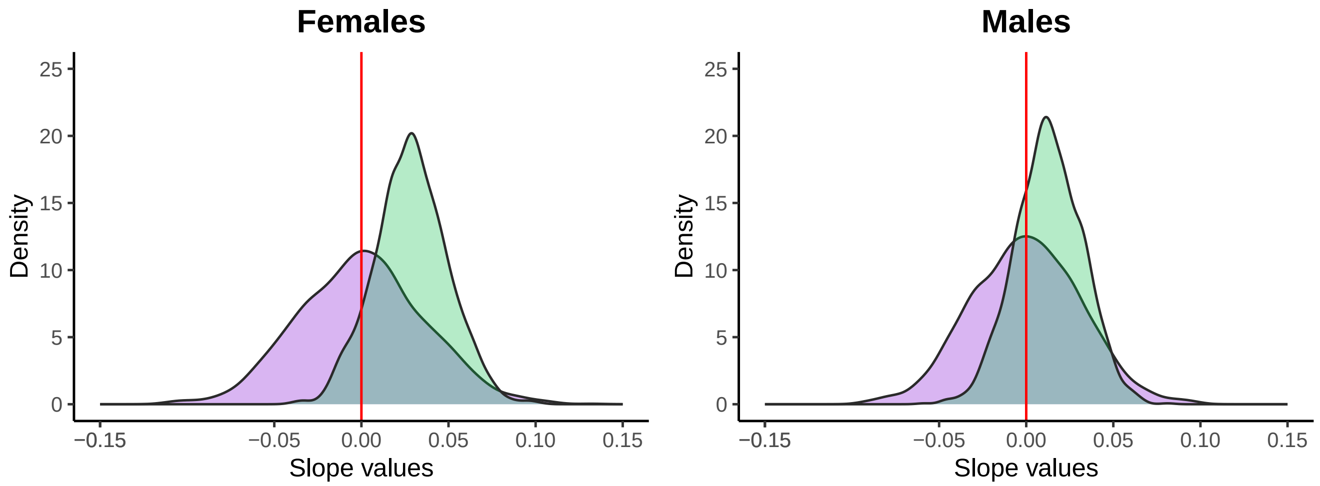


Figure B.2.: Posterior density plots for the slopes of mean predicted breeding values for female and male Alpine swifts in relation to their birth year from 1985 to 2018. The green filled distributions represents the posterior distribution of slopes in mean cohort breeding values, while the purple filled distributions represents the predict changes under genetic drift alone from simulated random breeding values.

Table B.13.: Posterior estimates of the slopes for the changes in predicted breeding values over the course of the study for female-trait and male-trait fork length in Alpine Swifts. Values represent the median of the slopes for the predicted breeding values obtained followed by the 95% Bayesian posterior interval of highest density in brackets, when considering all available data (top) or only birth years after 1999 (bottom).

	Female-Trait		**Male-Trait**	
	Predictd	**Drift**	**Predicted**	**Drift**
All birth years				
Intercept	0.0162 (-0.0532, 0.0792)	-0.00244 (-0.0823, 0.074)	-0.105 (-0.552, 0.316)	-0.000399 (-0.069, 0.07)
Birth Year	0.765 (0.367, 1.22)	-0.00103 (-0.0697, 0.0591)	0.762 (0.343, 1.21)	-0.000738 (-0.0533, 0.0556)
Birth years after 1999 (inclusive)				
Intercept	-0.0222 (-0.129, 0.0894)	-0.00355 (-0.0767, 0.077)	-0.657 (-1.37, 0.172)	0.00105 (-0.0674, 0.068)
Birth Year	1.28 (0.27, 2.33)	-0.00018 (-0.0662, 0.0714)	1.26 (0.209, 2.33)	0.000144 (-0.0619, 0.0581)

Appendix C

Supplementary for Chapter 4 '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'

C.1. Causes of variation in adult swift body mass and body condition

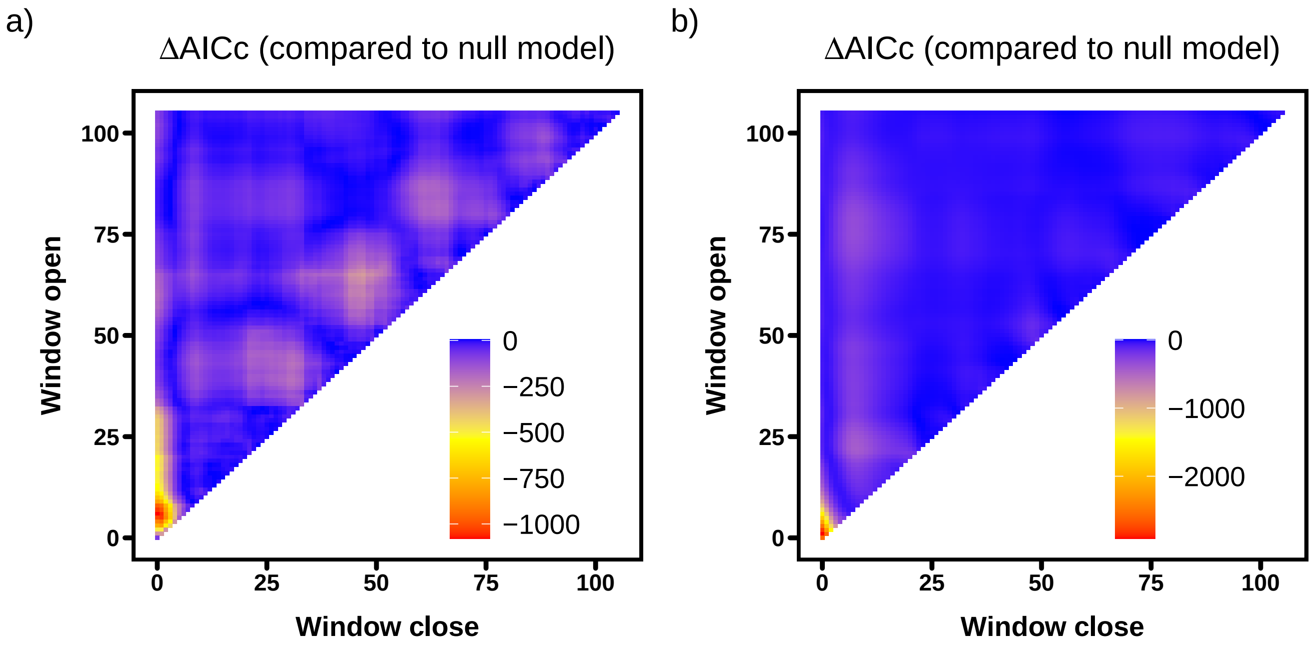


Figure C.1.: Output from the climwin model describing the effects of a) rainfall and b) ambient temperature on adult mass in the Alpine swift (models ran on 5387 weights from 1079 individuals measured between 1999 and 2021). The sliding windows were allowed to vary by day from the day of body mass measurement (0) up to 105 days before the measurement (April 15th, corresponding to average return dates to the breeding colonies from the overwintering grounds). The plots show the spread of delta AICc compared between a null model with no weather effects and each climate window being tested. The lowest delta AICc in red is indicative of best fit. While the delta AIC plot for rain is quite spotty, suggesting the possible presence of a second window, there is no biological reason to expect a second, further removed signal. For rain, the window from 0-6 days is the best supported, while for temperature, the window from 0-1 days is the best supported, with the lowest delta AICc.

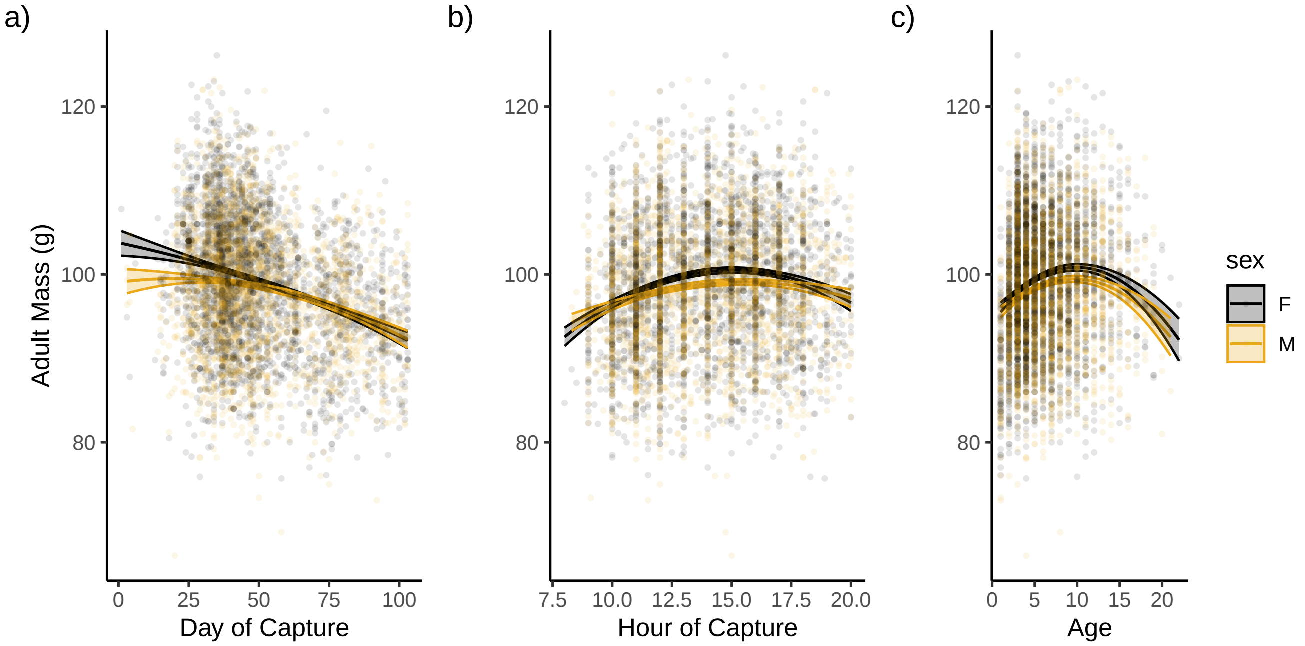


Figure C.2.: Association between day (panel a) and hour (panel b) of capture as well as individual age (panel c) and adult mass in two colonies of Alpine swifts captured between May 1st and August 10th from 1999 to 2021. Number of individuals: 1079; number of observations: 5387.

