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Shared genetic architecture and sex-specific fitness consequences of forked tails in the Alpine swift

Tachymarptis melba

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21 ABSTRACT

22   The evolution of deeply forked tails in highly aerial birds has been suggested to be driven by

23 sexual and viability selection. Using over 20 years of data on the Alpine swift, we investigated the sex-

24 specific predictors and fitness consequences of deeply forked tails, as well as the role of genetics in

25 shaping the evolutionary trajectory of this trait. In the Alpine swift, fork length shows moderate sexual

26 dimorphism, being 7% longer in males than in females. Longer forks were associated with increased

27 reproductive success in males and larger eggs in females, suggesting that this trait may be mutually

28 selected and signal aspects of individual condition in both sexes. In addition, fork length was heritable

29 and strongly genetically correlated between the sexes, with effectively the same genetic architecture

30 expressed in both sexes. However, genetic constraints between the sexes are unlikely to explain the

31 changes in fork length observed over the course of the study, as fork length increased more in females

32 than in males. Further studies will be required to understand why male fork length has not became

33 further elaborated, despite positive directional selection on this heritable trait.

34

35 INTRODUCTION

36   Sexual dimorphism is widespread in the animal kingdom, encapsulating differences between the

37 sexes in behaviour, physiology or morphology, and ranging from subtle to extreme while favouring one

38 sex or the other (Fairbairn *et al.,* 2007). Sexual dimorphism is expected to arise when the strength and

39 shape of selection on the sexes differs (Shine, 1989), reflecting adaptive differences in the optimal value

40 of the trait for each sex (Fairbairn *et al.,* 2007). For instance, both sexes of the barn swallow *Hirundo*

41 *rustica* have elongated tail streamers resulting in deeply forked tails. Deeply forked tails are expected to

42 impact maneuverability and agility, both of which play a crucial role in foraging and predator escape in

43 highly aerial species. The tail streamers of the barn swallow appear to be elaborated past the natural

44   selection optimum in males (Møller *et al.*, 1998) thereby increasing drag and incurring aerodynamic

45   costs (Evans & Thomas, 1992), and are considered a classical example of sexual selection. Males with

46   more deeply forked tails have higher levels of circulating testosterone and are preferred as mates by

47   females, but also suffer increased mortality (Møller *et al.,* 1998). Despite controversy around the

48   relative roles of natural *vs.* sexual selection in driving tail length and shape, especially in swallows (*e.g.,*

49   Evans et al., 2012; Aparicio & Moller, 2012), deeply forked tails may arise in both sexes as a product of

50   both natural and sexual selection.

51   Because traits expressed in both sexes typically have their origin in shared genetic architecture

52   (Roff, 1996; Poissant *et al.,* 2010), genetic constraints in the form of intra-locus sexual conflict could

53   impede the evolution of sex-specific phenotypic optima (Bonduriansky & Chenoweth, 2009). Intra-locus

54   sexual conflicts may be commonplace—especially so in cases of weak or subtle sexual dimorphism

55   where the conflict could be ongoing—and can be assessed by estimating the cross-sex genetic

56   correlation (*rMF*; Lande, 1980) and sex-specific selection of a shared trait. While an *rMF* approaching

57   one (positive or negative) suggests the presence of shared genetic architecture between the sexes, and

58   thus constraints on sex-specific evolution, a null correlation suggests little shared genetic architecture

59   and thus that both sexes may evolve to their own sex-specific optimums unhindered (Poissant *et al.,*

60   2010). Intra-locus sexual conflict is expected in cases were a positive *rMF* approaching one is coupled

61   with sexually antagonistic selection or were a negative *rMF* approaching one is coupled with sexually

62   concordant selection (Kruuk *et al.*, 2008). Intra-locus sexual conflict has chiefly been reported in lab-

63   based population, namely studies on *Drosophila melanogaster* (*e.g.,* Rice & Chippindale, 2001; Long &

64   Rice, 2007), though it has also been identified in wild populations (*e.g.,* collared flycatcher *Ficedula*

65   *albicollis,* Merilä *et al.,* 1997, 1998; mountain goats *Oreamnos americanus,* Mainguy *et al.*, 2009).

66   Such genetic constraints have been put forth as one of the explanations for monomorphism,

67   wherein secondary sexual traits are expressed in the non-signaling sex as a result of strong genetic

68   correlations between the sexes. In these cases, one sex would be expected to benefit from the over-

69   elaboration of the trait, while the other sex would only bear the costs. Indeed, this argument has been

70   used by some to explain the evolution of tail streamers in female barn swallows (Cuervo *et al.,* 1996),

71   wherein tail streamers that are longer than the aerodynamic optimum are sexually selected in males

72   and may be over expressed in females solely due to the genetic constraint. In line with this expectation,

73   experimentally elongated tail steamers in female barn swallows resulted in decreased reproductive

74   success in the year following the manipulation, suggesting long-term parental investment or flight

75   efficacy costs (Cuervo et al., 2003).

