

BACKGROUND: Sexual selection [1] plays an essential role in shaping the evolution and adaptation of a species to its natural environment, with individuals more proficient at securing mates achieving higher fitness [2]. Despite a positive correlation between duration of pair bond and lifetime reproductive success in monogamous species, mate choice need not be a static event, with some individuals abandoning a current mate for a new one while both partners are still alive (divorce [3]). Sexual selection is considered to drive the evolution of secondary sexual traits, which may be broadly categorized by function as those attracting mates (ornaments) or those repelling rivals (weapons) [1; 4]. Sexual selection can act at the pre-copulatory level (i.e., mating success; [1]) or at the post-copulatory level (i.e., fertilization success; [4]), and is further intrinsically linked to additional processes such as parental care [5] and sexual conflict [6]. Two central mechanisms may be distinguished in explaining the evolution of secondary sexual traits: inter- and intra-sexual selection, or (female) mate choice and (male-male) competition respectively. Inter- and intra-sexual selection remain the foundations of modern sexual selection theory after 150 years of study [4]. However, much of this research has focused disproportionately on males of polygynous species with pronounced sexual dimorphisms [4] where sexual selection seems to play an obvious role (e.g., female preference of elaborately ornamented male Long-tailed Widowbirds *Euplectes progne* [7]). This has led to a persistent gap in our understanding of how sexual selection operates within and between the sexes in a species with little apparent dimorphism.

More recently, research has addressed questions of sexual selection in females [8-11] and in species where both males and females are similarly ornamented [12; 13]. Two main hypotheses have been proposed to explain the evolution of mutual ornamentation: Lande's [14] genetic correlation hypothesis and Huxley's [15] mutual selection hypothesis. The genetic correlation hypothesis puts forward that ornamentation serves a functional purpose in one sex only, while the matching ornaments in the other sex are non-functional by-products of genetic correlations between the sexes. The mutual selection hypothesis suggests that the evolution of functional ornaments may occur in both sexes due to reciprocal mate choice, which is predicted to occur when quality is crucial to both male and female reproductive success (i.e., species with biparental care; [5]) and to result in assortative mating (a positive correlation between males and females [16]) by mate quality [17]. Despite significant improvements in our understanding of sexual selection in recent decades, open questions remain as to how secondary sexual traits can evolve in both sexes, how their evolution may relate to sexually antagonistic selection (wherein the sexes have conflicting fitness strategies) or be constrained due to shared genetic architecture between the sexes. Similarly, in species where biparental investment is high, mate choice decisions, sexual conflict over parental investment as well as the adaptive value of divorce (vs. mate retention) remain poorly understood.

AIMS & RESEARCH QUESTIONS (RQ): The aim of my PhD research is to investigate how sexual selection operates within and between the sexes in a monogamous species with little apparent sexual dimorphism. I will address four central questions. **RQ1:** How does sexual selection drive the evolution and maintenance of secondary sexual traits and what is their current signalling value? **RQ2:** What are the relative contributions of additive genetic (heritable) and environmental effects on phenotypic variation in secondary sexual traits? **RQ3:** 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? **RQ4:** Do nest location and composition reflect parental quality and how does experience affect male, female, and total parental investment (and in turn fitness)?

STUDY SPECIES: The Alpine Swift (*Tachymarptis melba*) is a long lived (lifespan: median of 7 years, maximum of 26 years), migrant and colonially nesting species. They live a highly aerial lifestyle, feeding and remaining on wing nearly year-round, with breeding as the exception [18]. 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 [19]. Although Alpine Swifts appear monomorphic to human observers, subtle sexual dimorphisms are present: the conspicuous white throat patch is larger in females while fork length is longer in males (P. Bize, unpublished). These traits are highly variable within each sex. The wild Swiss colonies that I will study have been closely followed at the individual level for over twenty years. As such, outstanding information has been collected for this system detailing individual secondary sexual traits, reproductive success, divorce and natal dispersal rates, as well as a detailed pedigree [20]. The existence of such a detailed pedigree, still relatively rare in wild populations, will allow me to perform state-of-the-art analyses of genetic variance [21; 22].

METHODS: I will investigate four secondary sexual traits: 1) achromatic throat patch size, 2) throat patch brightness, 3) tail fork length, and 4) breast patch melanization; as well as two mating strategies, a) divorce (vs. mate retention) and b) assortative (vs. non assortative) mating (following natal dispersal); and parental care. My research will build upon the existing individual-level long-term database with newly collected information on achromatic throat patch size and plumage UV reflectance using a novel photographic approach (obtaining joined size & reflectance information on the throat patch by capturing breeding pairs and non-breeding individuals in the colonies).

Quantitative genetic models: I will use animal models—mixed models linked to a pedigree [22]—to understand the genetic basis of secondary sexual traits and mating strategies. These models will allow me to make statistical inferences about the additive genetic (co)variance (heritability) in secondary sexual traits in both sexes and the genetic correlation between the sexes, and to test the direct and indirect influences of mating strategies and parental care on fitness in a species with little apparent sexual dimorphism.

RQ1: I will investigate the signalling values of secondary sexual traits in both sexes and will use selection models to test whether variation in these traits is sex-specific and related to measures of fitness (laying date, egg size, size of clutch and brood) *to shed light on the sex-specific selection acting on secondary sexual traits in a subtly dimorphic species.*

RQ2: I will quantify the sex-specific relative contributions of additive genetic (heritable) and environmental effects (estimated by weather condition variables, rank in the brood, and colony size) on secondary sexual trait expression using univariate animal models. I will investigate the potential for intra-locus sexual conflict—wherein alleles that increase fitness in one sex decrease fitness in the other sex—using bivariate animal models. *In conjunction with RQ1 this will allow for stronger conclusions about the selective pressures driving subtle dimorphisms in this species.*

RQ3: I will assess the adaptive value of divorce (vs. mate retention) and of assortative (vs. non-assortative) pairings following natal dispersal and how this may differ and reflect conflicts between the sexes using multivariate animal models, with *important implications for gene flow.*

RQ4: I will examine the link between parental quality and nest composition and location within the colony, and will analyse the effect of experience on male, female and total parental investment (and in turn on fitness) *to clarify the link between sexual selection and parental care.*

SIGNIFICANCE: My proposed study will shed new light on the evolution and maintenance of secondary sexual traits in species where these traits have evolved in both sexes, sexual conflicts underlying these traits and their potential resolution, as well as the fitness impacts of divorce assortative mating and parental care at both the phenotypic and genetic levels.