

# **Sexual selection and Mating Strategies in a Bird with Little Apparent Sexual Dimorphism**

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# 1 INTRODUCTION

## 1.1 *Sexual Selection*

Amongst the incredible diversity of phenotypic traits that exist in the natural world, the most extreme and bizarre are near-universally attributed to sexual selection. 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 [1]. In other words, sexual selection arises as a result of among-individual variations in the ability to attract mates or repel rivals and thus achieve higher fitness, measured as the number of offspring an individual contributes to the next generation [2]. As such, sexual selection may play an essential role in the evolution and adaptation of species to their natural environment, with the potential to shape population dynamics in any cases where matings are non-random.

Though Darwin’s view of sexual selection was largely limited to pre-copulatory selection (i.e., mating success; [1]), theory has since expanded to include post-copulatory selection (i.e., fertilization success; [3]), and further encompasses traits relating to parental care (e.g., territory defence and nest building; [4]). 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 [5]. This encompasses many secondary sexual traits, broadly categorized by function as those attracting mates (ornaments) or those repelling rivals (weapons) [3]. For instance, birdsong in male Passerines has been shown to serve both theses functions, to attract potential mates and/or to deter potential competitors [6]. Sexual selection may thus be characterized as either intra- or inter- sexual selection [3]. Intra-sexual selection occurs when individuals of one sex (generally females) mate preferentially with individuals displaying favoured traits, while inter-sexual selection occurs when

individuals of one sex (generally males) compete amongst themselves for access to mates and for the fertilization of gametes. Broadly, pre-copulatory sexual selection is typically described as female choice and male-male combat, while post-copulatory sexual selection is typically defined as cryptic female choice (“(1) when females primarily or only use sperm of preferred mates for fertilizing eggs; and (2) when they nurture only or primarily zygotes fertilized by superior mates” [7]), and sperm competition (“competition between the sperm from two or more males for the fertilization of a given set of ova” [8]).

For example, in peacocks *Pavo cristatus*, sexual selection has favoured the evolution of elaborate male trains by female choice, 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; [9]), which appear to correlate positively with male immune function and offspring survival [10]. While the benefits of such a trait have been demonstrated in terms of reproductive success, larger trains may also be costly, thus ensuring the honesty of this signal (Zahavi’s [11] handicap theory; e.g., colouration as an indicator of developmental stability Loyau et al. [12], but see Askew [13] and Thavarajah et al. [14]). 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 [15]. 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 [16]. Such example of inter- and intra- sexual selection are numerous in the literature, with the bulk of research centred on the males of polygamous and strongly sexually dimorphic species [3].

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' [4] General Framework for Sexual Selection) and experimentally (e.g., Bateman's [17] Principal, but see Hoquet et al. [18] for a rebuttal). Likewise, the opportunity for sexual selection may be stronger in polygamous than monogamous mating systems [3], and dimorphism and polygynous mating systems are widely acknowledged correlates of strong sexual selection. Indeed, sexual selection seems 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" [19]. 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 [3], at both the pre- and post- copulatory levels. And yet, what of species where both sexes are ornamented to similar extents (either 'dull' or 'extravagant' mutual ornamentation)? Are females truly only accessories in the evolution of ornamental 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: [25]). Researchers have increasingly been targeting species with female-specific ornaments [26], the ornamented males of monogamous species [27] and species where both males and females are similarly and extravagantly ornamented [23]. Indeed, in the wattled jacana *Jacana jacana*, larger and more ornamented females are more successful at defending territories and acquiring mates [28], and, in sympatric populations, northern jacana *Jacana spinosa* females are so successful in intra-sexual conflicts that they can monopolize males of both *J. spinosa* and *J. jacana* [29]. In the dance fly *Rhamphomyia tarsata*, females with larger abdominal air sacs are preferred by males, which may honestly signal fecundity [30]. 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 choosy males and showy & competitive females [31].

Of particular recent interest are cases of sexual selection in weakly dimorphic species, where ornamental traits may be expressed to similar degrees in both sexes [32]. For example, in the crested auklet *Aethla cristatella*, both sexes have long feather crests, and individuals of both sexes with longer crests not only outcompete those with shorter crests, but are also preferred as mates [33]. In the black swan *Cygnus atratus*, individuals of both sexes prefer mates with more curled black wing feathers, assortative pairings form based on their numbers, and individuals with more of these curled black feathers enjoy a more dominant status [34]. Thus, examples of inter- and intra-sexual selection exist in both sex-role reversed and weakly dimorphic species, highlighting the diverse and widespread nature of sexually selected traits in both sexes. Furthermore, though the evolution of sexually selected traits and their role in mediating social interactions remains captivating, sexual selection is intrinsically linked to a number of additional processes such as mating strategies, pairing decisions, parental care, and sexual conflict. Many questions concerning these and other topics have been left unanswered and are of particular interest in monomorphic or subtlety dimorphic species.

Despite 150 years of study and an extensive body of works, the scope and extent of sexual selection and the very definition of this evolutionary process are still under considerable debate (see [5] for an overview). The applicability of sexual selection to females has been put into question, as has the need to modify the scope of sexual selection theory to explicitly extend to social selection, wherein competition may take place over resources other than mates [35]. The former has been largely resolved thanks to increasing interest in recent decades (though there is still a need for empirical work extending to a broader range of model organisms and mating systems, e.g., [36]). The latter has yielded little consensus among authors, with some arguing for sexual selection to be seen as an extension of social selection without meaningful distinction between the two (e.g., [38], others arguing for the sake of a narrow-sense modern definition (e.g., [25]), and others still arguing that both options have as many pitfalls as benefits with the solution being a careful consideration of terminology (e.g., [36]). This lack of consensus as to the generalities of sexual selection theory

is especially relevant to the study of subtly dimorphic species and extends to a longstanding debate over how to define several fundamental concepts. For instance, ‘individual quality’ and ‘individual condition’ are often used interchangeably and rarely defined despite their ubiquitous presence in the sexual selection literature.

## 1.2 *Individual Quality and Condition*

Central to the question of mate choice (and of the signalling function of ornaments) lies variations in the relative quality and condition of individuals. If all individuals were of similar quality and condition, and thus associated with equivalent fitness, there would be no benefits associated with mate choice and rather only costs. The costs of 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 risk of predation. The benefits of mate choice are primarily offspring of greater ‘quality’ or in higher quantity (hence, higher fitness), which are contingent upon discerning such a nebulous ‘high quality’ mate. Individuals may signal aspects of quality and/or condition through greater expression of ornamental traits, with those of lower quality and/or condition unable to do so due to associated viability costs (but see [39] for a review of honest signalling in traits that are not costly to produce) 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 [40]: thus, trade-offs, defined as an increase in one trait which improves fitness resulting in a decrease in another trait which also improves fitness [41], will occur. These trade-off strategies are possible between functions (i.e., reproductive senescence, trade-off between self-maintenance and reproductive output [42]) or between traits (i.e., condition-dependent ornamentation in three-spined stickleback *Gasterosteus aculeatus* males [43]). 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 [44].

As illustrated by Wilson & Nussey [45], the absence of formal definitions for the terms ‘individual quality’ and ‘individual condition’ has resulted in subtly different usages by different researchers. Wilson & Nussey [45] 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 not necessarily informative. Hill [46] 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. 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), 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, greater resources allowing increased reproduction and survival). Condition then refers to intra-individual fluctuations in the allocation of available resources between competing traits, which will likewise impact fitness. Hill [46] further defines condition-dependent traits as a “feature of an organism that varies in expression depending on the capacity to withstand environmental challenges.” Condition-dependence is therefore a form of environmental plasticity. Given the expected costs of ornamental traits, it is predicted that ornamental traits will have greater condition-dependence than non-ornamental traits, and that this difference would increase as the trait becomes more exaggerated.

An important caveat in measuring individual condition arises from the need to control for inter-individual variations in body size and/or quality. Typical body condition indexes (BCIs) attempting to do so utilize ratios (i.e., relationship between body mass and a mea-



sure of length), among other morphological or physiological indexes of condition [47]. The aim of these BCIs is generally to measure the pools of resources available to individuals in the form of stored fat, and to document among individual differences after controlling for body size [47]. 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 (e.g., [51]). 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* reared in poorly diversified food environments (low individual condition) were less selective than females with a more highly diversified diet (high individual condition) ([52]; see [53] 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 the consequences on fitness.

### 1.3 *Sexual Dimorphism and Allometry*

Allometry describes the ways in which individual traits scale with body size and is often used to quantify the relative investment of different-sized individuals into various traits. Variations in the size and shape of various traits can occur independently or in tandem with sexual size dimorphism (SSD) [2]. Allometry is described as “static” when it applies to individuals of the same species and developmental stage, as “ontogenetic” when it applies to changes through individual development stages, and as “evolutionary” when it applies to mean trait and body size covariation between species [54]. The equation  $Y = aX^b$  is often used to describe an allometric relationship where  $Y$  and  $X$  are indices of trait and body size, such as an ornament and body mass, respectively. The log-transformation of this equation results in  $\log(Y) = \log(a) + b \cdot \log(X)$  where  $b$  is the allometric slope. Despite remaining

debates in the literature, the use of regressions to examine sexual dimorphism and trait scaling is widely accepted (normalize data and control for confounding variables; [55]).