76   As an alternative to the genetic correlation hypothesis, monomorphic traits could evolve as a

77   result of mutual selection (Kokko & Johnstone, 2002), wherein the trait would be sexually selected in

78   both sexes. Under mutual mate choice, deeply forked tails could act as a signal of individual condition in

79   both sexes, with individuals of higher condition able to carry the costs of more deeply forked tails.

80   Mutual selection is predicted to occur most often in monogamous species with bi-parental care, though

81   its prevalence remains uncertain (Kokko & Johnstone, 2002). Crested auklets *Aethia cristatella* of both

82   sexes prefer mates with longer feather crests (Jones & Hunter, 1999), and longer tail streamers were

83   associated with higher reproductive success in both sexes of an East Mediterranean population of barn

84   swallows *H. r. transitive* (Vortman *et al.,* 2011).

85   The aim of this study was to investigate the sex-specific fitness consequences and genetic

86   architecture of deeply forked tails in a wild population of Alpine Swifts *Tachymarptis melba*, a highly

87   aerial insectivore. We first quantified the sex-specific reproductive and viability selection acting on fork

88   length. As longer wings have been identified as a compensatory trait for deeply forked tails, minimizing

89   their aerodynamic costs (Fitzpatrick, 2008), and since the allometric scaling of fork length to wing length

90   is sex-specific (Dumas et al., in prep), we also considered direct and indirect selection acting on fork

91   length and wing length in both sexes. We expected deeply forked tails to provide benefits for males but

92   not females in terms of reproductive success, and costs for both sexes in terms of survival, consistent

93   with general theory on traits subject to sexual selection. Indeed, though the bulk of works on this topic

94   are on swallows, recent works have provided some support for the role of sexual selection in driving the

95   evolutionary of more deeply forked tails in male swifts (*e.g.,* Hasegawa & Arai, 2020, Jukema *et al.*,

96   2023). Because sexual conflict at the genetic level requires the traits in question to be heritable, we then

97   quantified the additive genetic variance and heritability of fork length in both sexes. We additionally

98   assessed the importance of genetic constraints in the evolution of sexual dimorphism in fork length by

99   estimating the cross-sex genetic correlation, with the expectation that such a correlation would be

100   strongly positive. Finally, we evaluated the micro evolutionary trajectory of fork length over the course

101   of the study.

102

103   METARIAL & METHODS

104   *Study site & species*

105   The Alpine swift is a long-lived (median lifespan: approx. 7 years; maximum: 26 years; Bize *et al.*,

106   2006; Moullec et al. 2023) and colonially nesting bird. They live a highly aerial lifestyle, capable of

107   remaining in constant flight for over six months at a time (Liechti *et al.,* 2013), and landing only during

108   the breeding period. Colonies of a few to a hundred pairs will nest on cliffs or in the roof spaces of tall

109   buildings when nesting in urban settings. Alpine swifts nest from May to August, with both parents

110   incubating their 1-4 eggs for approximately 18 days (Bize *et al.,* 2004). Chicks take approximately 50 to

111   70 days from hatching to fledging, during which time both parents will brood and feed them (Bize *et al.,*

112   2004). As such, males and females are expected to have similar parental allocation into reproduction,

113   with the exception of egg laying for which females alone pay the energetic costs (*e.g.,* females show a

114   more pronounced decrease in body mass over the season than males, Dumas *et al.,* 2024).

115   Since 1999 and 2000 respectively, two urban-nesting colonies have been intensively monitored

116   in the Swiss cities of Biel (60-100 breeding pairs) and Solothurn (40-55 breeding pairs). In both colonies,

117   birds are individually identified by permanently ringing them as nestlings or at their first capture at

118   adulthood if not already ringed as nestlings. Parents are caught by hand at the nest, their identity is

119   recorded, and their yearly reproductive success is determined (clutch size, brood size at hatching and

120   fledgling). As no extra-pair paternity (EPP) has been recorded in this population (C. M. Meier & P. Bize,

121   personal comm.), these behavioural observations are sufficient for pair-bond identification and to

122   construct a detailed social pedigree. Individuals are measured to the nearest millimetre using a ruler

123   (*e.g.,* wing, tail and fork lengths) or tenth of a millimetre using a caliper (*e.g.,* sternum length) and sexed

124   (DNA taken from blood or feathers; Griffiths *et al.,* 1998). Fork length is measured as the distance

125   between the tip of the inner tail feather and the tip of the outer tail feathers. The inner tail feather is

126   calculated as the difference between the outer tail feather and the fork length. These feather traits are

127   measured once per individual per year captured.