The inclusion of sternum length to correct body mass for skeletal size did not alter these meteorological windows, nor the relationship between body mass and age, hour or day of capture. Females were of higher body condition as compared to males.

Table C.1.: Estimates (posterior mean) and 95% credible intervals (Bayesian model in the R package MCMCglmm) for the relationships between body condition (mass corrected for skeletal size) and fixed effects for adult male and female Alpine swifts measured over the May-August breeding period (1999-2021). Estimates with 95% CIs that exclude 0 are deemed significant and bolded. Female is the reference level for sex. Biel is the reference level for colony.

	Estimate	**Lower 95% HDPI**	**Upper 95% HDPI**
Intercept	**0.15**	**0.064**	**0.23**
Sternum	**0.26**	**0.22**	**0.29**
Sex [M]	**-0.24**	**-0.32**	**-0.16**
Colony [Solothurn]	-0.056	-0.13	0.027
Age	**3.8**	**2.1**	**5.5**
Age ^2	**-5.8**	**-7.1**	**-4.4**
Rain Signal	**-9.0**	**-11**	**-7.4**

Rain Signal ^2	**3.0**	**1.6**	**4.2**
Temperature Signal	**39**	**37**	**40**
Temperature Signal ^2	**-7.7**	**-8.9**	**-6.4**
Hour of Capture	**11**	**9.3**	**12**
Hour of Capture ^2	**-1.8**	**-3.1**	**-0.59**
Day of Capture	**-31**	**-33**	**-29**
Day of Capture ^2	**7.3**	**5.7**	**9.1**
Sex [M] : Day of Capture	**5.7**	**3.2**	**8.1**
Sex [M] : Day of Capture ^2	**-3.0**	**-5.5**	**-0.80**

Table C.2.: Estimates (posterior mean) and 95% credible intervals (Bayesian model in the R package MCMCglmm) for the relationships between mass and fixed effects for adult male and female Alpine swifts measured over the May-August breeding period (1999-2021) including the sex by colony interaction. Estimates with 95% CIs that exclude 0 were deemed significant and bolded. References levels are as follows: females for sex, Biel for colony.

	Estimate	**Lower 95% HDPI**	**Upper 95% HDPI**
Intercept	0.051	-0.040	0.15
Sex [M]	-0.099	-0.21	0.0022
Colony [Solothurn]	-0.031	-0.14	0.088
Age	**4.5**	**2.7**	**6.3**
Age ^2	**-5.7**	**-7.2**	**-4.4**
Rain Signal	**-9.0**	**-11**	**-7.5**
Rain Signal ^2	**3.1**	**1.8**	**4.3**
Temperature Signal	**39**	**37**	**40**
Temperature Signal ^2	**-7.8**	**-9.0**	**-6.5**
Hour of Capture	**11**	**9.3**	**12**
Hour of Capture ^2	**-1.8**	**-3.2**	**-0.65**
Day of Capture	**-31**	**-33**	**-29**
Day of Capture ^2	**7.5**	**5.8**	**9.4**
Sex [M] : Day of Capture	**5.6**	**3.2**	**8.1**

Sex [M] : Day of Capture ^2	**-3.2**	**-5.7**	**-0.66**
Sex [M] * Colony [Solothurn]	0.0072	-0.15	0.16

C.2. Pedigree

Table C.3.: Summary statistics of the pruned social pedigree used in the quantitative genetic analyses. The pedigree was generated using the R package pedantics. The pedigree was built using data collected between 1999 and 2021 in a Swiss population of Alpine swifts.

	Sample Size
Total Sample Size	1162
Total Maternities	535
Total Paternities	518
Total Full Siblings	238
Total Maternal Siblings	488
Total Paternal Siblings	481
Total Pedigree Depth	5

Table C.4.: Summary statistics of the colony specific social pedigree used in the quantitative genetic analyses. The pedigree was build using data collected between 1999 and 2021 in a Swiss population of Alpine swifts from two colonies, Biel and Solothurn. At least 80 individuals have one or both parents originating from the other colony indicating strong gene flow across the two colonies: maternities denotes the total number of individuals with mother from the other colony, while paternities denotes the total number of individuals with fathers from the other colony, and both parents denotes the total number of individuals with both parents from the other colony.

Colony	Total Sample Size	Maternities	Paternities	Both Parents
Bienne	681	22	18	15
Solothurn	391	27	19	17

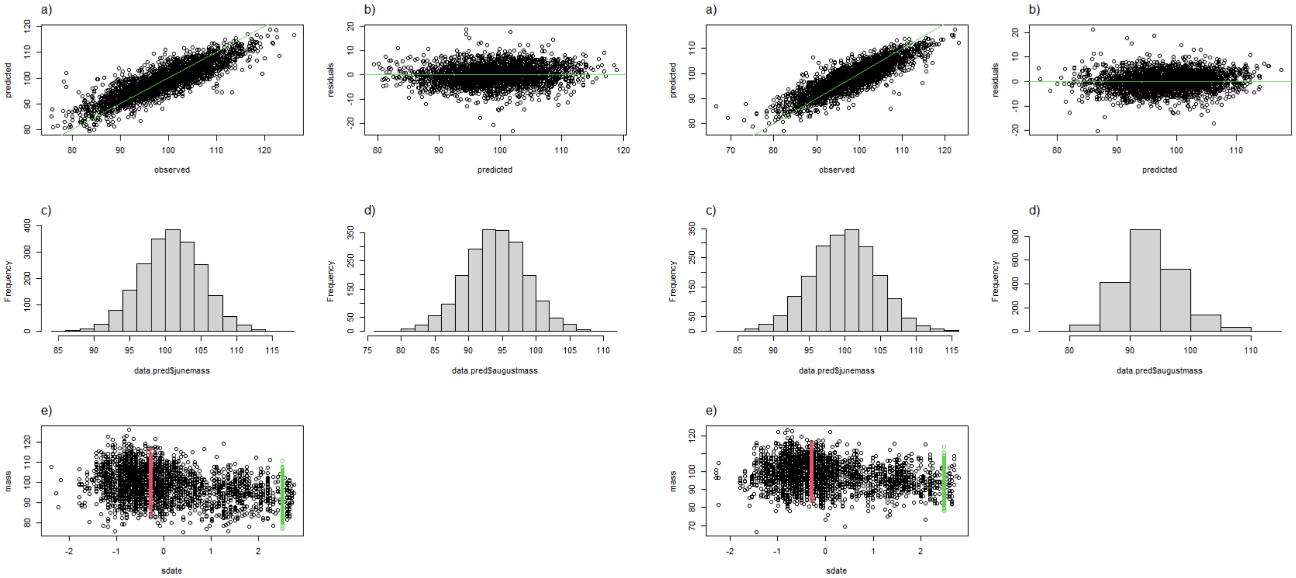
C.3. Heritability and cross-sex genetic correlation of adult swift body condition

Table C.5.: Variance component and ratio estimates (posterior mode) along with their 95% credible intervals for body condition (body mass corrected for skeletal size) in both adult female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment effect, and year effect. Given that variance components are bounded to zero, components for which the lower 95% HPDI was higher than 0.01 were deemed statistically significant and bolded. Evolvability is expressed as a percentage.

	Females	**Males**
Variance Components		
Additive Genetic Variance	0.111 [0.0684-0.167]	0.101 [0.058-0.17]
Permanent Environment	0.0866 [0.0505-0.13]	0.0994 [0.0597-0.158]
Year	0.0167 [0.00609-0.0341]	0.0178 [0.00897-0.0401]
Residual	0.316 [0.298-0.337]	0.301 [0.28-0.317]
Variance Ratios		
Heritability	0.203 [0.129-0.297]	0.202 [0.117-0.312]
Evolvability	0.123 [0.0777-0.144]	0.103 [0.0677-0.154]
Permanent Environment	0.166 [0.0959-0.241]	0.183 [0.109-0.283]
Year	0.0337 [0.0141-0.0634]	0.034 [0.0187-0.0732]
Cross-Sex Covariances		
Genetic	0.0619 [0.0163-0.108]	-
Yearly	0.0147 [0.00675-0.0321]	-
Cross-Sex Correlations		
Genetic	0.652 [0.208-0.923]	-
Yearly	0.943 [0.688-0.995]	-

C.4. Adjusted Mass

To allow comparison of body mass between years, measures taken in each year (between May 1st and August 10th) were standardized to 14h on June 13th (“June mass”), which corresponds to the median capture time and date. This date is representative of mean hatching throughout the study (June 15th; from year to year, mean hatching ranges from June 2nd to June 28th) and may reflect how much energy is available for reproduction. Mass was also standardized to July 31st, possibly reflecting the energy available at the end of the breeding season prior to migration (“July mass”). This second measure of late-season mass was used to assess the probability of overwinter survival as a consequence of varying reproductive investment. The best linear unbiased predictors (BLUPs) from linear mixed models including fixed effects of individual age, sternum length, and colony were used to obtain the standardized body masses for each individual in each year.



(a) Female adjusted mass

(b) Male adjusted mass

Figure C.3.: Adjusted June and August mass of adult female (left) and male (right) Alpine swifts using a frequentist approach. Relation between the a) predicted and observed and b) residual and predicted values of body mass. Distribution of c) June and d) August mass, as well as e) the spread of the data over the course of the season with June mass in red and August mass in green. Sdate corresponds to the scaled date (mean-centred and with a variance of 1). The slight deviation in the tails in panels a and b suggests error around our predictions of June and August mass. As such, further analyses were conducted using a Bayesian approach.

C.5. Sex-specific selection over body condition in adult swifts

Table C.6.: Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between body condition (mass corrected for size) and laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), and the weighted proportion of surviving fledglings (binomial distribution). Models were fitted on the 1000 sets of estimated mass from a Bayesian model. Estimates are the posterior mode with 95% HPDI for each parameter. Post P-value is the posterior mode of the p-values. Statistically significant estimates (P value < 0.05) were bolded. The reference level for colony is Biel. Data spans from 1999-2021.