An allometric slope can be described as “isometric”, “positive” or “negative”. In the case of isometry, relative trait size is constant for all body size with an allometric slope of 1, suggesting equal resource allocation between traits across sizes. In the case of positive allometry, trait size is relatively larger with larger body size ( $b > 1$ ), while for negative allometry, trait size is relatively smaller with larger body size ( $b < 1$ ). Many traits show some degree of allometric scaling with body size, but secondary sexual traits under directional sexual selection have historically been expected to demonstrate strong positive allometry (e.g., [56]). Indeed, positive allometry should evolve when relatively larger traits confer their bearers an advantage in sexual competition, either through direct advantage [57], honest signaling [58], or when the relative costs are lower for larger individuals [59]. Under a positive allometry hypothesis [56], sexually selected traits should be more positively scaled than non sexually selected traits. However, as illustrated by Bonduriansky [54], this association in the literature between strong sexual selection and positive allometry may rather reflect a sampling and publication bias, with some sexually selected traits displaying positive, negative, or isometric allometry. It has been suggested that secondary sexual traits under intra-sexual selection are likely to exhibit positive allometry [56], while traits under inter-sexual selection are likely to exhibit negative allometry [54]. These and other studies highlight the controversy still surrounding the subject, with additional research needed to explore these differences in allometric patterns in sexually selected traits.

Furthermore, sexual dimorphisms in traits independently of SSD can be established by assessing the static allometric slopes of male and female traits and contrasting the two, which further allows inferences about the selection pressures acting on shared traits [60]. Indeed, ornaments may in some cases be defined based on their allometric slopes: for examples, in the fly *Chymomyza exophthalma*, head width serves as a signal of male condition during courtship and is positively allometric in males but isometric in females [61]. However, this

sex-specific allometry need not be the case in species where a shared trait may serve a signalling or competitive function in both sexes (e.g., positive allometry of the bill in both sexes of the common moorhen *Gallinula chloropus*, [62]).

## 1.4 *Mutual Ornamentation*

Thus far the bulk of research on sexual selection has focused on strongly dimorphic species where ornaments are expected to display strong positive allometry in one sex only. The growing body of work on weakly dimorphic species has generated important discussions about the nature and extent of sexual selection in both sexes and has clarified three main hypotheses explaining the evolution of mutual ornamentation: 1) Lande’s [63] genetic correlation hypothesis, 2) Huxley’s [64] mutual selection hypothesis, and 3) West-Eberhard’s [35] social selection hypothesis. Though not mutually exclusive [32], these hypotheses generate different predictions and may be disentangled from one another.

First, Lande’s [63] genetic correlation hypothesis surmises that ornaments serve a functional purpose in males only, while the matching ornaments in females are non-functional. In this view, genetic correlations between the sexes would lead to the evolution of ornaments in females as by-products of the intense sexual selection acting on males. This notion is grounded in the fact that, even accounting for sex chromosomes, the sexes share the vast majority of their genome [65], and thus this shared genetic architecture is expected to constrain the evolution of sexual dimorphism [66]. To describe the extent to which a genotype will affect the phenotype of both sexes, the cross-sex genetic correlation can be estimated ( $r_{MF}$ , [63]). An  $r_{MF}$  approaching 1 indicates that a genotype would be expressed in similar ways in both sexes (in this case, mutual ornamentation), while an  $r_{MF}$  approaching 0 indicates that the sexes will express independent phenotypes (in this case, sexually dimorphic ornamentation). One key assumption of this hypothesis is that ornamentation should not be costly in females, as even weak costs would break down the cross-sex correlation of the trait over evolutionary

time [63]. Average estimates of rMF reported approach 1 [67], yet the recent finding that as many somatic monomorphic as dimorphic traits are expressed through sex-dependent genetic architecture [68] suggests that sex-specific architectures are more common than previously believed.

Second, Huxley’s [64] mutual selection hypothesis proposes that ornamental traits expressed to similar degrees in both sexes are the result of equivalent sexual selection acting on both sexes, which suggests an adaptive value of the ornament in males as well as in females. The evolution of female ornaments may therefore be ascribed to similar mechanisms as those operating in males [22], the fitness benefits of which have been demonstrated in numerous studies [23,24]. Mutual selection is expected when 1) variance in reproductive success is similar in both sexes and 2) mate choice is associated with low costs and high benefits (i.e., mate encounter rates are high and individual quality varies in both sexes) [69]. This is often the case in monogamous species exhibiting biparental care [4], where both parents are required to invest heavily in their offspring to achieve reproductive success. Mutual selection is further predicted to result in assortative mating by mate quality [70], as demonstrated by a positive correlation between the partners of a pair [71] (e.g., [33]).

Third, West-Eberhard’s [35] social selection hypothesis suggests that ornaments are used as honest signals in competitions over resources other than matings, such as food, territories, and shelters (reviewed in: [37]). Indeed, not all examples of ornamental traits serve an obvious purpose during mating decisions, and so do not seem to fall under the purview of sexual selection. For example, juvenile American coots *Fulica americana* are highly ornamented with vivid orange-red natal plumage, which has been shown to play a role in parental investment [72], possibly serving as a reliable signal of chick size and age since colour is influenced by laying order [73]. Though this example appears to contradict the general notion that ornamental traits evolve as a result of sexual selection shared by many evolutionary biologists [3], the general process is reminiscent of inter-sexual selection—here too, individuals displaying the ornamental trait are preferred.

The literature has not yet yielded a consensus as to the relative roles of genetic correlations or mutual sexual selection or social selection in the evolution of mutual ornamentation, which warrants additional study. We also know surprisingly little about how effects of selection on one trait may relate to those on another, at the phenotypic and genetic levels. Sexual selection may act on multiple signal components across multiple sensory modalities (reviewed in [74]). As such, the traits in question may convey redundant or complementary information about underlying individual qualities and may also transmit information about signaller motivation (e.g., courtship vs. territorial defence vs. other social interactions [75] to one or more receivers (e.g., multiple receiver hypothesis, [76]. Indeed, sexually selected traits may convey redundant or separate messages to one or different receivers in a suit of social interactions, which may be the case in weakly dimorphic species. In any case, mate choice is far from static, and may occur at multiple points throughout a breeding season or an individual's life.

## 1.5 *Sexual Conflict*

Sexual conflict occurs when sex-specific selection, reflecting the sexes' different reproductive strategies, results in different fitness optimums for each sex [77]. Indeed, the reproductive interests of males and females are not always aligned and thus cannot be simultaneously satisfied [78], 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 & cheap sperm vs. large & 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 [79], 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: [80]).

Two forms of sexual conflict have been described: intra-locus and inter-locus [77]. Inter-locus sexual conflict occurs as a result of different fitness optimums over the outcome of male-female interactions and involves genes at different loci. In such a situation, an allele that produces a phenotypic trait in one sex (males) which enhances their reproductive success but harms their mates (females) as a side effect may persist in a population and result in the appearance of an allele at another genetic locus mitigating that harm, thus resulting in sexually antagonistic coevolution. Bateman’s experiment on mating rate in *Drosophila melanogaster* [17] is often cited as a classical example of inter-locus conflict between the sexes. 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 [77]. This form of sexual conflict may be resolved by the evolution of sexual dimorphism and is therefore expected to be strong and ongoing in weakly dimorphic species. Estimating this potential for conflict may be done through cross-sex genetic correlations [63].

## 1.6 *Study Specie & Site*

The Alpine Swift (*Tachymarptis melba*) is a long-lived (lifespan: median of 7 years; maximum of up to 26 years), migrant and colonially nesting Apodiformes bird. They live a highly aerial lifestyle, remaining on wing at all times except during the breeding season [81]. As a result, their biology (and that of Apodidae as a whole) remain poorly understood, especially so outside the reproductive period. Alpine Swifts typically nest on cliffs, and in the past decades, in the roof spaces of tall buildings. They are socially monogamous, with

relatively low rates of extra-pair copulations (approaching zero; P. Bize, unpublished), and mate and nest site fidelity are high in both sexes. Both parents incubate their single yearly clutch of between 1-4 eggs for approximately 20 days, and provision offspring until they fledge at around 50-70 days [83]. Fledglings typically return to their natal colony the next year, and do not disperse once settled. Previous research in this species has demonstrated that dispersing individuals are a non-random subset of the population, generally corresponding to those who are less prone to risk taking behaviours and who may therefore reducing the costs associated with dispersal by favouring survival and integration into the new social environment [84]. Furthermore, Alpine Swifts are highly parasitized by the bloodsucking louse fly *Crataerina melbae*, which may entail differential resource allocation between current and future reproduction [83]. Bize et al. [85] demonstrated that female-biased mortality occurs in broods with experimentally heightened parasite infestations, and suggest that this phenomenon reflects heightened sibling competition and parental favouritism of male offspring.