128   Although Alpine swifts have historically been considered to be monomorphic like most swifts,

129   subtle sexual dimorphisms are present (*e.g.,* females are 1% heavier than males, Dumas *et al.*, 2024;

130   males have 7% more deeply forked tails than females, Dumas et al., in prep). Fork length in swifts range

131   from monomorphic in the Plain Swift *Apus unicolor* (Garcia-Del-Rey *et al.,* 2008), to minorly dimorphic in

132   the Comon swift *Apus apus* (males have more deeply forked tails than females, Jukema *et al.*, 2023), to

133   strongly dimorphic in the Black swift *Cypseloides niger borealis* (males have more deeply forked tails

134   than females, Gunn *et al.,* 2018), with sexual dimorphism in other feather and morphometric traits

135   documented in some species (*e.g.,* male Pallid swifts *Apus pallidus* have longer wings than females,

136   Boano *et al.,* 2015). Despite the presence of these slight sexual dimorphism, Alpine swifts appear

137   monomorphic to human observers, and hence field measurements are taken blind to the sex of the

138   individuals.

139   *Statistical analyses*

140   All statistical analyses were conducted in R version 4.3.1 "Beagle Scouts" (R Core Team, 2023),

141   using the R packages *lmerTest* (Kuznetsova *et al.*, 2017) and *MCMCglmm* (Hadfield, 2010). For all

142   models, we examined fork length, the fork to outer tail feather lengths ratio and the fork to inner tail

143   feather lengths ratio so as to account for differences in the fork length and depth relative to the outer

144   and inner tail feathers. Indeed, deeply forked tails can be produced by one of two mechanisms:

145   lengthening of outer tail feathers and/or shortening of inner tail feathers. Results from all three

146   approaches were qualitatively similar and hence only the fork length models are included in the

147   manuscript, while the relative fork depth models are reported in the supplemental. Absolute and

148   relative fork depths were mean-centered and scaled to a variance of 1, pooled across the sexes. Year, as

149   a continuous variable, was also mean-centered and scaled to a variance of 1. When included in the

150   analyses, quadratic effects were calculated using orthogonal polynomials. All models were first tested

151   with the inclusion of all biologically relevant interaction terms and quadratic effects; non-statistically

152   significant interaction terms (Engqvist, 2005) and non-statistically significant quadratic effects (Faraway,

153   2014) were dropped from the final models and are reported only in the supplemental. Data presented in

154   these analyses spans 1999-2021.

155   *Selection analyses*

156   In a first part, we investigated the fitness consequences of relatively deeply forked tails in both

157   sexes. We ran a series of linear and generalized linear mixed effects models to investigate the fitness

158   consequences of fork length on measures of reproductive success and overwinter survival. We

159   considered direct and indirect selection acting on fork length and wing length, as longer wings may

160   compensate for the aerodynamic costs of deeply forked tails. We further considered both female and

161   male traits as selection may operate differently on each sex. Overwinter survival was estimated for

162   breeding individuals only based on yearly records of capture, as the probability of recapturing birds in

163   this population is nearly one (Bize *et al.,* 2006).

164   Reproductive success traits considered were clutch size (Poisson distribution, log-link), brood

165   size at hatching (Poisson distribution, log-link) and at fledgling (Poisson distribution, log-link), and the

166   weighted proportion of surviving fledglings (binomial distribution, logit-link). The weighted proportion of

167   surviving fledglings was modelled as brood size at fledging over clutch size. Surviving fledglings are

168   defined as those that successfully leave the colony.

169   Since nonbreeding individuals have typically not yet reached sexual maturity, we also

170   considered the relation between fork length and breeding status (binomial distribution, logit-link). In

171   addition, we considered the relation between fork length and egg laying date (Gaussian distribution), as

172   laying date is strongly related to fitness in the Alpine swift (de Villemereuil *et al.,* 2020) despite not

173   being a fitness component *per se*. Laying date was modeled as day of the year and mean-centered and

174   scaled to a variance of 1. Finally, we considered the relation between fork length and egg volume

175   (Gaussian distribution), as previous studies have identified a trade-off between egg size and deeply

176   forked tails in swifts and swallows (females with more deeply forked tails produced smaller eggs;

177   Hasegawa & Arai, 2017, 2018). Egg volume was calculated as egg length x width^2 x π/6 following Bize *et*

178   *al.,* 2002.

179   For each reproductive parameter, we fit a model with reproductive success as a function of

180   female and male fork length, female and male wing length, and the colony. Female and male identity as

181   well as the year were included as random effects to account for repeated measurements on the

182   individual and yearly levels, respectively. These models were conducted at the pair level, as reproductive

183   success require concerted effort from both parents with both parents providing care to their offspring at

184   all stages. Models were fitted with both linear and quadratic effects for male and female fork length and

185   wing length, but the quadratic term was dropped from the final model as these were not statistically

186   significant (Table S2).