	Estimate	**95% HPDI**	**Post. P-Value**
Laying Date[1]			
Intercept	0.21	[0.20; 0.21]	0.18
Female mass	**-5.4**	**[-6.9; -3.5]**	**< 0.001**
Female mass^2	0.17	[-0.70; 1.2]	0.94
Male mass	**-2.5**	**[-3.6; -1.1]**	**0.0047**
Male mass^2	-0.76	[-1.5; 0.25]	0.21
Female sternum	**2.0**	**[1.4; 2.8]**	**0.045**
Female sternum^2	-0.59	[-0.82; -0.35]	0.60
Male sternum	-0.24	[-0.69; 0.32]	0.94
Male sternum^2	1.2	[0.95; 1.4]	0.14
Colony	**-0.34**	**[-0.35; -0.32]**	**< 0.001**
Clutch Size[2]			
Intercept	**0.98**	**[0.98; 0.99]**	**< 0.001**
Female mass	-0.15	[-0.42; 0.050]	0.83
Female mass^2	-0.22	[-0.38; 0.067]	0.72
Male mass	0.0032	[-0.21; 0.23]	0.95
Male mass^2	0.16	[0.0015; 0.38]	0.74
Female sternum	0.0040	[-0.089; 0.085]	0.98
Female sternum^2	-0.25	[-0.29; -0.22]	0.68
Male sternum	0.30	[0.20; 0.39]	0.66

Male sternum^2	-0.24	[-0.30; -0.19]	0.71
Colony	0.060	[0.058; 0.061]	0.075
Brood Size at Hatching[3]			
Intercept	**0.68**	**[0.68; 0.68]**	**< 0.001**
Female mass	0.37	[-0.18; 0.90]	0.61
Female mass^2	0.18	[-0.22; 0.78]	0.76
Male mass	-0.49	[-1.1; 0.046]	0.56
Male mass^2	0.71	[0.17; 1.2]	0.31
Female sternum	-0.77	[-0.99; -0.56]	0.32
Female sternum^2	-1.1	[-1.1; -0.99]	0.14
Male sternum	0.44	[0.26; 0.75]	0.56
Male sternum^2	-0.38	[-0.52; -0.19]	0.60
Colony	**0.17**	**[0.17; 0.17]**	**< 0.001**
Brood Size at Fledgling[4]			
Intercept	**0.45**	**[0.44; 0.45]**	**< 0.001**
Female mass	1.1	[0.45; 1.9]	0.12
Female mass^2	-0.18	[-0.87; 0.46]	0.86
Male mass	-0.32	[-1.2; 0.23]	0.74
Male mass^2	**1.2**	**[0.76; 1.9]**	**0.018**
Female sternum	-1.1	[-1.3; -0.70]	0.22
Female sternum^2	-1.1	[-1.1; -0.92]	0.20
Male sternum	0.039	[-0.37; 0.26]	0.96
Male sternum^2	-0.86	[-1.1; -0.72]	0.28
Colony	**0.19**	**[0.18; 0.19]**	**< 0.001**
Weighted Proportion of Surviving Fledglings[5]			
Intercept	**0.42**	**[0.40; 0.43]**	**0.012**
Female mass	**4.4**	**[1.2; 6.5]**	**0.050**
Female mass^2	**-2.7**	**[-5.2; -0.88]**	**0.0096**

Male mass	-3.0	[-5.8; -0.39]	0.18
Male mass^2	**5.6**	**[3.3; 7.8]**	**0.0011**
Female sternum	-3.4	[-4.4; -2.2]	0.12
Female sternum^2	-2.8	[-3.2; -2.4]	0.17
Male sternum	-0.65	[-1.8; 0.45]	0.95
Male sternum^2	-1.8	[-2.5; -1.3]	0.40
Colony	**0.37**	**[0.35; 0.39]**	**0.0069**
Overwinter Survival[6]			
Intercept	**0.91**	**[0.89; 0.93]**	**0.0052**
Sex	0.061	[0.026; 0.086]	0.46
August Mass	0.14	[0.044; 0.27]	0.052
Sternum	0.0022	[-0.016; 0.028]	0.92
Colony	**0.52**	**[0.51; 0.52]**	**< 0.001**
Breeding Status	0.031	[0.0050; 0.056]	0.81
August Mass : Breeding Status	**-0.19**	**[-0.32; -0.090]**	**0.042**

[1] Number of observations: 1328; Number of females: 464; Number of males: 427; Number of years: 23 [2] Number of observations: 1334; Number of females: 470; Number of males: 432; Number of years: 23 [3] Number of observations: 1332; Number of females: 465; Number of males: 428; Number of years: 23 [4] Number of observations: 1330; Number of females: 465; Number of males: 428; Number of years: 23 [5] Number of observations: 1323; Number of females: 464; Number of males: 428; Number of years: 23 [6] Number of observations: 4111; Number of individuals: 1072; Number of years: 23

C.6. Estimating selection gradients from GLM(M)s

To estimate selection gradients from GLMMs, we followed the approach described by Morrissey & Goudie (2022) for log-link models and extended it to logit-link models.

Briefly, following Lande & Arnold (1983), given a function W(z) for expected fitness of a (multivariate) phenotype z, general expressions for the directional and quadratic selection gradient vectors β and γ are:

$$\beta = \overline{W}^{-1} \int \frac{\partial W(z)}{\partial z} p(z) dz \tag{C.1}$$

$$\gamma = \overline{W}^{-1} \int \frac{\partial^2 W(z)}{\partial z^2} p(z) dz \tag{C.2}$$

Where p(z) is the probability density function of phenotype, with z being a column vector, and $\overline{W}$ is mean fitness. Mean fitness can itself be obtained by $\overline{W} = \int W(z)p(z)dz$.

For log-link models, Morrissey & Goudie (2022) then showed that if b and g are the linear and quadratic slope from the model then the (average) linear, β, and quadratic, γ, selection gradient can be obtained as: $\beta = \frac{b}{1-g}$ and $\gamma = \frac{b^2+g(1-g)}{(1-g)^2}$

For logit-link models, Janzen & Stern (1998) provided a way to estimate the linear selection gradient but not the quadratic one. Based on both Janzen & Stern (1998) and Morrissey & Goudie (2022), we extended the approach for logit-link models. For GLMs with a logit-link function, we can write the fitness function as

$$W(z) = \frac{e^{f(z)}}{1 + e^{f(z)}} \tag{C.3}$$

where $f(z) = a + b'z + \frac{1}{2}z'gz$

Calculating the first and second order differentials of equation (C.3) for z, we get

$$\frac{\partial W(z)}{\partial z} = (b + gz)W(z)\left(1 - W(z)\right) \tag{C.4}$$

and

$$\frac{\partial^2 W(z)}{\partial z^2} = \frac{2(b+gz)^2 e^{3f(z)}}{\left(1+e^{f(z)}\right)^3} - \frac{\left(3(b+gz)^2 + g\right) e^{2f(z)}}{\left(1+e^{f(z)}\right)^2} + \frac{\left((b+gz)^2 + g\right) e^{f(z)}}{1+e^{f(z)}} \tag{C.5}$$

Now, using equations (C.1) and (C.2), substituting values from equations (C.4) and (C.5) and not making any assumptions about $p(z)$, we can approximate the average fitness and average gradients numerically for a sample population of size N as:

$$\overline{W} = \frac{1}{N}\sum_{i=1}^{N} W(z) \tag{C.6}$$

$$\begin{aligned}\beta &= \overline{W}^{-1}\frac{1}{N}\sum_{1}^{N}\frac{\partial W(z)}{\partial z}\\ &= \frac{1}{\sum_1^N W(z)}\sum_{1}^{N}(b+gz)\,W(z)\,(1-W(z))\end{aligned} \tag{C.7}$$

$$\begin{aligned}\gamma &= \overline{W}^{-1}\frac{1}{N}\sum_{1}^{N}\frac{\partial^2 W(z)}{\partial z^2}\\ &= \frac{1}{\sum_1^N W(z)}\sum_{1}^{N}\frac{2(b+gz)^2 e^{3f(z)}}{\left(1+e^{f(z)}\right)^3} - \frac{\left(3(b+gz)^2+g\right)e^{2f(z)}}{\left(1+e^{f(z)}\right)^2} + \frac{\left((b+gz)^2+g\right)e^{f(z)}}{1+e^{f(z)}}\end{aligned} \tag{C.8}$$

Appendix D

Supplementary for Chapter 5 ‘Who keeps the house after divorcing? Partner and nest (in)fidelity in the long-lived Alpine swift’