Although Alpine Swifts appear monomorphic to human observers, subtle sexual dimorphisms are present and likely reflect secondary sexual traits: the white throat patch is larger in females while fork length is longer in males, and the rachis of the breast patch feathers is likewise more highly melanized in males (P. Bize, unpublished). These traits are highly variable within each sex, and breast patch melanization is highly heritable [86]. Tail fork length is likely (or was) under directional sexual selection. As demonstrated by Hasegawa & Arai [87] in a comparative study between Swifts and Swallows, deeply forked tails in male Swifts of the Apodini and Collocaliini tribes ( $n = 39$ ) occurred as a result of decreasing central feather length, which impairs tail lift. Forked tails seem to be associated with agility and maneuverability in a number of avian species, and thus forks longer than the aerodynamic optimum of the species may result from sexual selection. The selection mechanisms favouring deeply forked tails and the relative importance of direct and indirect benefits of mate choice based on this preference remains to be clarified. Further, fluctuating asymme-

try reflects the deviation from symmetry in bilateral morphological traits [88] such as forked tails, and is expected to occur as a result of the trade-off between growth and maintenance. Hence, fluctuating asymmetry in fork tail length may play a role in sexual selection as a signal of individual quality and/or condition. Similarly, white feather spots are subject to increased breakage, abrasions, and parasites in many bird species [89], which, if only high-quality/condition individuals are able to display such a costly signal, might grant them the capacity of honest signaling. In addition, reproductive success is highly variable in the Alpine Swift, with approximately 25% of breeding individuals account for 80% of offspring production [90], further suggesting a role of sexual selection in this species: sexual selection has the potential to be extremely strong when variance in reproductive success is high. Thus, there is reasonable evidence that these traits fulfill the roles of ornaments and have evolved, at least partly, by sexual selection.



Figure 1: Alpine Swift in flight. The characteristic long narrow wings, achromatic throat patch and forked tail are visible, as are the dark rachis of the melanized breast patch feathers. Photo credited to Gordon Speirs, 2017.

The wild colonies of Alpine Swifts in Switzerland which I will study during my doc-



toral thesis have been closely followed at the individual level for over twenty years: Bienne (~100 breeding pairs) since 2000, and Solothurn (~50 breeding pairs) since 1999. As such, outstanding information has been collected for this system detailing morphological traits (including tail fork length, throat patch size, and breast patch melanization), sex (accurately determined from blood cell DNA [91]), reproductive success, natal dispersal, divorce, as well as a detailed pedigree [84]. This full pedigree pertains to 8465 individuals, with 72.89% maternity assignment (6170 individuals) and 71.16% paternity assignment (6024 individuals), 17162 full siblings, and a maximum pedigree depth of 6. In addition, there may be opportunities throughout my PhD to utilize data collected from other colonies in Switzerland with similarly extensive individual-based data (e.g., Baden, where the colony has been followed since 1990 as well as Seengen & Luzern which have both been followed since 2017), and to visit these colonies to collect data on traits such as throat patch size and brightness.

The availability of such a detailed pedigree, still relatively rare for wild populations, will allow me to perform analyses of genetic variance [93]. In particular, animal models will be used, which are linear mixed-effects models fitted to estimate the relative contributions of genetic or environmental factors of phenotypic variations [93]. Since the traits I will be studying are expressed in both sexes with subtle sexual dimorphism in their appearance, multiple questions about how sexual selection has shaped signal evolution in the wild may be explored, namely sex-based differences in their signaling value at both the phenotypic and genotypic level, the genetic architecture of ornamental traits and the potential for inter-locus sexual conflict, the adaptive value of mating strategies such as divorce, and inter-individual variations in parental care. Importantly, few studies have addressed these questions in both sexes simultaneously. Thus, the Alpine Swift is an excellent model species for my doctoral thesis, which will shed new light on the evolution and maintenance of ornamental traits expressed to similar degrees in both sexes, as well as the adaptive value of mating strategies such as divorce, at both the phenotypic and genetic level, in a wild population.

## 1.7 *Scope & Thesis Objectives*

The main objective of my doctoral thesis is to investigate how sexual selection operates within and between the sexes in an Apodiformes bird with little apparent sexual dimorphism, the Alpine Swift. I will investigate within and between individual variations in ornamental traits as well as fitness variations associated with mating and parental strategies in both sexes. I will consider four potentially ornamental traits: 1) tail fork length, 2) achromatic throat patch size and 3) throat patch brightness, 4) breast patch melanization; and two mating strategies: 1) divorce (vs. mate fidelity), and 2) natal dispersal (as assortative or non-assortative pairings); as well as components of parental investment. My doctoral thesis will answer the following questions, each corresponding to one chapter.

1. How does sexual selection drive the evolution and maintenance of secondary sexual traits and what is their current signalling function?
2. What are the relative contributions of additive genetic (heritable) and environmental effects on phenotypic variation in secondary sexual traits?
3. What are the adaptive advantages of divorce (vs. mate retention) and of assortative (vs. non-assortative) pairings following natal dispersal in the context of local adaptation?
4. Does nest location and composition reflect parental quality and how does experience affect male, female, and total parental investment (and in turn fitness)?

## 2 CHAPTER 1

Explaining the evolution and astounding diversity of secondary sexual traits found in nature has been a central question in evolutionary biology for over a century. Evolutionary theory predicts that sexually selected traits should demonstrate higher phenotypic variation than other traits [44], and further predicts that directional sexual selection may generate

positive allometry in relation to body size [56] (but see [94]). Despite a longstanding focus on ornamented males of sexually dimorphic species, these signals can occur adaptively in either or both sexes in the context of sexual selection. In subtly dimorphic species, an intriguing question is whether the selective pressures shaping the evolution and maintenance of ornamental traits differ between the sexes, potentially resulting in different signaling functions of a shared ornament.

In my first chapter, I will investigate the selection pressures shaping and maintaining four sexually dimorphic and potentially ornamental traits (tail fork length, breast patch melanization, throat patch size & brightness) as well as the signaling values of these traits in both sexes of the Alpine Swift. In a first part, I will describe the morphology and subtle sexual dimorphism of the Alpine Swift. Sexual dimorphism—and specifically sexual dichromatism, as in the case of breast patch melanization and the achromatic throat patch—may occur as a result of sexual selection [95], and thus shed light on the sex-specific selection of specific traits. I predict a stronger effect of sexual selection on tail fork length in males and on throat patch size in females, demonstrated by male and female biased trait expression, respectively. To further understand the role of sexual selection in ornamental trait evolution in this species, I will compare their allometric slopes between the sexes. In a second part, I will investigate the signalling value and fitness benefits of these traits in relation to individual quality, condition and body size (allometry) in both sexes. I will explore if the correlation between these traits and individual condition differs between the sexes; should the trait serve a similar signaling function in both sexes, the correlation would be positive in both sexes, while a lack of function would result in a null correlation in one or both sexes (illustrated in figure 2.) Because Alpine Swifts are (socially & genetically) monogamous, and because biparental care is required to ensure the successful fledgling of a brood, mutual mate choice is predicted to occur [32]. Mutual mate choice is predicted to result in assortative mating; condition dependence of a shared trait in both sexes may likewise suggest that the trait is used to guide mating decisions by both sexes.

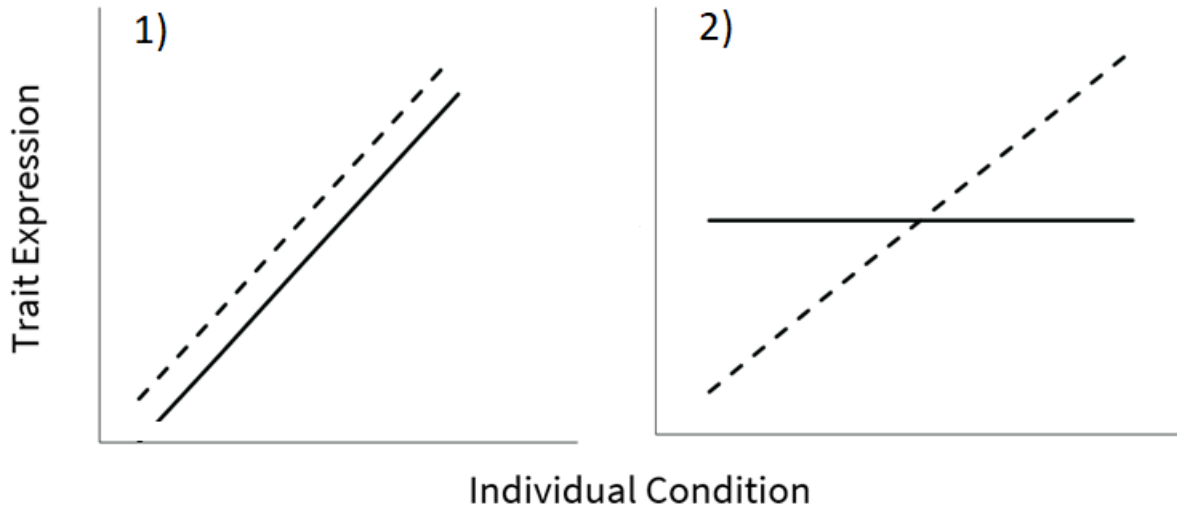


Figure 2: Predicted relationship between the potentially ornamental trait (tail fork length, breast patch melanization, throat patch size and brightness) and individual condition in male and female Alpine Swifts in two different signaling scenarios. This relationship may indicate 1) a similar signaling function in both sexes (positive correlation in both sexes), or 2) a lack of signaling function in one sex (positive correlation in one sex and null correlation in the other).

Hence, in this first chapter I aim to clarify the role of sexual selection in shaping the evolution and maintenance of four weakly dimorphic traits and investigate the relationships between individual quality, condition, body size, fitness and these traits in both sexes. I will do so using 23 years of data on fork tail length, throat patch size and breast patch melanization, and 2 years of data on throat patch size and brightness using a photographic approach. While detailed data on tail fork length, throat patch size, and other individual based information such as nest location and reproductive success is included in the long-term database (spanning from 1999-2020; as well as feathers collected to analyze brightness from 2008), subsequent data on throat patch size & brightness will be simultaneously collected using a photographic approach. This approach will allow me to explore the potential for plumage variations to reveal subtle sex differences and trait signalling functions with greater

precision (data on throat patch size collected with a calliper may not be repeatable and highly dependent on the bird's body position). As such, the following subsections details the pilot study on throat patch size assessment via photography and the preliminary analyses of that data as well as data from the long-term database. During the 2021 field season, data on the achromatic throat patch was collected for over 200 individuals using both the photographic and calliper approaches, hence these methods will be compared.