187   The breeding status (binomial distribution, logit-link) and overwinter survival models (binomial

188   distribution, logit-link) were run at the individual level, and thus included sex as a fixed effect. We fit

189   breeding status as a function of sex, fork length (linear and quadratic terms), and colony, with individual

190   identity and year as random effects to account for repeated measures. We also included the two-way

191   interaction term between sex and fork length (linear and quadratic), but these were removed the final

192   model as they were not statistically significant (Table S2). We fit overwinter survival as a function of sex,

193   fork length, and colony, with individual identity and year as random effects to account for repeated

194   measures. We also included the two-way interaction term between sex and fork length but it was

195   removed from the final model as it was not statistically significant (Table S2).

196   *Quantitative genetic analyses*

197   In a second part, we investigated the predictors of fork length in female and male Alpine swifts.

198   We assessed the sexual dimorphism in fork length, with the expectation that males would have more

199   deeply forked tails than females, as shown in previous work on the Alpine swift (Dumas et al., in prep),

200   and since previous studies have suggested a sexually selected role of deeply forked tails in males

201   (Hasegawa & Arai, 2020). As Alpine swifts have been subject to rapid morphometric changes over the

202   past two decades (*e.g.,* wing and tail lengths have increased in both sexes, Masoero *et al.,* in prep), we

203   considered sex-specific changes in fork length over the course of the study. As such, we fitted a

204   generalized linear mixed effects model with fork length as a function of sex, the year (linear and

205   quadratic), and colony as fixed effects, with an interaction term between sex and year to investigate

206   whether fork length changed in the same ways over the course of the study in both sexes. We further

207   considered the effect of male and female age (linear and quadratic) on fork length, as previous studies

208   on the Alpine swift have revealed sex specific ageing trajectories of morphometric traits (Moullec *et al.,*

209   2023). Since the quantitative genetic analyses results with and without the age effects were qualitatively

210   similar, and including individual age decreases the available sample size by approximately 30%, we

211   report age effects only in the supplemental (Table S6, Table S7).

212   We estimated quantitative genetic parameters of fork length by including pedigree data (an

213   'animal model', Kruuk *et al.,* 2008). Animal models allow users to decompose total variance between

214   environmental and genetic sources, and hence make inferences about the evolutionary potential of a

215   trait (Kruuk *et al.,* 2008; Wilson *et al.,* 2009). We estimated the following sex-specific variance

216   components: additive genetic variance (individual identity linked to the pedigree), permanent

217   environment variance (individual identity), yearly variance (year of observation) and residual variance. In

218   addition, we estimated the cross-sex genetic and yearly covariances and correlations, to assess the

219   presence of genetic constraints on the evolutionary potential of fork length. Variance parameters were

220   estimated as the median, mean and posterior mode following Pick *et al.* (2023) and reported with their

221   95% highest posterior density intervals (HPDI) (the mean and posterior mode are reported in the

222   supplemental only, Table S9). Variance ratio estimates were calculated as the proportion of total

223   phenotypic variation explained by the given variance parameter, *i.e.,* heritability conditioned on the

224   fixed effects was estimated as the sex-specific additive genetic variance divided by the (conditional) total

225   phenotypic variance. The pruned social pedigree used in this study was 5 generations deep and included

226   data on 1396 individuals, with 590 maternities and 571 paternities (Table S5). The social pedigree

227   statistics were determined using the R package *pedantics* (Morrissey, 2018).

228   For the residuals and the permanent environment effect, for which cross-sex correlations

229   cannot be estimated, we used standard priors with V = diag(2), nu = 1.002. For the additive genetic and

230   year effects, we used expanded priors, adapted for models estimating cross-sex correlations (*i.e.,* V =

231   diag(2) * 0.02, nu = 3, alpha.mu = rep(0, 2), and alpha.V = diag(2) * 1000). The model had a burn-in

232   period of 50000 iterations and was sampled every 2000 iterations for a total effective sample size of

233   1500. Plot traces were visually assessed, and absolute autocorrelation values were verified to be <0.1.

234   We verified chain convergence for each parameter using the Heidelberger and Welch's convergence

235   diagnostic (heidel.diag function) as recommended by Hadfield (2010); all converged well.

236   In addition, we refitted the previous animal model without the inclusion of year as a fixed or

237   random effect in order to assess whether or not there have been genetic changes in this trait over the

238   course of the study. To do so, we estimated the predicted breeding values (PBV) of female and male fork

239   length using best linear unbiased predictors (BLUPs) based on individual phenotypic information as well

240   as that of relatives (Henderson, 1950). We then fit the female-trait and male-trait breeding values as a

241   function of the year of birth of each individual (linear and quadratic) to investigate changes in PBV over

242   the course of the study. The quadratic effect of the year of birth was non-statistically significant and

243   hence was dropped from the model. These linear regressions were fit on the PBVs of each posterior

244   sample from the animal model, allowing us to estimate the posterior distribution (median) of the slope

245   (Hadfield *et al.,* 2010). We further simulated random breeding values following the pedigree for each

246   posterior sample in order to estimate the changes in PBV over time due to genetic drift, and to assess

247   whether the change in female-trait and male-trait PBVs over time were stronger than those expected

248   under drift alone (Hadfield *et al.,* 2010).