D.1. Patterns of Partner & Nest Fidelity

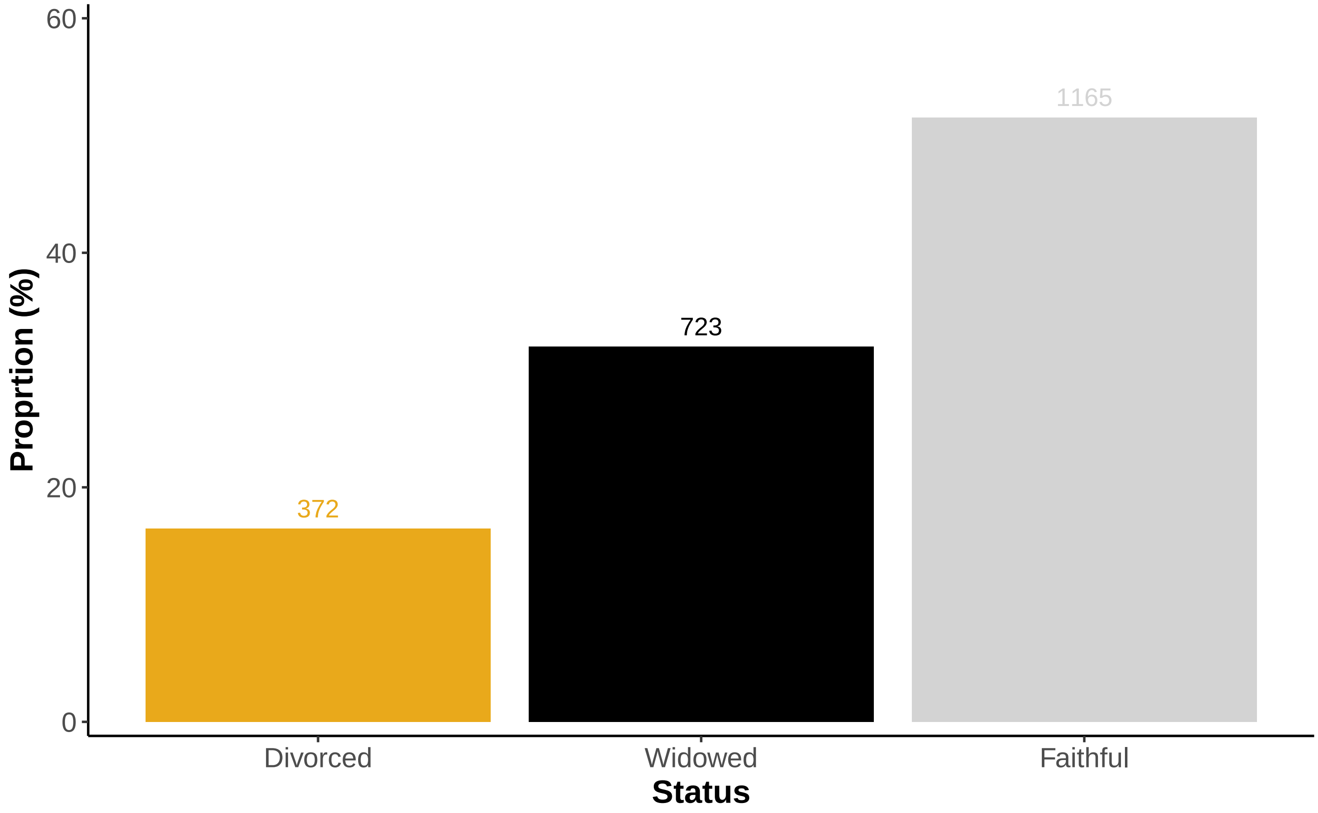


Figure D.1.: Proportion of Alpine swift pairs from three Swiss colonies (Baden, Biel and Solothurn) which ended in divorced (gold) or widowing (black), and pairs for which partners remained with the same partner (grey) from one year to the next. The number of pairs in each category are displayed above the corresponding proportion. Data spans 1991-2021.

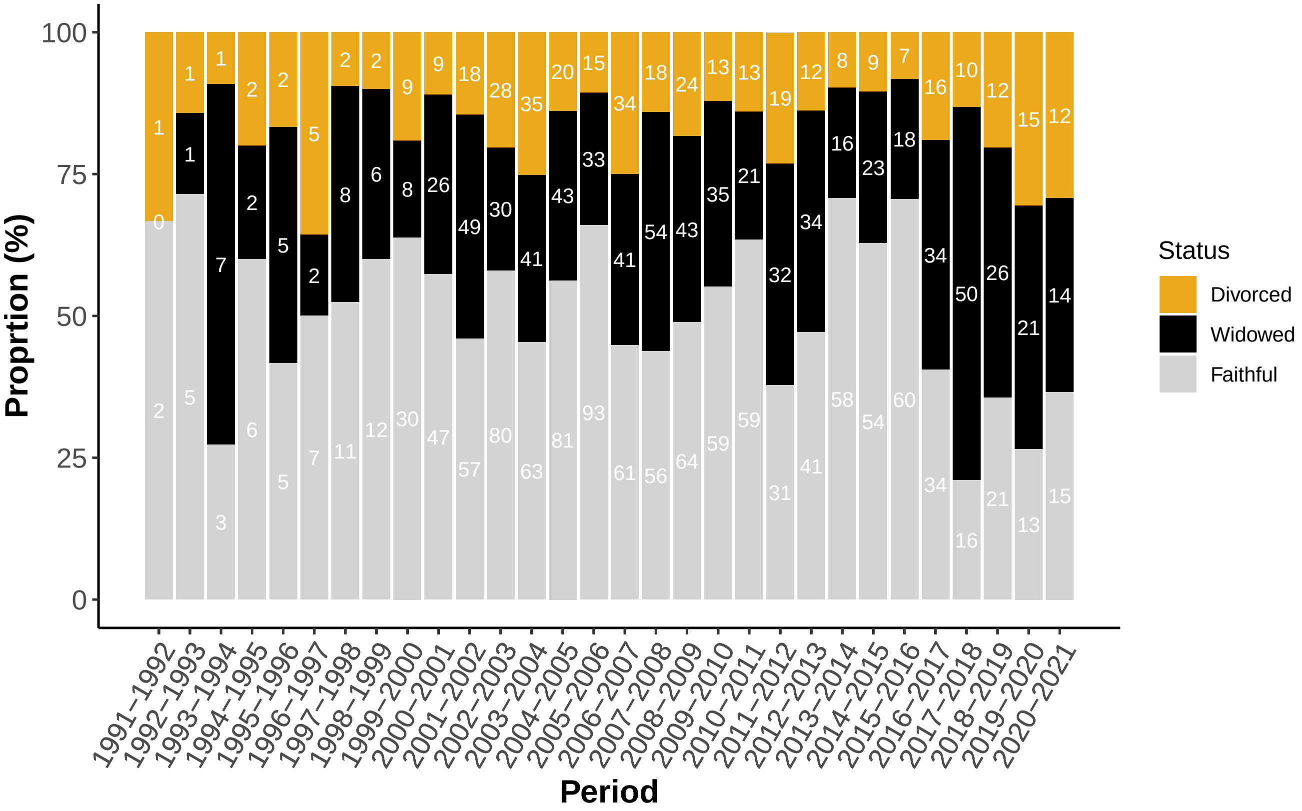


Figure D.2.: Proportion of Alpine swift pairs from three Swiss colonies (Baden, Biel and Solothurn) which ended in divorced (gold, top) or widowing (black, middle), and pairs for which partners remained with the same partner (grey, bottom) from one year to the next for all periods of the study (1991-2021). The number of pairs in each category are displayed within the corresponding proportion.

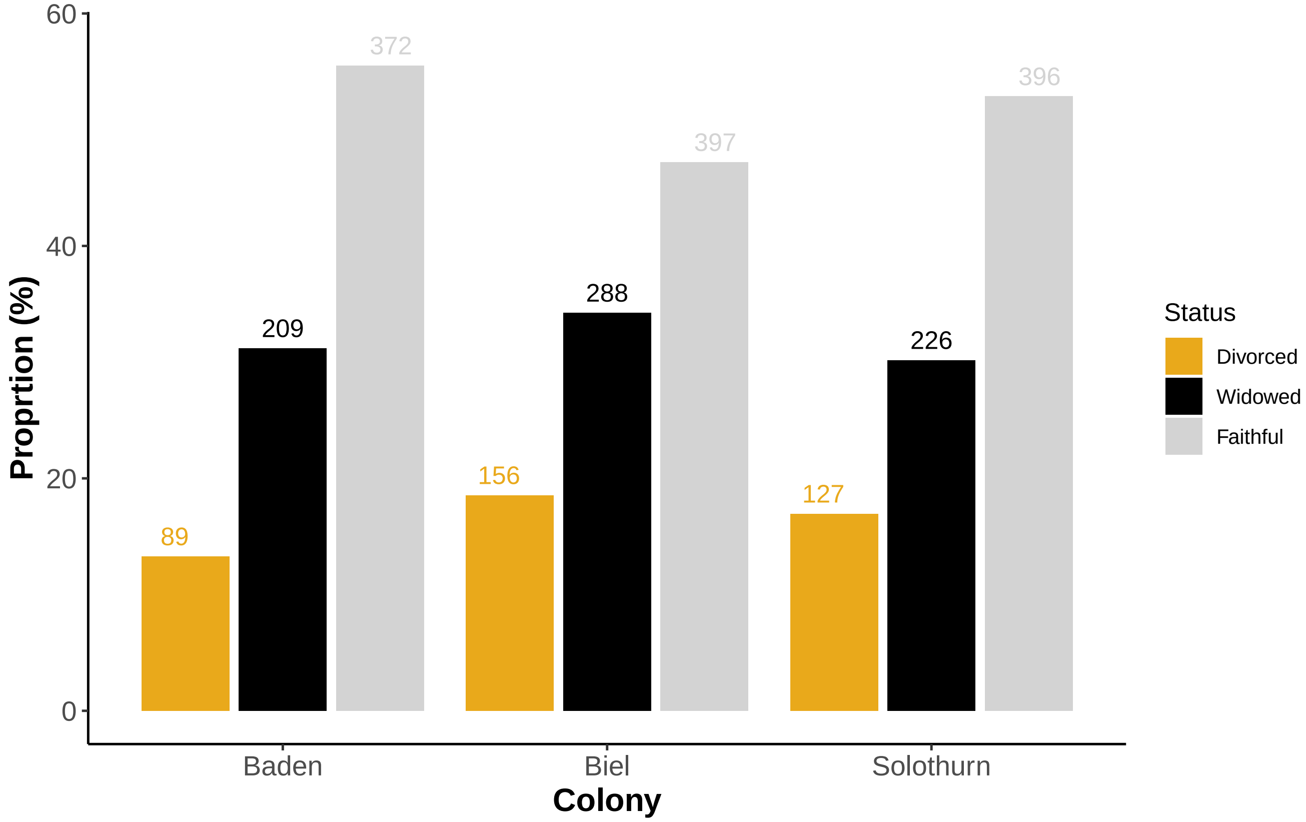


Figure D.3.: Proportion of Alpine swift pairs which ended in divorced (gold) or widowing (black), and pairs for which partners remained with the same partner (grey) from one year to the next across three Swiss colonies (Baden, Biel and Solothurn). The number of pairs in each category are displayed above the corresponding proportion. Data spans 1991-2021.