## ***2.1 Achromatic Throat Patch Pilot Study***

The achromatic throat patch was photographed by holding each bird against a ruled background at a standard distance from the camera lens. I measured throat patch area using a standardized thresholding procedure in ImageJ software (U.S. National Institute of Health; <http://rsb.info.nih.gov/ij/>) after converting the photos to 8-bit greyscale. Using ImageJ, I also measured width and length of the throat patch, as well as width of the body at the shoulders, length of the achromatic patch at the shoulder, and total head patch length (achromatic patch + brown collar).

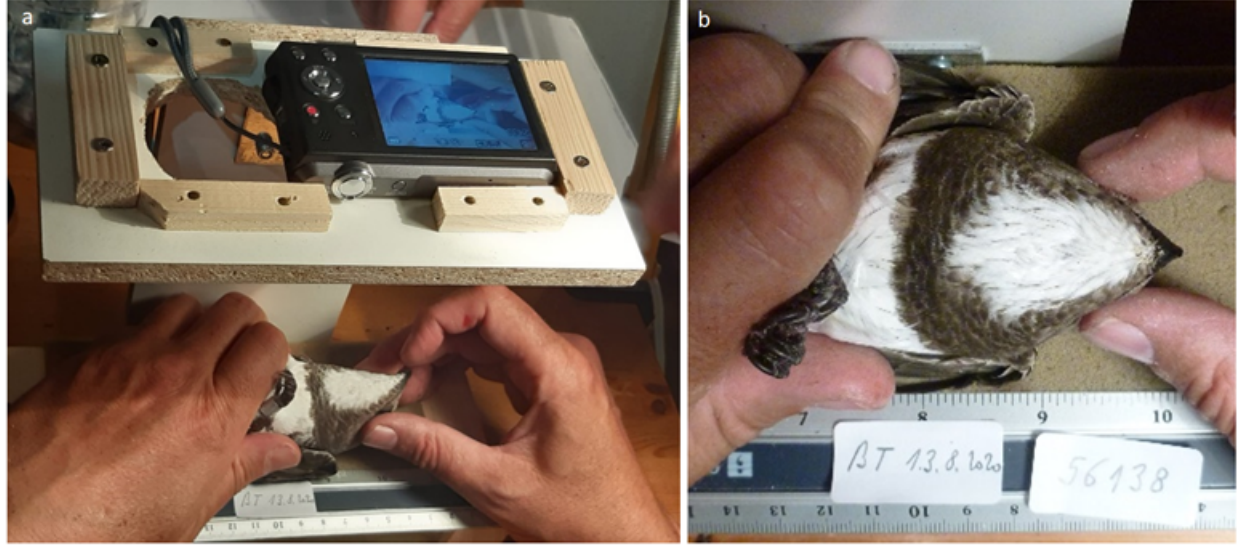


Figure 3: a. Equipment used to photograph the achromatic throat patch. b. Resulting photo of an individual, with the achromatic throat patch clearly visible, wings folded, and head in a neutral position. Breast feather melanization is visible (dark rachis of the feathers), which is another ornamental trait that may be further assessed during my thesis. Photos credited to Pierre Bize.

An initial 22 individuals were used to assess measurement repeatability, for which the photos of the achromatic white patch were deemed of ‘high quality.’ These photos were selected based on the following criteria: neutral position of the head, even lighting of the achromatic throat patch, feathers not too ruffled, and wings closed and tucked against the body in a neutral position. The six measures listed above as well as pixel value of the scale were recorded four times independently of one another, and repeatability was then estimated using the *rptR* package [96] in R version 4.0.4 “Lost Library Book” [97]. All measures were highly repeatable, indicating a very small measurement error: Pixel Scale ( $R = 0.945$ ,  $CI = [0.884, 0.964]$ ); Area ( $R = 0.968$ ,  $CI = [0.934, 0.981]$ ); Width ( $R = 0.918$ ,  $CI = [0.804, 0.952]$ ); Length ( $R = 0.909$ ,  $CI = [0.818, 0.949]$ ); Length including Brown Collar ( $R = 0.915$ ,  $CI = [0.841, 0.948]$ ); Width at Shoulder ( $R = 0.972$ ,  $CI = [0.949, 0.984]$ ); Length at Shoulder ( $R = 0.989$ ,  $CI = [0.979, 0.994]$ ).

Next, 11 individuals were used to assess variation between individuals, for which two independent photos were taken. Inter-individual variation was estimated: Area ( $R = 0.679$ ,  $CI = [0.274, 0.894]$ ); Width ( $R = 0.33$ ,  $CI = [0, 0.754]$ ); Length ( $R = 0.191$ ,  $CI = [0, 0.65]$ ). Though the sample size is extremely small and thus results for width and length of achromatic throat patch are not statistically significant with a very large confidence interval, inter-individual variance is detected and suggests that this photography-based protocol is sufficient to analyze variances in this ornament.

Finally, preliminary analyses were conducted for the 22 (12 female, 10 male) individuals with known molecular sex. The achromatic throat patch area is of 8.53 ( $CI = [8.06, 9.00]$ )  $\text{cm}^2$  in females and of 8.22 ( $CI = [7.70, 8.73]$ )  $\text{cm}^2$  in males. Though the sample size is small and the confidence intervals overlap, this 3.64% difference in throat patch area is in line with the current expectation that the achromatic throat patch is larger in females. In future analyses with larger sample sizes, individual body size will also be controlled by sternum size (tarsus length is not an accurate proxy of size in the Alpine Swift as a result of their morphology). Further, time between observations may explain variations in phenotypic expression otherwise attributed to individual identity [98]; to account for this potential confounding source of variation, the date of measurement will also be included in future analyses. In the 2021 field season, data for over 200 individuals was collected, many of whom were captured and photographed at two different time points to assess within-year individual repeatability. Current results suggest that while males are overall larger than females, achromatic throat patch area is larger in females than in males, suggesting either sex-specific costs or sex-specific signalling functions of this trait in both sexes.

## ***2.2 Preliminary Analyses: Long-Term Data***

The data set (1999-2020) includes information for 1508 individuals, of which 1271 are of known sex. The data pertains to 657 females (252 from Solothurn (BT), 405 from Bienne

(SK)) and 614 males (229 from Solothurn (BT), 385 from Bienne (SK)). Blood samples have been taken from all individuals, and hence the individuals of unknown sex will be molecularly sexed in the year to come.

In a first part, I began assessing the presence of subtle sexual dimorphism in ten morphometric traits: wing length, tail length, tail fork length, tail fork fluctuating asymmetry, sternum length, breast patch melanization, throat patch width, throat patch length, throat patch area, and beak length (Table 1.). Sexual dimorphism, summary statistics (sample size, mean, confidence interval; Table 1.) and repeatability (Table 2.) are reported for all ten morphometric traits in relation to sex. In addition, univariate linear mixed effects models were fitted using the R package lmerTest [99] with each morphometric trait as response variable and sex as fixed effect, and individual identity and year as random effects (Table 1.). Assumptions of the models were verified, and where needed (e.g., fork fluctuating asymmetry) data were log transformed to account for non-normal distributions.

Table 1: Descriptive statistics reporting: sample size (N individuals), mean, and 95% confidence intervals in [lower; upper] for both sexes, the percentage of sexual dimorphism (SD; estimated as (male.trait – female.trait) / female.trait \*100), as well as the result of linear mixed-effects models testing for differences between the sexes after controlling for individual identity and year as random effects. A positive value of SD denotes male trait > female trait while a negative value denotes male trait < female trait (in %).

	Females			Males			SD (%)	Estimate	SE	df	t	P
	N	Mean	CI	N	Mean	CI						
Wing Length	648	225.5	[225.2; 225.8]	610	227.9	[227.5; 228.2]	1.05	2.4	0.2	1237.6	9.89	<0.001
Tail Length (mm)	648	87.2	[87.0; 87.4]	609	88.8	[88.6; 89.0]	1.83	1.6	0.2	1242.1	10.49	<0.001
Fork Length (mm)	648	22.4	[22.2; 22.5]	608	24	[23.9; 24.2]	7.49	1.6	0.1	1223.7	13.54	<0.001
Fork Fluctuating Asymmetry (mm)	597	1.2	[1.1; 1.3]	558	1.2	[1.1; 1.3]	1.59	0.01	0.02	864.9	0.49	0.624
Sternum (mm)	589	40	[39.9; 40.1]	556	40.7	[40.6; 40.8]	1.64	0.7	0.1	1140.9	9.28	<0.001
Breast Coloration (0-3)	593	1.1	[1.0; 1.2]	562	1.2	[1.1; 1.3]	10.5	0.1	0.1	1151.4	1.79	0.074
Throat Width (mm)	385	22.13	[22.0; 22.3]	386	22.06	[21.9; 22.2]	-0.3	-0.1	0.1	632.5	-0.81	0.417
Throat Length (mm)	385	42.04	[41.9; 42.2]	386	41.75	[41.6; 41.9]	-0.71	-0.2	0.1	647.6	-2.57	0.01
Throat Patch Area (mm2)	385	931.73	[923.6; 939.9]	386	922.38	[914.6; 930.2]	-1	-7.9	4	676	-1.97	0.05
Beak Size (mm)	392	8.5	[8.5; 8.6]	375	8.7	[8.6; 8.7]	1.52	0.1	0.03	705.8	4.91	<0.001



Table 2: Individual-based repeatability and 95% confidence interval in [lower; upper] after conditioning on sex (LMM models with individual identity and year as random effects), as well as total number of individuals (N) and observations (n) considered.