249   *Ethical note*

250   Adult swifts were caught at the nest between 8h00 and 20h00 (usually between 9h00 and

251   18h00) to avoid disturbing the adults during periods of intense social activity (dawn and dusk) (Meier *et*

252   *al.,* 2018). We minimized the number of captures and disturbances during severe weather events to

253   avoid extra stress to the birds. To further limit stress to the birds, swifts were placed in cloth bags and

254   handled quickly, typically 5-15 minutes depending on data collection. All individuals were released at the

255   colony site. All handlers were trained by PB or senior members of the field team. All work was

256   conducted in accordance with international standards on animal welfare and in compliance with Swiss

257   local and national regulations (ringing permit 2235 & project 72 delivered to Pierre Bize by the Swiss

258   Federal Office for the Environment).

259

260   RESULTS

261   *Selection analyses*

262   On average, there were more breeding females than breeding males, and breeders had more

263   deeply forked tails than nonbreeders with a non-linear increase in breeding probability in relation to

264   fork length (Table 1). Female but not male fork and wing length had a positive effect on egg volume

265   (Table 1). There were no detectable effects of either female or male fork length or wing length on egg

266   laying date (Table 1). Likewise, there was no detectable selection on female or male fork length or wing

267   length in relation to clutch size (Table 1). However, males with more deeply forked tails had larger brood

268   sizes at hatching and fledgling as well as a greater weighted proportion of surviving fledglings than males

269   with less deeply forked tails (Table 1, Figure 1). In addition, males with shorter wings had larger brood

270   sizes at hatching than males with longer wings (Table 1). There were no statistically significant effects of

271   female fork length or wing length in relation to brood size at hatching nor fledgling, or to the weighted

272   proportion of surviving fledglings (Table 1). There were no statistically significant differences in

273   overwinter survival in relation to sex, fork length or wing length (Table 1). There were statistically

274   significant colony differences for all measures of reproductive success as well as breeding status, laying

275   date and overwinter survival, with more breeding individuals, earlier laying dates, larger eggs, larger

276   clutch and brood sizes (hatching, fledgling, weighted proportion of surviving fledglings) as well as

277   greater overwinter survival in Solothurn as compared to Biel (Table 1). These results were qualitatively

278 similar when looking at the relative fork depth (ratio of fork length to inner or outer tail feather length)

279 rather than absolute fork length (Table S3), and when removing wing length from the models (Table S4).

280 Table 1. Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association

281 between fork length and breeding status (binomial distribution), laying date (gaussian distribution),

282 clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson

283 distribution), the weighted proportion of surviving fledglings (binomial distribution) and overwinter

284 survival (binomial distribution). The T-Value is reported for the laying date model, while the Z-Value is

285 reported for all other models. Statistically significant estimates ($P < 0.05$) were bolded. The reference

286 levels are: females for sex, Biel for colony, and nonbreeders for breeding status. Data spans from 1999-

287 2021.

	Estimate	Standard Error	T- or Z-Value	P-Value
Breeding Status				
Number of observations: 5341; Number of individuals: 1445; Number of years: 24				
Intercept	**2.77**	**0.21**	**13.11**	**<0.001**
Sex [M]	**-0.55**	**0.12**	**-4.51**	**<0.001**
Fork Length	**16.98**	**4.30**	**3.95**	**<0.001**
Fork Length ^2	**-11.77**	**3.09**	**-3.81**	**<0.001**
Wing length	**28.41**	**4.52**	**6.28**	**<0.001**
Wing Length ^2	**-11.14**	**3.72**	**-3.00**	**0.003**
Colony [Solothurn]	**-0.28**	**0.12**	**-2.47**	**0.014**
Laying Date				
Number of observations: 1941; Number of females: 611; Number of males: 567; Number of years: 24				
Intercept	0.18	0.12	1.45	0.160
Female Fork Length	-0.03	0.02	-1.20	0.231

	Estimate	Standard Error	T- or Z-Value	P-Value
Male Fork Length	-0.03	0.02	-1.43	0.154
Female Wing Length	-0.04	0.02	-1.43	0.152
Male Wing Length	0.02	0.02	1.12	0.263
Colony [Solothurn]	**-0.34**	**0.05**	**-6.68**	**<0.001**

Egg Volume

Number of observations: 5051; Number of females: 593; Number of males: 554; Number of nests: 1655; Number of years: 24

	Estimate	Standard Error	T- or Z-Value	P-Value
Intercept	**5.76**	**0.03**	**214.93**	**<0.001**
Female Fork Length	**0.05**	**0.01**	**3.90**	**<0.001**
Male Fork Length	0.01	0.01	1.32	0.188
Female Wing Length	**0.03**	**0.01**	**2.59**	**0.010**
Male Wing Length	0.01	0.01	1.22	0.223
Colony [Solothurn]	**0.07**	**0.04**	**2.08**	**0.038**