There were four instances in which a pair divorced, the two partners divorced again, and then re paired with their original partner. From Biel, one pair divorced after the 2005 season and re-paired during the 2008 season. From Baden, one pair divorced after the 1996 season and re-paired during the 1998 season. Also from Baden, another pair divorced after the 1999 season, re-paired during the 2001-2002 seasons, then divorced again after the 2002 season, only to repair once again for the 2007 season (following which the female died and the male re-paired with a different female). From Solothurn, one pair divorced following the 2017 season and re-paired during the 2019 season.

The patterns of lifetime divorce and re-pairing following widowing were comparable between sexes (Figure 5.1 A): 21% of females and males divorced once, and 41% of females and 40% of males re-paired after being widowed once; 6% of females and 8% of males divorced twice, and 11% of females and 13% of males re-paired after being widowed twice; 2% of females and males divorced three times, 4% of females and 5% males re-paired after being widowed three times; and <1% of males and females divorced or re-paired after being widowed four and five times. 6% of females and 6% of males remained with the same partner throughout their entire lifetime.

D.2. Predictors of Partner & Nest Fidelity

Table D.1.: Summary statistics of the pruned social pedigree used in the quantitative genetic analyses. The pedigree was generated using the R package pedantics. The pedigree was built using data collected between 1999 and 2021 in a Swiss population of Alpine swifts from three colonies, Baden, Biel and Solothurn.

	Sample Size
Total Sample Size	1596
Total Maternities	653
Total Paternities	640
Total Full Siblings	264
Total Maternal Siblings	539
Total Paternal Siblings	550
Total Pedigree Depth	5

Table D.2.: Repeatability, variance component as well as variance ratio estimates (median, mean and mode) along with their 95% HDP intervals for divorce in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, permanent environment and year effects. The cross-sex covariances and correlations are estimated as between the sexes and hence displayed in the table only once.

	Females	**Males**	R_{fm}
Model I - Median -			
Repeatability	0.11 [0.017; 0.19]	0.023 [6.4e-08; 0.09]	
Model I - Mean -			
Repeatability	0.11 [0.017; 0.19]	0.03 [6.4e-08; 0.09]	
Model I - Mode -			
Repeatability	0.11 [0.017; 0.19]	0.00059 [6.4e-08; 0.09]	
Model II - Median - Variance Components			

Additive Genetic Variance	0.23 [3.8e-08; 0.74]	0.079 [7.2e-09; 0.4]	0.13 [-0.82; 0.94]
Permanent Environment	0.31 [4.3e-08; 0.85]	0.069 [3.8e-09; 0.4]	
Year	0.16 [0.017; 0.41]	0.16 [0.017; 0.41]	
Model II - Median - Variance Ratios			
Heritability	0.046 [7.8e-09; 0.14]	0.017 [1.5e-09; 0.082]	
Permanent Environment	0.061 [8.9e-09; 0.16]	0.015 [8.9e-09; 0.08]	
Model II - Mean - Variance Components			
Additive Genetic Variance	0.28 [3.8e-08; 0.74]	0.13 [7.2e-09; 0.4]	0.09 [-0.82; 0.94]
Permanent Environment	0.35 [4.3e-08; 0.85]	0.12 [3.8e-09; 0.4]	
Year	0.19 [0.017; 0.41]	0.19 [0.017; 0.41]	
Model II - Mean - Variance Ratios			
Heritability	0.054 [7.8e-09; 0.14]	0.026 [1.5e-09; 0.082]	
Permanent Environment	0.067 [8.9e-09; 0.16]	0.024 [8.9e-09; 0.08]	
Model II - Mode - Variance Components			
Additive Genetic Variance	0.0041 [3.8e-08; 0.74]	0.0017 [7.2e-09; 0.4]	0.55 [-0.82; 0.94]
Permanent Environment	0.0056 [4.3e-08; 0.85]	0.0017 [3.8e-09; 0.4]	
Year	0.13 [0.017; 0.41]	0.13 [0.017; 0.41]	
Model II - Mode - Variance Ratios			
Heritability	0.00078 [7.8e-09; 0.14]	0.00052 [1.5e-09; 0.082]	
Permanent Environment	0.00063 [8.9e-09; 0.16]	0.00053 [8.9e-09; 0.08]	

Table D.3.: Variance component and ratio estimates (median, mean and mode) along with their 95% HDP intervals of divorce in female Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, pair, and year. Variance ratios: heritability, permanent environment and year.

	Estimate	**95% HPDI**
Median - Variance Components		

Additive Genetic Variance	0.294	[9.15e-10-0.827]
Permanent Environment	0.291	[2.1e-07-0.91]
Pair	0.491	[2.28e-06-1.92]
Year	0.181	[0.0269-0.467]
Median - Variance Ratios		
Heritability	0.0514	[1.26e-10-0.138]
Permanent Environment	0.0518	[2.56e-08-0.149]
Year	0.0317	[0.00519-0.077]
Mean - Variance Components		
Additive Genetic Variance	0.332	[9.15e-10-0.827]
Permanent Environment	0.347	[2.1e-07-0.91]
Pair	0.651	[2.28e-06-1.92]
Year	0.206	[0.0269-0.467]
Mean - Variance Ratios		
Heritability	0.0566	[1.26e-10-0.138]
Permanent Environment	0.0589	[2.56e-08-0.149]
Year	0.035	[0.00519-0.077]
Mode - Variance Components		
Additive Genetic Variance	0.00471	[9.15e-10-0.827]
Permanent Environment	0.00303	[2.1e-07-0.91]
Pair	0.00845	[2.28e-06-1.92]
Year 1	0.127	[0.0269-0.467]
Mode - Variance Ratios		
Heritability	0.000692	[1.26e-10-0.138]
Permanent Environment	0.000908	[2.56e-08-0.149]
Year	0.0249	[0.00519-0.077]

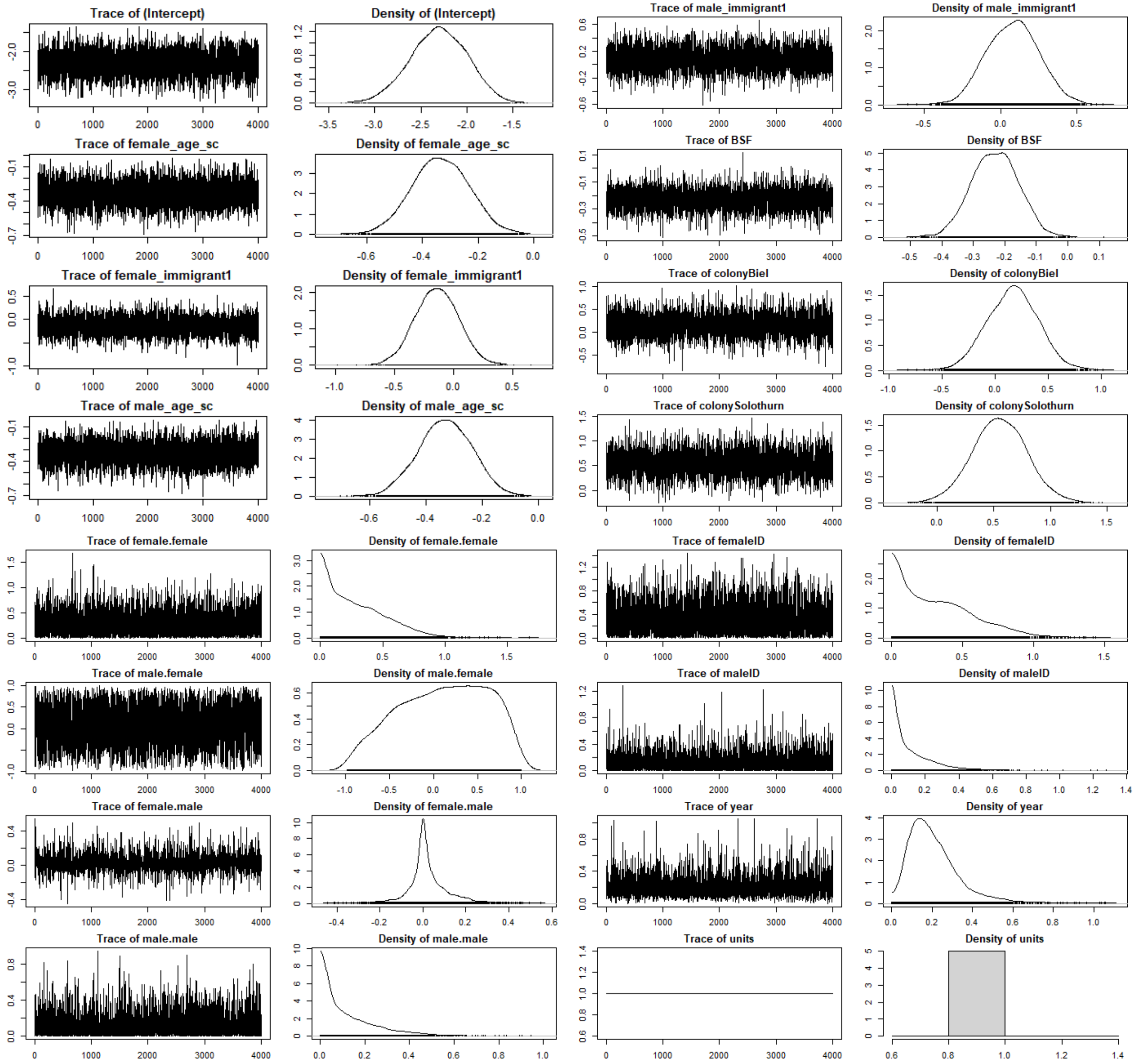


Figure D.4.: The posterior distributions of the fixed effects (upper) and variance components (lower) of divorce in female and male Alpine swifts (model II). Female.female and male.male refer to thefemale and male additive genetic variance, respectively, while femaleID and maleID refer to the female and male permanent environment effect, respectively. Male.female reference to the cross-sex genetic correlation, while female.male referes to the cross-sex genetic covariation. Units were fixed to 1.