	<b>N</b>	<b>n</b>	<b>Repeatability</b>	<b>CI</b>
Wing Length (mm)	1258	4759	84.2	[81.3; 86.2]
Tail Length (mm)	1257	4722	81.4	[79.8; 83.0]
Fork Length (mm)	1256	4724	70.9	[65.8; 74.9]
Fork Fluctuating Asymmetry (mm)	1155	4174	7.4	[4.9; 9.6]
Sternum (mm)	1145	3872	94.9	[94.2; 95.4]
Breast Coloration (0-3)	1155	4258	84.9	[83.3; 85.8]
Throat Width (mm)	557	2592	23.1	[14.5; 31.5]
Throat Length (mm)	771	2592	27.6	[21.7; 35.5]
Throat Patch Area (mm <sup>2</sup> )	771	2592	26.5	[18.0; 39.0]
Beak Size (mm)	767	2166	46.6	[35.5; 56.9]

I report sexual dimorphism ranging from 0.3% to 10.35% in the Alpine Swift. If allometric slopes were similar between the sexes for all traits, we might also expect that sexual dimorphism would likewise be expressed in the same way for all traits. Hence, the reported mix of male- and female- biased sexual dimorphism suggests these traits are expressed in different ways between the sexes, with the potential to be sexually selected ornaments and to have different allometric slopes. Of interest, males have 7.49% longer tail forks than females, and females have 1% larger throat patch areas than males, which is in line with my prediction that sexual selection acts more strongly on male fork tail length and female throat patch size. Tail fork length is highly repeatable after conditioning on sex ( $R = 70.9\%$ ,  $CI = [65.8; 74.9]$ ), and males have on average 1.6mm longer fork tails than females, associated with a p-value  $< 0.001$ . Repeatability of throat patch area after conditioning on sex is lower ( $R = 26.5\%$ ,  $CI = [18.0; 39.0]$ ), and while females have on average 7.9mm<sup>2</sup> larger throat patch areas than males the difference is associated with a p-value of 0.05. The low individual-based repeatability after conditioning for sex of throat patch area may be due to relatively

low measurement precision for which minute differences in bird body position strongly impact results, hence my intention of pursuing a photography-based approach methodology to study this possible ornament. Breast patch melanization of the feather rachis also appears dimorphic with a 10.5% difference between sexes (males tend towards a higher melanization score than females) and will be further investigated in a similar fashion. I will subsequently begin assessing the condition dependence and fitness correlates of these ornamental traits (and will also do the same for throat patch brightness & size with the photographic approach once sufficient data has been collected; pilot studies are to take place this summer). Data on laying date, egg size, hatching date, brood size at fledgling and lifetime number of recruits will be used to assess individual fitness, and parasite load, body condition, and age will be used as proxies for individual condition.

### 3 CHAPTER 2

Evolutionary change in natural populations requires that any generational changes in phenotypic diversity—be they due to nature or sexual selection—be passed on to the next generation via genes. A quantitative genetic approach may be used to quantify this genetic architecture, for which the phenotypic trait of interest is likely to be influenced by multiple genes as well as environmental factors [93]. Relevant (and statistically estimable) parameters include the additive genetic variance ( $V_A$ ) of the trait, its heritability ( $h^2$ , where  $h^2 = V_A / \text{total phenotypic variance } V_P$ ), and any genetic correlations with other traits. In addition, trade-offs between different components of fitness are generally assumed to affect evolutionary processes, thus implying a genetic basis of these traits. As illustrated by Kruuk et al. [93], genetically based trade-offs require either: 1) a negative genetic correlation between two traits which are selected in the same direction, or 2) a positive genetic correlation between two traits which are selected in opposing directions. These trade-offs can occur at different levels, such as between environments (e.g., GXE interactions), between generations

(e.g., maternal effects), or between the sexes (e.g., intra-locus sexual conflict), and can be applied to either the same trait expressed in these different conditions or two different traits entirely [93].

In the case of intra-locus sexual conflict, alleles that increase fitness in one sex may decrease it in the other sex [100], with sexual dimorphism potentially resolving this conflict. However, significant shared genetic architecture between the sexes will hamper the evolution of sexual dimorphism [101] and can be assessed by the cross-sex genetic correlation ( $rFM$ , a standardized measure of the additive genetic covariance between males and females for a given trait [63]). Indeed, an  $rFM$  approaching 1 indicated a strong correlation between the sexes reflecting shared genetic architecture [67], wherein selection on the trait in one sex will result in correlated selection on the trait in the other sex. An  $rFM$  approaching 0 would rather indicate no or little additive genetic correlation between the sexes and thus the possibility for each sex to evolve to their own trait optima [102]. Hence, sexually dimorphic traits are likely to have experienced (or are potentially experiencing ongoing) intra-locus conflict, especially so in subtly dimorphic species. As such, the Alpine Swift provides an excellent opportunity to examine the sex-specific genetic architecture of traits expressed in both sexes as well as the cross-sex genetic correlations between them. Few studies have explicitly quantified the extent of shared genetic architecture between males and females for ornamental traits, making it difficult to assess the generality of cross-sex correlations and their impact on evolution and requiring further study. Furthermore, though cross-sex genetic correlations are population and environment specific (different allele frequencies, GXE interactions, respectively; [103], there are still relatively few studies estimating  $rFM$  in different populations of the same species, which is likewise relevant in the Alpine Swift as multiple distinct colonies have been studied.

In my second chapter, I will examine the sex-specific genetic variance and cross-sex genetic correlations of four traits (tail fork length, breast patch melanization, throat patch size & brightness). In a first part, I aim to quantify the relative contributions of additive genetic

(heritable) and environmental effects for each of these traits using univariate animal models (mixed models with individual identity linked to a pedigree [93]). The long-term database includes pedigree informing pertaining to 8465 individuals with ~70% parental assignment extending over a maximum of 6 generations (restrained to individuals of known sex: 1290 individuals; molecular sexing is still ongoing). Since repeatability is accepted as a preliminary indication of heritability [104], fork tail length is likely to be heritable ( $R = 70.9\%$ ,  $CI = [65.8; 74.9]$  after conditioning on sex), with throat patch size & brightness remaining to be assessed using the photographic approach. Next, I will investigate the potential for intra-locus conflict for each of these traits using bivariate animal models (sex-specific variation & cross-sex genetic correlations). Indeed, evidence of cross-sex genetic correlations in combination with the sex-specific selection gradients identified in my first chapter will allow for stronger conclusions about the mechanisms driving dimorphism in this specie. Finally, I am interested in population specific (i.e., differences between colonies) and GXE interaction differences in these cross-sex genetic correlations, if identified in the previous step. I will assess both the early (nestling stage) and late (adulthood) socio-ecological environments in these analyses, estimated by measures of weather conditions (temperature, precipitation in the year of bird and of measure), offspring rank in the brood (hatch date, number of siblings), and colony size (number of breeding pairs).

## 4 CHAPTER 3

Adaptive mate choice should result in a positive effect on fitness, occurring on the basis of traits assessed prior to mating (including ornaments, territories, or parental care). Changes in the social environment play a key role in the adaptive value of mating systems and may for example include those driven by natal dispersal—the movement of individuals from the site of their birth to a removed breeding site. Indeed, the dispersal of a non-random subset of the population may have important implication for gene flow, which, in the context of local

adaptation, may further impact pairing decisions on the basis of dispersal status (assortative or non-assortative matings) [105]. 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 [71]. The condition dependence of sexually selected traits has been shown to vary with environment [106], as a possible response to the different costs and benefits of these traits in a given micro-environment.

In many bird species, a positive relationship exists between the duration of the pair bond and lifetime reproductive success [107,108]. However, some individuals seek additional mating opportunities in the form of extra-pair copulations and even abandon a current partner, potentially incurring the loss of the brood (divorce, also called mate switching). 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 [109]. These modifications of the initial mating decision may be adaptive, should they increase an individual's reproductive success, and potentially reflect the existence of suboptimal pairings. In a recent phylogenetic meta-analysis, Culina et al. [109] highlight the adaptive nature of divorce in female birds of monogamous species, where low breeding success in a breeding season  $X$  triggers divorce and results in improved breeding success in season  $X+1$ . The costs of divorce (i.e., time spent searching for and assessing new mates, delays in egg laying, poor coordination of parental duties due to unfamiliarity, [110] are likely to differ between the sexes, and the possibility of cross-sex genetic covariance could generate sexual conflict [77]. The evolutionary causes of divorce are still under considerable debate, though it is a probable outcome of sexual selection and several hypotheses have been formulated to explain this phenomenon (reviewed in [110]. Indeed, 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 [23], assuming that such variation underlying the trait is heritable. Very few studies have examined the heritability of divorce in birds (e.g., Wheelwright & Teplitsky [111] report no additive genetic variance in Savannah sparrows,

while Germain et al. [112] report low but non-zero heritability of divorce in both sexes in song sparrows *Melospiza melodia*). While low heritability would limit the possibility for evolution, these studies do highlight the complex relationship between divorce, breeding success, and species-specific life-history traits (such as natal dispersal) which warrants further study.