Clutch Size

Number of observations: 1939; Number of females: 613; Number of males: 578; Number of years: 24

	Estimate	Standard Error	T- or Z-Value	P-Value
Intercept	**0.99**	**0.02**	**52.09**	**<0.001**
Female Fork Length	0.01	0.01	0.50	0.616
Male Fork Length	0.00	0.01	0.24	0.807
Female Wing Length	0.00	0.01	0.24	0.807
Male Wing Length	0.00	0.01	0.33	0.741
Colony [Solothurn]	0.05	0.03	1.74	0.083

Brood Size at Hatching

Number of observations: 1949; Number of females: 613; Number of males: 578; Number of years: 24

	Estimate	Standard Error	T- or Z-Value	P-Value
Intercept	**0.63**	**0.04**	**15.08**	**<0.001**
Female Fork Length	0.02	0.02	0.85	0.396

	Estimate	Standard Error	T- or Z-Value	P-Value
Male Fork Length	**0.05**	**0.02**	**2.67**	**0.008**
Female Wing Length	0.00	0.02	0.09	0.926
Male Wing Length	**-0.04**	**0.02**	**-2.47**	**0.013**
Colony [Solothurn]	**0.18**	**0.04**	**5.16**	**<0.001**

Brood Size at Fledgling

Number of observations: 1946; Number of females: 613; Number of males: 577; Number of years: 24

	Estimate	Standard Error	T- or Z-Value	P-Value
Intercept	**0.34**	**0.06**	**5.45**	**<0.001**
Female Fork Length	0.03	0.02	1.29	0.198
Male Fork Length	**0.04**	**0.02**	**2.03**	**0.042**
Female Wing Length	0.01	0.02	0.55	0.583
Male Wing Length	-0.03	0.02	-1.58	0.114
Colony [Solothurn]	**0.22**	**0.04**	**5.28**	**<0.001**

Weighted Proportion of Surviving Fledglings

Number of observations: 1934; Number of females: 612; Number of males: 577; Number of years: 24

	Estimate	Standard Error	T- or Z-Value	P-Value
Intercept	0.22	0.17	1.30	0.195
Female Fork Length	0.08	0.06	1.45	0.146
Male Fork Length	**0.16**	**0.05**	**3.10**	**0.002**
Female Wing Length	0.02	0.06	0.40	0.686
Male Wing Length	-0.10	0.06	-1.75	0.079
Colony [Solothurn]	**0.59**	**0.14**	**4.30**	**<0.001**

Overwinter Survival

Number of observations: 4585; Number of individuals: 1300; Number of years: 24

	Estimate	Standard Error	T- or Z-Value	P-Value
Intercept	**-0.71**	**0.22**	**-3.16**	**0.002**
Sex [M]	-0.07	0.07	-0.91	0.365
Fork Length	0.00	0.04	0.09	0.931