Table D.4.: Sex-specific nest site fidelity (0: different nest site; 1: same nest site) in relation to pair bond status (divorced, widowed, or faithful) from one year to the next. The chi-squared value is displayed for status and colony estimated from a type II Anova, while z-values are displayed for the intercept and sex estimates. Statistically significant ($p < 0.05$) estimates are bolded (P-values from the Anova are reported for status and colony). Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**Z-Value/chi-squared**	**P-Value**
Females				
Intercept	**-0.82**	**0.23**	**-3.5**	**< 0.001**
Status			**220**	**< 0.001**
Widowed	**1.8**	**0.23**		
Faithful	**4.2**	**0.29**		
Colony			**6.0**	**0.050**
Biel	**-0.54**	**0.23**		
Solothurn	**-0.18**	**0.25**		
Males				
Intercept	**0.48**	**0.21**	**2.3**	**0.022**
Status			**200**	**< 0.001**
Widowed	**1.6**	**0.21**		
Faithful	**3.2**	**0.23**		
Colony			**21**	**< 0.001**
Biel	**-1.0**	**0.23**		
Solothurn	**-0.90**	**0.24**		

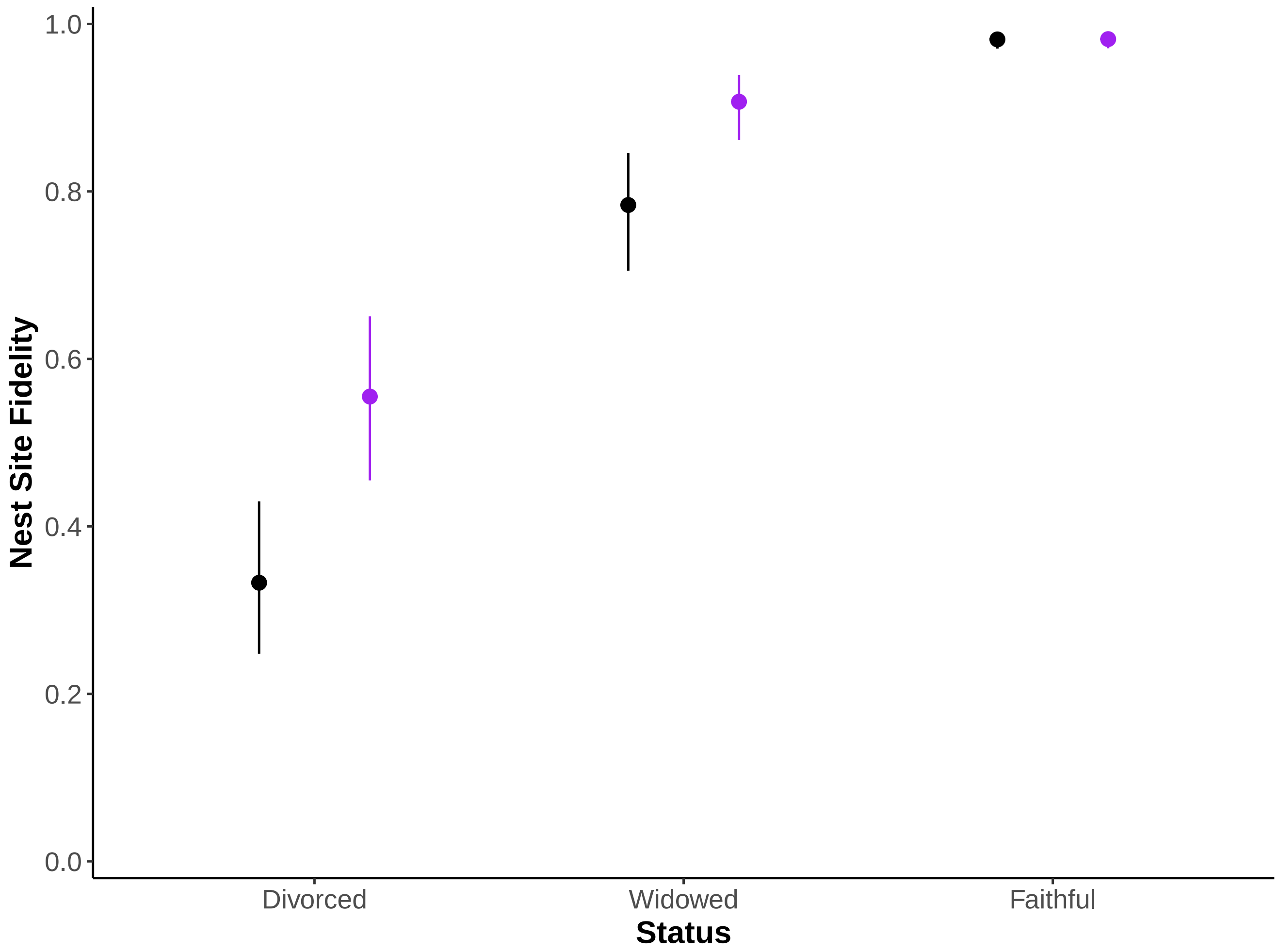


Figure D.5.: Probability of retaining the nest site (0: different nest; 1: same nest) in relation to pair bond status (divorced, widowed, faithful) from one year to the next for both female (black) and male (purple) Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn). Error bars correspond to the 95% confidence intervals. Data spans 1991-2021.

D.3. Fitness Consequences of Partner Fidelity

Table D.5.: Subseuqent reproductive success (year X+1) in relation to pair bond status (divorced, widowed, or faithful), with the inclusion of the status by sex interaction term. The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant ($P < 0.05$) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	Standard Error	T-Value or Chisq	P-Value
Laying Date[1]				
Intercept	0.096	0.13	0.71	0.48
Sex [M]	0.029	0.029	1.0	0.32
Status			**84**	**< 0.001**
Widowed	**-0.086**	**0.047**		
Faithful	**-0.32**	**0.038**		
Solothurn	**-0.27**	**0.030**	**-9.0**	**< 0.001**
Sex [M] : Status			2.6	0.28
Sex [M] : Widowed	0.032	0.055		
Sex [M] : Faithful	-0.034	0.032		
Clutch Size[2]				
Intercept	**1.0**	**0.037**	**27**	**< 0.001**
Sex [M]	0.0059	0.048	0.12	0.90
Status			1.2	0.55
Widowed	0.025	0.048		
Faithful	0.041	0.038		
Colony			3.0	0.22
Biel	-0.016	0.025		
Solothurn	0.025	0.025		
Sex [M] : Status			0.35	0.84

Sex [M] : Widowed	-0.034	0.066		
Sex [M] : Faithful	-0.0059	0.054		
Brood Size at Hatching[3]				
Intercept	**0.86**	**0.045**	**19**	**< 0.001**
Sex [M]	0.0020	0.055	0.036	0.97
Status			4.0	0.13
Widowed	0.039	0.054		
Faithful	0.082	0.043		
Colony			**40**	**< 0.001**
Biel	**-0.17**	**0.028**		
Solothurn	**-0.047**	**0.028**		
Sex [M] : Status			1.2	0.55
Sex [M] : Widowed	-0.063	0.075		
Sex [M] : Faithful	-0.0020	0.061		
Brood Size at Fledgling[4]				
Intercept	**0.74**	**0.055**	**13**	**< 0.001**
Sex [M]	-0.017	0.061	-0.27	0.78
Status			**8.5**	**0.014**
Widowed	**0.041**	**0.059**		
Faithful	**0.12**	**0.047**		
Colony			**130**	**< 0.001**
Biel	**-0.35**	**0.031**		
Solothurn	**-0.18**	**0.030**		
Sex [M] : Status			1.1	0.58
Sex [M] : Widowed	-0.050	0.083		
Sex [M] : Faithful	0.017	0.068		
Weighted Proportion of Surviving Fledglings[5]				
Intercept	**2.0**	**0.21**	**9.9**	**< 0.001**

Sex [M]	-0.11	0.13	-0.82	0.41
Status			**11**	**0.0041**
Widowed	**0.13**	**0.20**		
Faithful	**0.47**	**0.16**		
Colony			**160**	**< 0.001**
Biel	**-1.8**	**0.15**		
Solothurn	**-1.3**	**0.14**		
Sex [M] : Status			1.1	0.57
Sex [M] : Widowed	-0.070	0.23		
Sex [M] : Faithful	0.11	0.15		

[1] Number of: Observations: 2546; Nests: 1566; Pairs: 930; Individuals: 790; Years: 23 [2] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [3] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [4] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [5] Number of: Observations: 3586; Nests: 2197; Pairs: 1251; Individuals: 1075; Years: 31

Table D.6.: Changes in reproductive success (year X+1 - year X) in relation to pair bond status (divorced, widowed, or faithful), with the inclusion of the status by sex interaction term. The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant ($P < 0.05$) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**T-Value or Chisq**	**P-Value**
Laying Date[1]				
Intercept	-0.18	0.21	-0.84	0.41
Sex [M]	0.019	0.028	0.68	0.50
Status			**6.4**	**0.041**
Widowed	**0.045**	**0.071**		
Faithful	**-0.092**	**0.056**		

Solothurn	0.054	0.040	1.4	0.18
Sex [M] : Status			4.9	0.086
Sex [M] : Widowed	0.14	0.076		
Sex [M] : Faithful	-0.019	0.032		
Clutch Size[2]				
Intercept	0.091	0.048	1.9	0.060
Sex [M]	0.029	0.019	1.5	0.13
Status			1.5	0.48
Widowed	-0.054	0.050		
Faithful	-0.043	0.040		
Colony			0.46	0.80
Biel	0.023	0.035		
Solothurn	0.016	0.035		
Sex [M] : Status			**6.4**	**0.041**
Sex [M] : Widowed	-0.13	0.052		
Sex [M] : Faithful	-0.029	0.021		
Brood Size at Hatching[3]				
Intercept	0.16	0.089	1.8	0.072
Sex [M]	0.014	0.038	0.37	0.71
Status			2.6	0.28
Widowed	-0.15	0.096		
Faithful	-0.057	0.076		
Colony			0.25	0.88
Biel	**-0.020**	**0.066**		
Solothurn	**-0.033**	**0.066**		
Sex [M] : Status			0.44	0.80
Sex [M] : Widowed	-0.066	0.10		
Sex [M] : Faithful	-0.014	0.042		