In my third chapter, I will examine patterns of divorce (vs. mate retention) and of natal dispersal (assortative vs non-assortative pairings). In a first part, I will determine overall patterns in divorce and natal dispersal in the Alpine Swift, including their likelihood, annual rates, sex and age differences, and occurrences of overlap. In the Alpine Swift, divorce occurs in 11.1% of females and 10.5% of males, ranging from 2.4% (2015) to 16.9% (2003) overall per year between 1999 and 2019. Natal dispersal occurred in 221 of 590 females and 250 of 540 males followed between 1999 and 2020 (additional data to be made available following molecular sexing of individuals captured during this period). I will subsequently compare annual reproductive success (estimated by laying date, clutch & egg size, hatching & fledgling success) between the mate retention, divorce, and mate loss subgroups, and between philopatric and dispersing individuals (including assortative vs. non-assortative pair formation between immigrants and residents) for both sexes. This will allow me to assess long-term reproductive success in the different subgroups as well as to compare their relative reproductive success. In a second part, I will determine the predictors of divorce and dispersal and their overlap (if occurring in sufficient numbers) by evaluating the ways in which social environmental variations (estimated by sibling status, number of breeding pairs, and natal dispersal), age, personality traits (e.g., risk taking in nest defence), and degree of ornamental trait expression (depending on final results from chapters 1 & 2) shape the fitness of mate retention versus divorce versus mate loss and of assortative versus non-assortative natal-colony pair formation in dispersing individuals. I will do so with multivariate animal models, which will also allow for the partitioning of additive genetic variance for these traits, their covariance, and the possible genetic correlations between sexes.

## 5 CHAPTER 4

Reproductive success is not only contingent on the choice of a partner before mating, but also on parental care. This is particularly true in monogamous species, where exclusive pair bonds are formed with a single partner for at least one reproductive event [113], and where bi-parental care is frequently required to successfully rear a brood. Indeed, parents of many species contribute far more to their offspring than only genes, and the quality of these non-genetic parental contributions and their impact on offspring viability can vary significantly between individuals and between the sexes. In addition, bi-parental care requires that both parents cooperate in the rearing of their brood, which seems likely to occur in long-lived species where repeated interactions occur over time, resulting in overlap between the lifetime reproductive success of an individual and their partner—equal care is predicted to increase with pair-bond duration, with positive impacts on reproductive success [114]. As such, parental investment remains an important topic in evolutionary biology and in any study of sexual selection, though the evolutionary link between the two is not always straightforward (i.e., differences in parental investment can affect mate availability, competition, and choice, and parental investment may itself be a sexually selected trait; reviewed in [115]). In birds, parental investment can include a wide range of complex behaviours (e.g., nest building, incubation, and offspring provisioning; [80]) which increase the fitness of the offspring at the cost of the parents' future reproduction and survival [4]. The costs of parental care are especially high in time and energy and can reduce future parental survival and limits opportunities for additional matings [116]. Nest building and incubation are especially important parental behaviours, as this parentally controlled micro-environment directly relates to embryo development and hatching success [117]. In altricial species where chicks are entirely dependent upon care provided by their parents, feeding rate is further strongly correlated with nestling growth and survival [118]. The highly aerial lifestyle and specialized biology of the Alpine Swift makes nest-building an especially time consuming and

costly process: as a result of their short legs suited for clinging to cliff walls and little else, all nesting materials must be collected on wing, and as such may directly reflect parental condition and investment.

In my fourth chapter, I will investigate the signaling value and fitness benefits associated with nest location and composition, in relation with the individual quality and condition of the parents. I predict that pairs with larger-sized nests will have greater fitness than pairs with smaller-sized nests. If data availability makes it possible, I will also investigate the role that age (and thus experience) will play in male, female, and total parental investment. I will estimate parental investment using measures of nest location within the colony (since some parts of the colony are more infested by the bloodsucking louse fly than others [119], nest size & shape (quantity of nesting material at hatching, assessed via photos), nest defence behaviours, and offspring provisioning frequency (possible proxy: nestling growth rate over a fixed period). These measures will reflect pair-level parental investment, and as such do not allow conclusions as to sex-specific variations in parental investment. Indeed, though sex-specific differences in parental investment at the nest building, incubation and offspring provisioning stages may be difficult to assess, this information would enable stronger conclusions as to the link between sexual selection and parental care in this species and will potentially be investigated over two consecutive field seasons using RFID technology (to accurately monitor individual appearances at the nest) and by video analysis. I would like to assess if reproductive success is jointly determined by own and partner investment by correlating male, female, and total parental investment (as sex-specific quality of nesting material provided, duration of incubation, and offspring provisioning frequency) with lay date, hatching date, offspring growth rate, and fledgling success. Pursuing this additional avenue of research will depend on speed of progress and results of previous chapters.



# BIBLIOGRAPHY

1. Darwin C. 1871 *The descent of man, and selection in relation to sex*. Vol. 2. London, UK: John Murray.
2. Westneat DF, Fox CW. 2010 *Evolutionary Behavioral Ecology*. Oxford University Press.
3. Andersson M. 1994 *Sexual selection. Monographs in behaviour and ecology*. Princeton, NJ: Princeton University Press.
4. Trivers RL. 1972 Parental investment and sexual selection. In *Sex. Sel. Descent man darwinian pivot*, pp. 136–179. (doi:10.4324/9781315129266-7)
5. Shuker DM. 2010 Sexual selection: endless forms or tangled bank? *Anim. Behav.* **79**, e11–e17. (doi:10.1016/j.anbehav.2009.10.031)
6. Kroodsma DE, Byers BE. 1991 The Function(s) of Bird Song. *Am. Zool.* **328**, 318–328.
7. Thornhill R. 1983 Cryptic female choice and its implications in the scorpionfly *Harpobittacus nigriceps*. *Am. Nat.* (doi:10.1086/284170)
8. Parker GA. 1970 Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* (doi:10.1111/j.1469-185x.1970.tb01176.x)
9. Petrie M, Tim H, Carolyn S. 1991 Peahens prefer peacocks with elaborate trains. *Anim. Behav.* (doi:10.1016/S0003-3472(05)80484-1)
10. Petrie M. 1994 Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* (doi:10.1038/371598a0)
11. Zahavi A. 1975 Mate selection-A selection for a handicap. *J. Theor. Biol.* (doi:10.1016/0022-5193(75)90111-3)
12. Loyau A, Gomez D, Moureau B, Théry M, Hart NS, Jalme MS, Bennett ATD, Sorci G. 2007 Iridescent structurally based coloration of eyespots correlates with mating success in the peacock. *Behav. Ecol.* **18**, 1123–1131. (doi:10.1093/beheco/arm088)
13. Askew GN. 2014 The elaborate plumage in peacocks is not such a drag. *J. Exp. Biol.* **217**, 3237–3241. (doi:10.1242/jeb.107474)
14. Thavarajah NK, Tickle PG, Nudds RL, Codd JR. 2016 The peacock train does not handicap cursorial locomotor performance. *Sci. Rep.* **6**, 1–6. (doi:10.1038/srep36512)
15. Hongo Y. 2007 Evolution of male dimorphic allometry in a population of the Japanese horned beetle *Trypoxylus dichotomus septentrionalis*. *Behav. Ecol. Sociobiol.* (doi:10.1007/s00265-007-0459-2)

16. McCullough EL. 2014 Mechanical limits to maximum weapon size in a giant rhinoceros beetle. *Proc. R. Soc. B Biol. Sci.* (doi:10.1098/rspb.2014.0696)
17. Bateman AJ. 1948 Intra-sexual selection in *Drosophila*. *Heredity (Edinb)*. (doi:10.1038/hdy.1948.21)
18. Hoquet T, Bridges WC, Gowaty PA. 2020 Bateman’s Data: Inconsistent with ‘Bateman’s Principles’. *Ecol. Evol.* **10**, 10325–10342. (doi:10.1002/ece3.6420)
19. Andersson M, Simmons LW. 2006 Sexual selection and mate choice. *Trends Ecol. Evol.* **21**, 296–302. (doi:10.1016/j.tree.2006.03.015)
20. Andersson M. 1982 Female choice selects for extreme tail length in a widowbird. *Nature* (doi:10.1038/299818a0)
21. Amundsen T. 2000 Female Ornaments: Genetically Correlated or Sexually Selected? *Anim. signals Signal. signal Des. Anim. Commun.*
22. Clutton-Brock T. 2007 Sexual selection in males and females. (doi:10.1126/science.1133311)
23. Clutton-Brock T. 2009 Sexual selection in females. *Anim. Behav.* **77**, 3–11. (doi:10.1016/j.anbehav.2008.08.026)
24. Rosvall KA. 2011 Intrasexual competition in females: Evidence for sexual selection? (doi:10.1093/beheco/arr106)
25. Hare RM, Simmons LW. 2019 Sexual selection and its evolutionary consequences in female animals. *Biol. Rev.* **94**, 929–956. (doi:10.1111/brv.12484)
26. Amundsen T, Forsgren E. 2001 Male mate choice selects for female coloration in a fish. *Proc. Natl. Acad. Sci. U. S. A.* (doi:10.1073/pnas.211439298)
27. Regosin JV, Pruett-jones S. 2001 Sexual selection and tail-length dimorphism in scissor-tailed flycatchers. *Auk* **118**, 167–175. (doi:http://www.jstor.org/stable/4089766)
28. Emlen ST, Wrege PH. 2004 Size dimorphism, intrasexual competition, and sexual selection in Wattled Jacana (*Jacana jacana*), a sex-role-reversed shorebird in Panama. *Auk* (doi:10.2307/4090403)
29. Lipshutz SE. 2017 Divergent competitive phenotypes between females of two sex-role-reversed species. *Behav. Ecol. Sociobiol.* **71**. (doi:10.1007/s00265-017-2334-0)
30. LeBas NR, Hockham LR, Ritchie MG. 2003 Nonlinear and correlational sexual selection on ‘honest’ female ornamentation. *Proc. R. Soc. B Biol. Sci.* **270**, 2159–2165. (doi:10.1098/rspb.2003.2482)