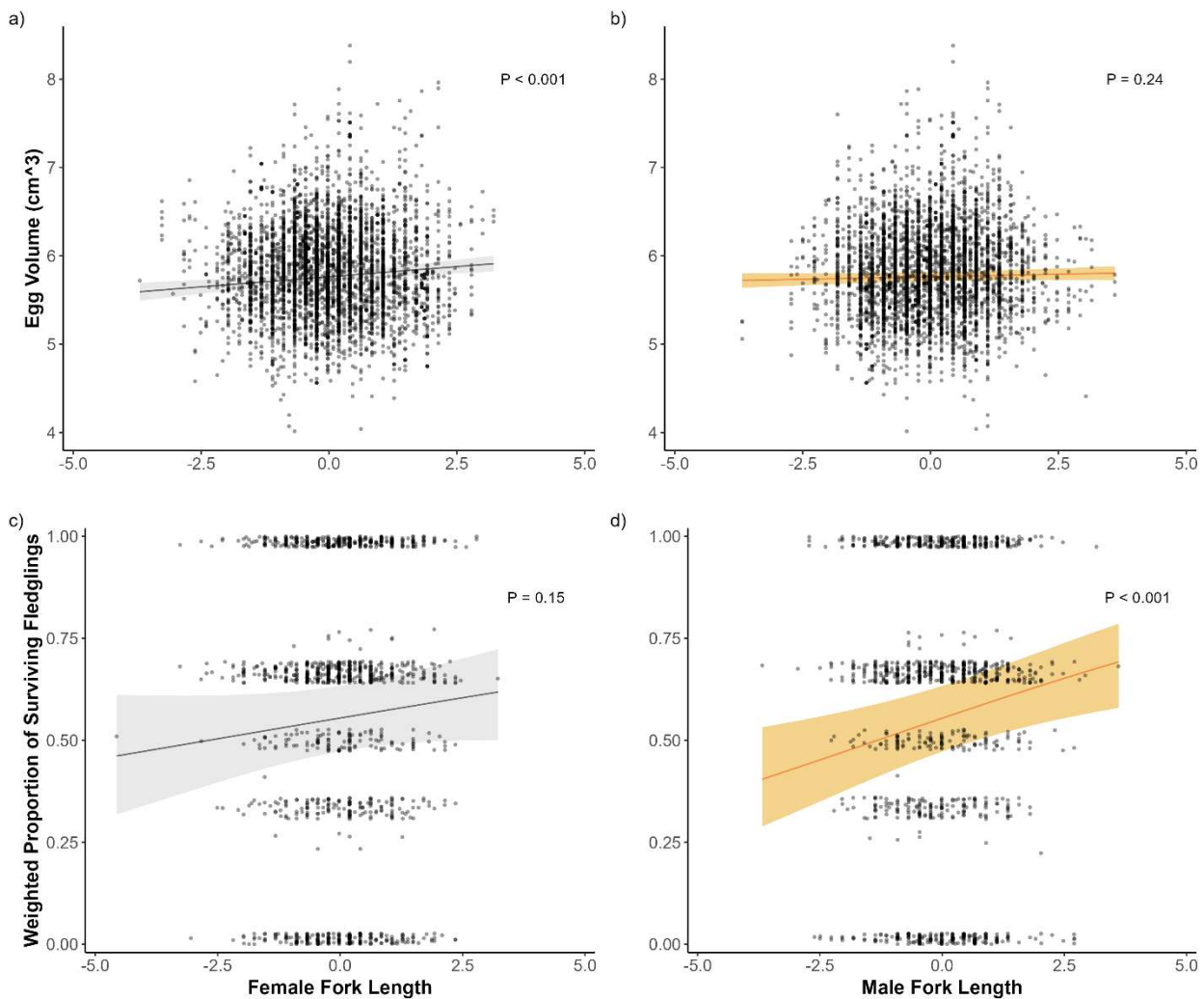|	Estimate	Standard Error	T- or Z-Value	P-Value
Wing Length	0.06	0.04	1.42	0.156
Colony [Solothurn]	**-0.34**	**0.07**	**-4.62**	**<0.001**

288

290 Figure 1. Association between female (left) and male (right) fork length and egg volume (panels a and b)

291 as well as the weighted proportion of surviving fledglings (panels c and d) in a Swiss population of Alpine

292 swifts (data spans 1999-2021). The data points correspond to the raw data.

293 *Quantitative genetic analyses*

294   This population of Alpine swifts showed moderate sexual dimorphism in fork length (Table 2),

295   with males' fork length being on average 7% deeper than that of females. Average fork length was of

296   24.1 mm in males and 22.5 mm in females (raw data, Table S1). The inner tail feather length was

297   comparable between sexes, with longer outer tail feathers in males than in females (Table S1). On

298   average, birds of both sexes in Biel had more deeply forked tails than birds in Solothurn (Table 2). Fork

299   length has increased over time, with a more pronounced increase in females, such that fork length has

300   become more similar between the sexes over the course of the study (Table 2).

301   We report relatively high additive genetic variance in both sexes, of 0.56 [0.45; 0.67] (median

302   [95% HPDI]) in females and 0.44 [0.32; 0.55] in males (Table 3). Heritability was likewise high in both

303   sexes, explaining of 60% [51; 68] of the variance in females and 52% [41; 62] of the variance in males.

304   Despite appearing slightly higher in females than in males, additive genetic variance and heritability

305   were comparable between the sexes: a model for which additive genetic variance was constrained to

306   the same value for both sexes performing no better than one where they were permitted to vary (Table

307   S8). The permanent environment explained 14% [7; 22] of the variance in females and 16% [7; 25] of the

308   variance in males (Table 3). The year effect explained only a small proportion of variance in fork length

309   accounting for 4% [2; 7] in females and 6% [3; 10] in males. There were strongly positive cross-sex

310   genetic (0.89 [0.76; 0.99]) and year (0.95 [0.86; 0.99]) correlations in fork length (Table 3, Figure 2). The

311   cross-sex genetic correlation was effectively 1, as a model estimating the correlation did not perform

312   better than one where it was fixed to 1 (Table S8). The median, mean and mode of the posterior

313   distribution were all comparable and are reported in the supplemental (Table S9). A model with a single

314   estimate pooled across the sexes for each of the variance components and ratios likewise performed

315   similarly (Table S9). Results for the relative fork length (inner or outer tail feather) where likewise

316   qualitatively similar (Table S10 & S11).