Brood Size at Fledgling[4]				
Intercept	0.15	0.11	1.4	0.15
Sex [M]	-0.022	0.036	-0.60	0.55
Status			3.4	0.18
Widowed	**-0.18**	**0.10**		
Faithful	**-0.066**	**0.080**		
Colony			1.1	0.57
Biel	**-0.072**	**0.071**		
Solothurn	**-0.026**	**0.071**		
Sex [M] : Status			0.30	0.86
Sex [M] : Widowed	0.013	0.10		
Sex [M] : Faithful	0.022	0.040		
Weighted Proportion of Surviving Fledglings[5]				
Intercept	0.15	0.11	1.4	0.16
Sex [M]	-0.025	0.036	-0.71	0.48
Status			3.3	0.20
Widowed	**-0.18**	**0.10**		
Faithful	**-0.067**	**0.080**		
Colony			1.4	0.49
Biel	**-0.080**	**0.070**		
Solothurn	**-0.023**	**0.071**		
Sex [M] : Status			0.41	0.81
Sex [M] : Widowed	0.017	0.10		
Sex [M] : Faithful	0.025	0.040		

[1] Number of: Observations: 2546; Nests: 1566; Pairs: 930; Individuals: 790; Years: 23 [2] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [3] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [4] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [5] Number of: Observations: 3586; Nests: 2197; Pairs: 1251; Individuals: 1075; Years: 31

Table D.7.: Changes in reproductive success (year X+1 – year X) in relation to pair bond status (divorced, widowed, or faithful) for pairs with null reproductive success in the year X. The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant ($p < 0.05$) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**T-Value or Chisq**	**P-Value**
Laying Date[1]				
Intercept	**-0.54**	**0.25**	**-2.1**	**0.038**
Sex [M]	-0.050	0.063	-0.79	0.43
Status			0.76	0.68
Widowed	0.17	0.22		
Faithful	0.11	0.16		
Solothurn	-0.13	0.13	-0.97	0.33
Sex [M] : Status			1.1	0.59
Sex [M] : Widowed	0.20	0.22		
Sex [M] : Faithful	0.050	0.074		
Clutch Size[2]				
Intercept	**0.47**	**0.15**	**3.1**	**0.0025**
Sex [M]	-0.052	0.047	-1.1	0.27
Status			4.1	0.13
Widowed	-0.28	0.14		
Faithful	-0.16	0.11		

Colony			1.8	0.41
Biel	0.11	0.14		
Solothurn	-0.0046	0.15		
Sex [M] : Status			1.3	0.51
Sex [M] : Widowed	-0.059	0.15		
Sex [M] : Faithful	0.052	0.056		
Brood Size at Hatching[3]				
Intercept	**1.6**	**0.28**	**5.6**	**< 0.001**
Sex [M]	0.044	0.11	0.41	0.68
Status			0.085	0.96
Widowed	-0.0053	0.27		
Faithful	-0.054	0.21		
Colony			0.72	0.70
Biel	-0.19	0.26		
Solothurn	-0.23	0.27		
Sex [M] : Status			1.0	0.60
Sex [M] : Widowed	-0.29	0.28		
Sex [M] : Faithful	-0.044	0.13		
Brood Size at Fledgling[4]				
Intercept	**1.9**	**0.22**	**8.6**	**< 0.001**
Sex [M]	-0.025	0.099	-0.25	0.80
Status			0.97	0.62
Widowed	0.19	0.20		
Faithful	0.030	0.16		
Colony			**12**	**0.0026**
Biel	-0.48	0.20		
Solothurn	-0.094	0.20		
Sex [M] : Status			0.26	0.88

Sex [M] : Widowed	-0.069	0.22		
Sex [M] : Faithful	0.030	0.12		
Weighted Proportion of Surviving Fledglings[5]				
Intercept	**1.9**	**0.22**	**8.6**	**< 0.001**
Sex [M]	-0.025	0.099	-0.25	0.80
Status			0.97	0.62
Widowed	0.19	0.20		
Faithful	0.030	0.16		
Colony			**12**	**0.0026**
Biel	-0.48	0.20		
Solothurn	-0.094	0.20		
Sex [M] : Status			0.26	0.88
Sex [M] : Widowed	-0.069	0.22		
Sex [M] : Faithful	0.030	0.12		

[1]Number of: Observations: 484; Nests: 307; Pairs: 280; Individuals: 351; Years: 23 [2]Number of: Observations: 527; Nests: 336; Pairs: 306; Individuals: 394; Years: 27 [3]Number of: Observations: 527; Nests: 336; Pairs: 306; Individuals: 394; Years: 27 [4]Number of: Observations: 527; Nests: 336; Pairs: 306; Individuals: 394; Years: 27 [5]Number of: Observations: 527; Nests: 336; Pairs: 306; Individuals: 394; Years: 27

Table D.8.: Subseuqent reproductive success (year X+1) in relation to pair bond status (divorced, widowed, or faithful), with the inclusion of prior investment and age as fixed effects and the sex by status interaction. The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant ($P < 0.05$) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	Standard Error	T-Value or Chisq	P-Value
Laying Date[1]				

Intercept	0.11	0.13	0.82	0.42
Sex [M]	0.027	0.033	0.82	0.41
Status			**82**	**< 0.001**
Widowed	**-0.040**	**0.049**		
Faithful	**-0.31**	**0.039**		
Colony [Solothurn]	**-0.26**	**0.030**	**-8.6**	**< 0.001**
Age	**-2.9**	**0.51**	**-5.7**	**< 0.001**
Age^2	**1.4**	**0.46**	**3.0**	**0.0024**
Prior Investment	-0.019	0.013	-1.5	0.14
Sex [M] : Status			**-5.7**	**< 0.001**
Sex [M] : Widowed	**0.0065**	**0.058**		
Sex [M] : Faithful	**-0.029**	**0.037**		
Clutch Size[2]				
Intercept	**1.0**	**0.045**	**22**	**< 0.001**
Sex [M]	0.0018	0.050	0.036	0.97
Status			0.84	0.66
Widowed	0.022	0.050		
Faithful	0.036	0.040		
Colony			2.9	0.24
Biel	-0.014	0.027		
Solothurn	0.028	0.026		
Age	0.72	0.60	1.2	0.23
Age^2	-0.35	0.60	-0.57	0.57
Prior Investment	0.0043	0.010	0.42	0.68
Sex [M] : Status			1.2	0.23
Sex [M] : Widowed	-0.030	0.069		
Sex [M] : Faithful	-0.0051	0.057		
Brood Size at Hatching[3]				

Intercept	**0.75**	**0.054**	**14**	**< 0.001**
Sex [M]	-0.0041	0.057	-0.071	0.94
Status			2.8	0.25
Widowed	0.025	0.056		
Faithful	0.069	0.045		
Colony			**26**	**< 0.001**
Biel	**-0.15**	**0.031**		
Solothurn	**-0.034**	**0.030**		
Age	-0.11	0.68	-0.15	0.88
Age^2	-0.17	0.69	-0.25	0.80
Prior Investment	**0.056**	**0.012**	**4.6**	**< 0.001**
Sex [M] : Status			-0.15	0.88
Sex [M] : Widowed	-0.051	0.079		
Sex [M] : Faithful	-0.00049	0.064		
Brood Size at Fledgling[4]				
Intercept	**0.63**	**0.065**	**9.7**	**< 0.001**
Sex [M]	-0.017	0.064	-0.26	0.79
Status			**6.1**	**0.048**
Widowed	**0.014**	**0.062**		
Faithful	**0.10**	**0.050**		
Colony			**95**	**< 0.001**
Biel	**-0.33**	**0.033**		
Solothurn	**-0.17**	**0.032**		
Age	0.80	0.75	1.1	0.28
Age^2	-0.70	0.76	-0.93	0.35
Prior Investment	**0.060**	**0.014**	**4.4**	**< 0.001**
Sex [M] : Status			1.1	0.28
Sex [M] : Widowed	-0.042	0.087		

Sex [M] : Faithful	0.013	0.071		
Weighted Proportion of Surviving Fledglings[5]				
Intercept	**1.6**	**0.25**	**6.3**	**< 0.001**
Sex [M]	-0.16	0.14	-1.1	0.27
Status			**8.3**	**0.016**
Widowed	**0.010**	**0.20**		
Faithful	**0.38**	**0.16**		
Colony			**140**	**< 0.001**
Biel	**-1.7**	**0.14**		
Solothurn	**-1.2**	**0.14**		
Age	0.23	2.4	0.097	0.92
Age^2	-2.7	2.3	-1.2	0.23
Prior Investment	**0.23**	**0.062**	**3.8**	**< 0.001**
Sex [M] : Status			0.097	0.92
Sex [M] : Widowed	-0.0063	0.24		
Sex [M] : Faithful	0.15	0.16		

[1] Number of: Observations: 2546; Nests: 1566; Pairs: 930; Individuals: 790; Years: 23 [2] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [3] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [4] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [5] Number of: Observations: 3586; Nests: 2197; Pairs: 1251; Individuals: 1075; Years: 31

Table D.9.: Changes in reproductive success (year X+1 – year X) in relation to pair bond status (divorced, widowed, or faithful), with the inclusion of prior investment and age as fixed effects and the sex by status interaction. The chi-squared value is displayed for status estimated from a type III Anova, while t-values are displayed for all other estimates. Baden is the reference level for colony (Biel, Solothurn) for all models except the laying date model, for which Biel is the reference level for colony (Solothurn). Statistically significant ($p < 0.05$) estimates are bolded. Data corresponds to male and female Alpine swifts from three Swiss colonies (Baden, Biel and Solothurn) spanning 1991-2021.