31. Eens M, Pinxten R. 2000 Sex-role reversal in vertebrates: Behavioural and endocrinological accounts. *Behav. Processes* **51**, 135–147. (doi:10.1016/S0376-6357(00)00124-8)
32. Kraaijeveld K, Kraaijeveld-Smit FJL, Komdeur J. 2007 The evolution of mutual ornamentation. *Anim. Behav.* **74**, 657–677. (doi:10.1016/j.anbehav.2006.12.027)
33. Jones L, Hunter FM. 1993 Monogamous Seabird. **362**, 238–239.
34. Kraaijeveld K, Gregurke J, Hall C, Komdeur J, Mulder RA. 2004 Mutual ornamentation, sexual selection, and social dominance in the black swan. *Behav. Ecol.* (doi:10.1093/beheco/arh023)
35. West-Eberhard M. 1979 Sexual selection, social competition, and evolution. *Proc. Am. Philos. Soc.* **123**, 222–234.
36. Fritzsche K, Booksmythe I. 2013 The measurement of sexual selection on females and males. *Curr. Zool.* **59**, 558–563. (doi:10.1093/czoolo/59.4.558)
37. Tobias JA, Montgomerie R, Lyon BE. 2012 The evolution of female ornaments and weaponry: Social selection, sexual selection and ecological competition. *Philos. Trans. R. Soc. B Biol. Sci.* **367**, 2274–2293. (doi:10.1098/rstb.2011.0280)
38. Lyon BE, Montgomerie R. 2012 Sexual selection is a form of social selection. (doi:10.1098/rstb.2012.0012)
39. Roulin A. 2016 Condition-dependence, pleiotropy and the handicap principle of sexual selection in melanin-based colouration. *Biol. Rev.* **91**, 328–348. (doi:10.1111/brv.12171)
40. Stearns SC. 1989 Trade-Offs in Life-History Evolution. *Funct. Ecol.* **3**, 259–268.
41. Flatt T, Heyland A, editors. 2011 *Mechanisms of Life History Evolution: The Genetics and Physiology of Life History Traits and Trade-Offs*. Oxford University Press.
42. Nussey DH, Coulson T, Festa-Bianchet M, Gaillard JM. 2008 Measuring senescence in wild animal populations: Towards a longitudinal approach. *Funct. Ecol.* **22**, 393–406. (doi:10.1111/j.1365-2435.2008.01408.x)
43. Candolin U. 1999 The relationship between signal quality and physical condition: Is sexual signalling honest in the three-spined stickleback? *Anim. Behav.* **58**, 1261–1267. (doi:10.1006/anbe.1999.1259)
44. Rowe L, Houle D. 1996 The lek paradox and the capture of genetic variance by condition dependent traits. *Proc. R. Soc. B Biol. Sci.* **263**, 1415–1421. (doi:10.1098/rspb.1996.0207)

45. Wilson AJ, Nussey DH. 2009 What is individual quality? An evolutionary perspective. *Trends Ecol. Evol.* **25**, 207–214. (doi:10.1016/j.tree.2009.10.002)
46. Hill GE. 2011 Condition-dependent traits as signals of the functionality of vital cellular processes. *Ecol. Lett.* **14**, 625–634. (doi:10.1111/j.1461-0248.2011.01622.x)
47. Stevenson RD, Woods WA. 2006 Condition indices for conservation: New uses for evolving tools. *Integr. Comp. Biol.* **46**, 1169–1190. (doi:10.1093/icb/icl052)
48. Peig J, Green AJ. 2009 New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos* **118**, 1883–1891. (doi:10.1111/j.1600-0706.2009.17643.x)
49. Peig J, Green AJ. 2010 The paradigm of body condition: A critical reappraisal of current methods based on mass and length. *Funct. Ecol.* **24**, 1323–1332. (doi:10.1111/j.1365-2435.2010.01751.x)
50. Labocha MK, Hayes JP. 2012 Morphometric indices of body condition in birds: A review. *J. Ornithol.* **153**, 1–22. (doi:10.1007/s10336-011-0706-1)
51. Labocha MK, Schutz H, Hayes JP. 2014 Which body condition index is best? *Oikos* **123**, 111–119. (doi:10.1111/j.1600-0706.2013.00755.x)
52. Lerch A, Rat-Fischer L, Gratier M, Nagle L. 2011 Diet quality affects mate choice in domestic female canary *Serinus canaria*. *Ethology* **117**, 769–776. (doi:10.1111/j.1439-0310.2011.01929.x)
53. Cotton S, Small J, Pomiankowski A. 2006 Sexual Selection and Condition-Dependent Mate Preferences. *Curr. Biol.* **16**, 755–765. (doi:10.1016/j.cub.2006.08.022)
54. Bonduriansky R. 2006 Sexual selection and allometry: A critical reappraisal of the evidence and ideas. *Evolution (N. Y.)*. **61**, 838–849. (doi:10.1111/j.1558-5646.2007.00081.x)
55. Packard GC, Boardman TJ. 1999 The use of percentages and size-specific indices to normalize physiological data for variation in body size : Wasted time , wasted effort ? The use of percentages and size-specific indices to normalize physiological data for variation in body size : waste. *Comp. Biochem. Physiol.* **122**, 37–44. (doi:10.1016/S1095-6433(98)10170-8)
56. Kodric-Brown A, Sibly RM, Brown JH. 2006 The allometry of ornaments and weapons. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 8733–8738. (doi:10.1073/pnas.0602994103)
57. Green AJ. 1988 Positive allometry is likely with mate choice , competitive display and other functions. *Wildfowl Wetl.*, 2–4.
58. Naturalist TA. 1987 Vol. 129, No. 5 The American Naturalist May 1987. *Am. Nat.* **129**, 775–776.

59. Petrie M. 1992 Are all secondary sexual display structures positively allometric and , if so , why ? *Anim. Behav.* **43**, 173–175.
60. Emlen DJ. 2008 The Evolution of Animal Weapons. *Annu. Rev. Ecol. Evol. Syst.* **39**, 387–413. (doi:10.1146/annurev.ecolsys.39.110707.173502)
61. Eberhard WG. 2002 Natural history and behavior of *Chymomyza mycopelates* and *C. exophthalma* ( Di ptera : Drosophilidae ), and allometry of structures used as signals , weapons , and spore collectors. *Can. Entomol.* **134**, 667–687. (doi:https://doi.org/10.4039/Ent134667-5)
62. Petrie M. 1988 Lnterspecific variation in structures that display competitive ability: Large animals invest relatively more. *Anim. Behav.* **36**, 1174–1179.
63. Lande R. 1980 Sexual Dimorphism, Sexual Selection, and Adaptation in Polygenic Characters. *Evolution (N. Y.)*. **34**, 292. (doi:10.2307/2407393)
64. Huxley JS. 1914 The Courtship habits of the Great Crested Grrebe (*Podiceps cristatus*); with an addition to the Theory of Sexual Selection. *Proc. Zool. Soc. London* (doi:10.1111/j.1469-7998.1914.tb07052.x)
65. Bachtrog D *et al.* 2014 Sex Determination: Why So Many Ways of Doing It? *PLoS Biol.* **12**, 1–13. (doi:10.1371/journal.pbio.1001899)
66. Stewart AD, Rice WR. 2018 Arrest of sex-specific adaptation during the evolution of sexual dimorphism in *Drosophila*. *Nat. Ecol. Evol.* **2**, 1507–1513. (doi:10.1038/s41559-018-0613-4)
67. Poissant J, Wilson AJ, Coltman DW. 2010 Sex-specific genetic variance and the evolution of sexual dimorphism: A systematic review of cross-sex genetic correlations. *Evolution (N. Y.)*. **64**, 97–107. (doi:10.1111/j.1558-5646.2009.00793.x)
68. Bijl W van der, Mank JE. 2021 Widespread cryptic variation in genetic architecture between the sexes. *Evol. Lett.* **5**, 359–369. (doi:10.1002/evl3.245)
69. Kokko H, Johnstone RA. 2002 Why is mutual mate choice not the norm? Operational sex ratios, sex roles and the evolution of sexually dimorphic and monomorphic signalling. *Philos. Trans. R. Soc. B Biol. Sci.* (doi:10.1098/rstb.2001.0926)
70. Parker GA. 1983 Mate quality and mating decisions. In *Mate choice* (ed P Bateson), pp. 141–166. Cambridge University Press.
71. Class B, Dingemanse NJ, Jon YGA. 2017 A statistical methodology for estimating assortative mating for phenotypic traits that are labile or measured with error. **2017**, 1910–1919. (doi:10.1111/2041-210X.12837)
72. Lyon BE, Eadie JM, Hamilton LD. 1994 Parental choice selects for ornamental plumage in American coot chicks. *Nature* (doi:10.1038/371240a0)