	Estimate	**Standard Error**	**T-Value or Chisq**	**P-Value**
Laying Date[1]				
Intercept	-0.39	0.22	-1.8	0.083
Sex [M]	0.0061	0.032	0.19	0.85
Status			**13**	**0.0017**
Widowed	**-0.010**	**0.073**		
Faithful	**-0.17**	**0.057**		
Colony [Solothurn]	0.021	0.041	0.51	0.61
Age	**2.4**	**0.55**	**4.4**	**< 0.001**
Age^2	**-1.6**	**0.49**	**-3.2**	**0.0016**
Prior Investment	**0.16**	**0.019**	**8.2**	**< 0.001**
Sex [M] : Status			**4.4**	**< 0.001**
Sex [M] : Widowed	**0.16**	**0.079**		
Sex [M] : Faithful	**-0.012**	**0.036**		
Clutch Size[2]				
Intercept	**0.44**	**0.055**	**7.9**	**< 0.001**
Sex [M]	0.024	0.020	1.2	0.24
Status			0.52	0.77
Widowed	-0.019	0.051		
Faithful	0.011	0.040		
Colony			**6.4**	**0.040**
Biel	**-0.090**	**0.035**		
Solothurn	**-0.056**	**0.035**		
Age	-0.49	0.40	-1.2	0.23
Age^2	0.46	0.36	1.3	0.20
Prior Investment	**-0.17**	**0.014**	**-12**	**< 0.001**
Sex [M] : Status			-1.2	0.23
Sex [M] : Widowed	-0.13	0.054		

Sex [M] : Faithful	-0.023	0.023		
Brood Size at Hatching[3]				
Intercept	**1.5**	**0.097**	**16**	**< 0.001**
Sex [M]	-0.023	0.042	-0.55	0.58
Status			4.4	0.11
Widowed	-0.025	0.087		
Faithful	0.10	0.068		
Colony			**51**	**< 0.001**
Biel	**-0.42**	**0.060**		
Solothurn	**-0.29**	**0.059**		
Age	-0.23	0.80	-0.29	0.77
Age^2	-0.44	0.73	-0.60	0.55
Prior Investment	**-0.65**	**0.023**	**-28**	**< 0.001**
Sex [M] : Status			-0.29	0.77
Sex [M] : Widowed	-0.095	0.094		
Sex [M] : Faithful	0.025	0.047		
Brood Size at Fledgling[4]				
Intercept	**2.0**	**0.097**	**21**	**< 0.001**
Sex [M]	-0.063	0.040	-1.6	0.12
Status			**13**	**0.0017**
Widowed	**-0.0066**	**0.079**		
Faithful	**0.18**	**0.062**		
Colony			**130**	**< 0.001**
Biel	**-0.63**	**0.055**		
Solothurn	**-0.37**	**0.055**		
Age	0.31	0.77	0.40	0.69
Age^2	-0.98	0.69	-1.4	0.16
Prior Investment	**-0.91**	**0.021**	**-43**	**< 0.001**

Sex [M] : Status			0.40	0.69
Sex [M] : Widowed	-0.030	0.086		
Sex [M] : Faithful	0.062	0.045		
Weighted Proportion of Surviving Fledglings[5,6]				
Intercept	**2.0**	**0.097**	**21**	**< 0.001**
Sex [M]	-0.078	0.040	-1.9	0.054
Status			**12**	**0.0025**
Widowed	**-0.011**	**0.079**		
Faithful	**0.17**	**0.062**		
Colony			**130**	**< 0.001**
Biel	**-0.64**	**0.055**		
Solothurn	**-0.37**	**0.055**		
Age	0.41	0.76	0.54	0.59
Age^2	-1.1	0.69	-1.5	0.12
Prior Investment	**-0.90**	**0.021**	**-43**	**< 0.001**
Sex [M] : Status			0.54	0.59
Sex [M] : Widowed	-0.015	0.086		
Sex [M] : Faithful	0.076	0.045		

[1] Number of: Observations: 2546; Nests: 1566; Pairs: 930; Individuals: 790; Years: 23 [2] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [3] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [4] Number of: Observations: 3597; Nests: 2201; Pairs: 1251; Individuals: 1075; Years: 31 [5] Number of: Observations: 3586; Nests: 2197; Pairs: 1251; Individuals: 1075; Years: 31 [6] Model did not converge succesfully.

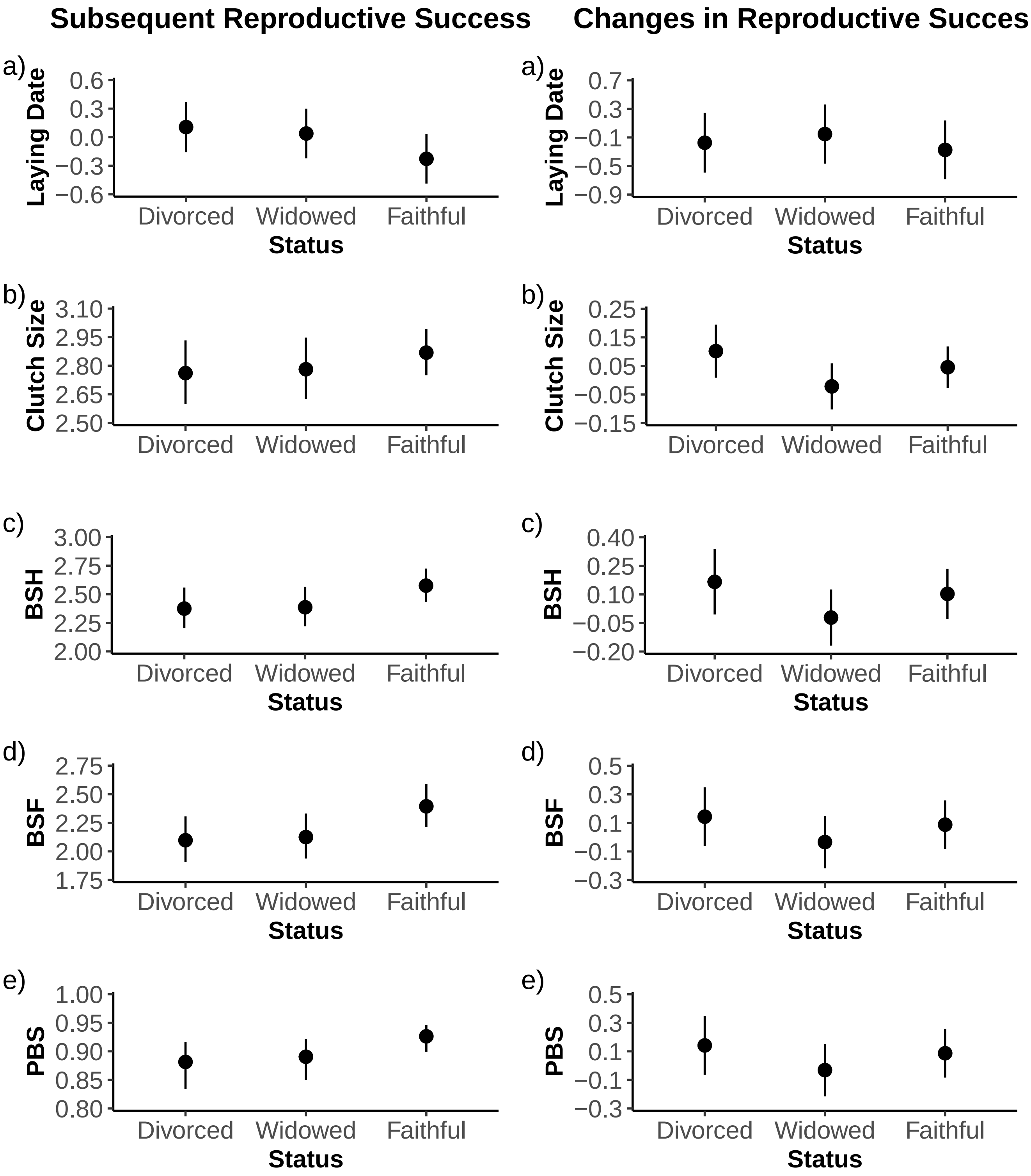


Figure D.6.: Subsequent reproductive success (left) as well as the changes in reproductive success (right) in relation to pair bond status. Reproductive success was modeled as laying date (a), clutch size (b), brood size at hatching (BSH) (c), brood size at fledgling (BSF) (d), and the weighted proportion of surviving fledglings (PBS) (e). Error bars correspond to the 95% confidence intervals. Data corresponds to male and female Alpine swifts from three Swiss colonies. Data spans 1991-2021.

Appendix E

R Packages

Table E.1.: Packages used to generate this thesis

Package	Version	Citation
asreml	4.1.0.149	Butler (2021)
base	4.3.1	R Core Team (2023)
car	3.1.2	Fox and Weisberg (2019a)
climwin	1.2.3	van de Pol et al. (2016b); Bailey and van de Pol (2016)
effects	4.2.2	Fox (2003); Fox and Hong (2009); Fox and Weisberg (2018); Fox and Weisberg (2019b)
ellipse	0.5.0	Murdoch and Chow (2023)
emmeans	1.8.9	Lenth (2023)
fable	0.3.4	O'Hara-Wild et al. (2024a)
feasts	0.3.2	O'Hara-Wild et al. (2024b)
flextable	0.9.4	Gohel and Skintzos (2023)
ggeffects	1.3.2	Lüdecke (2018)
ggpattern	1.0.1	FC et al. (2022)
ggthemes	4.2.4	Arnold (2021)
grateful	0.2.4	Francisco Rodriguez-Sanchez and Connor P. Jackson (2023)
gridExtra	2.3	Auguie (2017)
gt	0.10.1.9000	Iannone et al. (2024)
kableExtra	1.3.4.9000	Zhu (2023)

Table E.1.: Packages used to generate this thesis

Package	Version	Citation
knitr	1.46	Xie (2014); Xie (2015); Xie (2024)
lme4	1.1.34	Bates et al. (2015)
lmerTest	3.1.3	Kuznetsova et al. (2017)
MCMCglmm	2.35	Hadfield (2010)
nadiv	2.17.2	Wolak (2012)
patchwork	1.1.3	Pedersen (2023)
pedantics	1.7.1	Morrissey (2023)
plyr	1.8.9	Wickham (2011)
rmarkdown	2.26	Xie et al. (2018); Xie et al. (2020); Allaire et al. (2024)
rptR	0.9.22	Stoffel et al. (2017)
tidyverse	2.0.0	Wickham et al. (2019)
tinytex	0.48	Xie (2019); Xie (2023)
tsibble	1.1.4	Wang et al. (2020)
viridis	0.6.4	Garnier et al. (2023)
visreg	2.7.0	Breheny and Burchett (2017)
writexl	1.4.2	Ooms (2023)