73. Lyon BE, Shizuka D. 2020 Extreme offspring ornamentation in American coots is favored by selection within families, not benefits to conspecific brood parasites. *Proc. Natl. Acad. Sci. U. S. A.* (doi:10.1073/pnas.1913615117)
74. Candolin U. 2003 The use of multiple cues in mate choice. (doi:10.1017/S1464793103006158)
75. Schaedelin FC, Taborsky M. 2009 Extended phenotypes as signals. *Biol. Rev.* **84**, 293–313. (doi:10.1111/j.1469-185X.2008.00075.x)
76. Andersson S, Pryke SR, Örnborg J, Lawes MJ, Andersson M. 2002 Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *Am. Nat.* **160**, 683–691. (doi:10.1086/342817)
77. Bonduriansky R. 2016 Sexual Conflict Introduction : The Development of., 1–7. (doi:10.1002/9780470015902.a0003669.pub3)
78. Parker GA. 1979 Sexual selection and sexual conflict. In *Sex. Sel. Reprod. Compet. insects*, (doi:10.1016/b978-0-12-108750-0.50010-0)
79. Arnqvist G, Rowe L. 2005 *Sexual conflict*. Princeton, NJ: Princeton University Press.
80. Clutton-Brock T. 1991 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
81. Liechti F, Witvliet W, Weber R, Bächler E. 2013 First evidence of a 200-day non-stop flight in a bird. *Nat. Commun.* (doi:10.1038/ncomms3554)
82. Bize P, Roulin A, Bersier L, Pflüger D, Richner H. 2003 Parasitism and developmental plasticity in Alpine swift nestlings. *J. Anim. Ecol.* **72**, 633–639. (doi:10.1046/j.1365-2656.2003.00734.x)
83. Bize P, Roulin A, Tella JL, Bersier LF, Richner H. 2004 Additive effects of ectoparasites over reproductive attempts in the long-lived alpine swift. *J. Anim. Ecol.* (doi:10.1111/j.0021-8790.2004.00880.x)
84. Bize P, Daniel G, Viblanc VA, Martin JGA, Doligez B. 2017 Negative phenotypic and genetic correlation between natal dispersal propensity and nest-defence behaviour in a wild bird. *Biol. Lett.* **13**, 7–10. (doi:10.1098/rsbl.2017.0236)
85. Bize P, Roulin A, Tella JL, Richner H. 2005 Female-biased mortality in experimentally parasitized Alpine Swift *Apus melba* nestlings. *Funct. Ecol.* (doi:10.1111/j.1365-2435.2005.00995.x)
86. Bize P, Gasparini J, Klopfenstein A, Altwegg R. 2006 Melanin-Based Coloration Is a Nondirectionally Selected Sex-Specific Signal of Offspring Development in the Alpine Swift. *Evolution (N. Y.)*. **60**, 2370–2380.

87. Hasegawa M, Arai E. 2020 Fork tails evolved differently in swallows and swifts. *J. Evol. Biol.* **33**, 911–919. (doi:10.1111/jeb.13622)
88. Van Valen L. 1962 A Study of Fluctuating Asymmetry. *Evolution (N. Y.)*. **16**, 125–142.
89. Kose M, Mänd R, Møller AP. 1999 Sexual selection for white tail spots in the barn swallow in relation to habitat choice by feather lice. *Anim. Behav.* **58**, 1201–1205. (doi:10.1006/anbe.1999.1249)
90. Tettamanti F, Witvliet W, Bize P. 2012 Selection on age at first and at last reproduction in the long-lived Alpine Swift *Apus melba*. *Ibis (Lond. 1859)*. **154**, 338–344. (doi:10.1111/j.1474-919X.2012.01215.x)
91. Griffiths R, Double MC, Orr K, Dawson RJG. 1998 A DNA test to sex most birds. *Mol. Ecol.* (doi:10.1046/j.1365-294x.1998.00389.x)
92. Lynch M, Walsh B. 1998 *Genetics and Analysis of Quantitative Traits*. Sunderland, MA: Sinauer.
93. Kruuk LEB, Slate J, Wilson AJ. 2008 New answers for old questions: The evolutionary quantitative genetics of wild animal populations. (doi:10.1146/annurev.ecolsys.39.110707.173542)
94. Bonduriansky R, Day T. 2003 THE EVOLUTION OF STATIC ALLOMETRY IN SEXUALLY SELECTED TRAITS. *Evolution (N. Y.)*. **57**, 2450–2458.
95. Dunn PO, Armenta JK, Whittingham LA. 2015 Natural and sexual selection act on different axes of variation in avian plumage color. *Evol. Biol.*, e1400155.
96. Stoffel MA, Nakagawa S, Schielzeth H. 2017 rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. (doi:10.1111/2041-210X.12797)
97. R Core Team. 2021 *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
98. Biro PA, Stamps JA. 2015 Using repeatability to study physiological and behavioural traits : ignore time-related change at your peril. *Anim. Behav.* **105**, 223–230. (doi:10.1016/j.anbehav.2015.04.008)
99. Kuznetsova A, Brockhoff PB, Christensen RHB. 2017 lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software* **82**, 1–26. (doi:10.18637/jss.v082.i13)
100. Rice WR, Chippindale AK. 2001 Intersexual ontogenetic conflict. *J. Evol. Biol.* **14**, 685–693. (doi:10.1046/j.1420-9101.2001.00319.x)

101. Harano T, Okada K, Nakayama S, Miyatake T, Hosken DJ. 2010 Intralocus sexual conflict unresolved by sex-limited trait expression. *Curr. Biol.* **20**, 2036–2039. (doi:10.1016/j.cub.2010.10.023)
102. Bonduriansky R, Chenoweth SF. 2009 Intralocus sexual conflict. *Trends Ecol. Evol.* **24**, 280–288. (doi:10.1016/j.tree.2008.12.005)
103. Falconer DS. 1989 *Introduction to Quantitative Genetics*. Ed. 3. Essex, UK: Harlow : Longman Scientific & Technical.
104. Falconer DS, Mackay TFC. 1996 *Introduction to Quantitative Genetics*. Essex: Longman.
105. Tamin T, Doligez B. 2021 Assortative mating for between- patch dispersal status in a wild bird population : Exploring the role of direct and indirect underlying mechanisms. *J. Evol. Biol.*, 1–14. (doi:10.1111/jeb.13925)
106. Giery ST, Layman CA. 2015 Interpopulation Variation in a Condition-Dependent Signal : Predation Regime Affects Signal Intensity and Reliability. *Am. Nat.* **186**, 187–195. (doi:10.1086/682068)
107. Pyle P, Sydeman WJ, Hester M. 2001 Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin’s auklets. *J. Anim. Ecol.* (doi:10.1046/j.0021-8790.2001.00567.x)
108. Charmantier A, Perrins C, McCleery RH, Sheldon BC. 2006 Quantitative genetics of age at reproduction in wild swans: Support for antagonistic pleiotropy models of senescence. *Proc. Natl. Acad. Sci. U. S. A.* **103**, 6587–6592. (doi:10.1073/pnas.0511123103)
109. Culina A, Radersma R, Sheldon BC. 2015 Trading up: The fitness consequences of divorce in monogamous birds. *Biol. Rev.* **90**, 1015–1034. (doi:10.1111/brv.12143)
110. Choudhury SE. 1995 Divorce in birds: a review of the hypotheses. *Anim. Behav.* **50**, 413–429. (doi:10.1006/anbe.1995.0256)
111. Wheelwright NT, Teplitsky C. 2017 Divorce in an Island bird population: Causes, consequences, and lack of inheritance. *Am. Nat.* **190**, 557–569. (doi:10.1086/693387)
112. Germain RR, Wolak ME, Reid JM. 2018 Individual repeatability and heritability of divorce in a wild population. *bioRxiv* (doi:10.1101/254151)
113. Kleiman DG. 1977 Monogamy in Mammals. *Q. Rev. Biol.* **52**, 39–69.
114. Van De Pol M, Heg D, Bruinzeel LW, Kuijper B, Verhulst S. 2006 Experimental evidence for a causal effect of pair-bond duration on reproductive performance in oystercatchers (*Haematopus ostralegus*). *Behav. Ecol.* **17**, 982–991. (doi:10.1093/beheco/arl036)



- 115. Kokko H, Jennions MD. 2008 Parental investment, sexual selection and sex ratios. *J. Evol. Biol.* **21**, 919–948. (doi:10.1111/j.1420-9101.2008.01540.x)
- 116. Balshine S, Kempenaers B, Székely T. 2002 Philosophical transactions of the royal society: Introduction. *Philos. Trans. R. Soc. B Biol. Sci.* **357**, 237–240. (doi:10.1098/rstb.2001.0933)
- 117. Olson CR, Vleck CM, Vleck D. 2006 Periodic cooling of bird eggs reduces embryonic growth efficiency. *Physiol. Biochem. Zool.* **79**, 927–936. (doi:10.1086/506003)
- 118. Bellier E, Kéry M, Schaub M. 2018 Relationships between vital rates and ecological traits in an avian community. *J. Anim. Ecol.* **87**, 1172–1181. (doi:10.1111/1365-2656.12826)
- 119. Roulin A, Ducrest A-L, Jeamonod J. 1998 Prévalence et intensité parasitaire d'un Hippoboscide (Diptera) chez les jeunes martinets à ventre blanc *Apus melba*. *Nos Oiseaux* **45**, 185–190.