317   The predicted breeding values of female-trait fork length and male-trait fork length may both

318   have increased slightly over the course of the study (Figure 3), though the estimates were near zero and

319   with credible intervals crossing zero (median of the slopes (with lower and upper 95% HPDI): female-

320   trait 0.02 (-0.02; 0.06); male-trait 0.01 (-0.03; 0.04); Table S12). The estimated rate of increase in female-

321   trait and male-trait fork length over the study period was greater than expected under genetic drift

322   alone in 70.1% and 61.7% of cases, respectively (Pr[$slope_e$ > $slope_d$] Table S12). As PBVs could be

323   estimated both for individuals born before the start of data collection and individuals with no collected

324   data based on ancestry information, we also ran the analyses with all PBVs, the results of which were

325   qualitatively similar and presented in the supplemental (Figure S1, Table S12, Table S13).

326   Table 2. Estimates (median) and 95% credible intervals (Bayesian model in R package MCMCglmm) for

327   the relationships between fork length and fixed effects for male and female swifts (1999-2021). Female

328   is the reference level for sex. Biel is the reference level for colony.

	Estimate	Lower 95%HPDI	Upper 95%HPDI
Intercept	**-0.22**	**-0.32**	**-0.12**
Sex [M]	**0.63**	**0.53**	**0.71**
Year	**15.87**	**11.51**	**20.51**
Year^2	**-9.83**	**-13.34**	**-6.02**
Colony [Solothurn]	**-0.16**	**-0.27**	**-0.07**
Sex [M] : Year	**-9.05**	**-13.51**	**-4.66**
Sex [M] : Year^2	-2.34	-5.72	0.82

329

330   Table 3. Variance component as well as variance ratio estimates (median of the posterior distribution)

331   along with their [upper; lower] 95% HDP intervals of fork length in female and male Alpine swifts.

332   Variance component estimates: additive genetic variance, permanent environment, year and residual

333   variance. Variance ratios: heritability, permanent environment and year effects. We bolded estimates

334   for which the 95% HPD interval did not cross zero, deemed statistically significant.

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

335

336
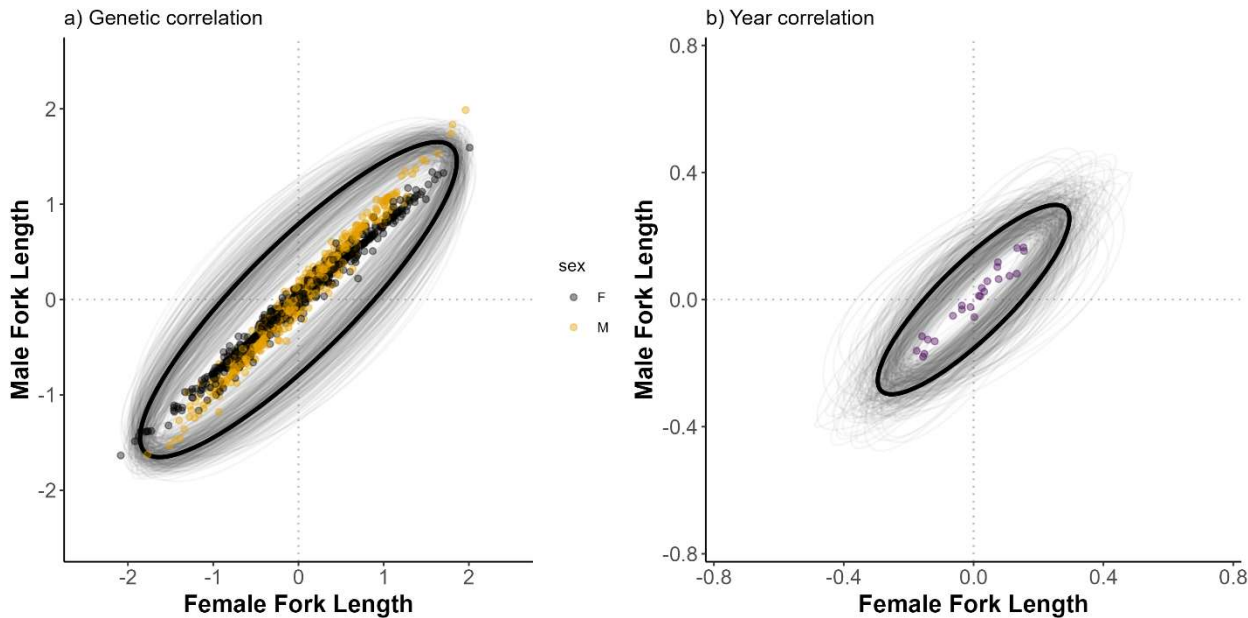
337   Figure 2. The cross-sex a) genetic and b) yearly correlations in Alpine swift fork length. The points

338   represent the posterior mode of the best linear unbiased predictors (BLUPs) from the MCMCglmm

339   model. For the genetic correlation plot, points in black are females and yellow are males, while for the

19

340   yearly correlation plot, points in purple correspond to each year (1999-2021). Ellipses represent the

341   correlation estimate. The bold ellipses were estimated from the posterior mode while the grey ellipses

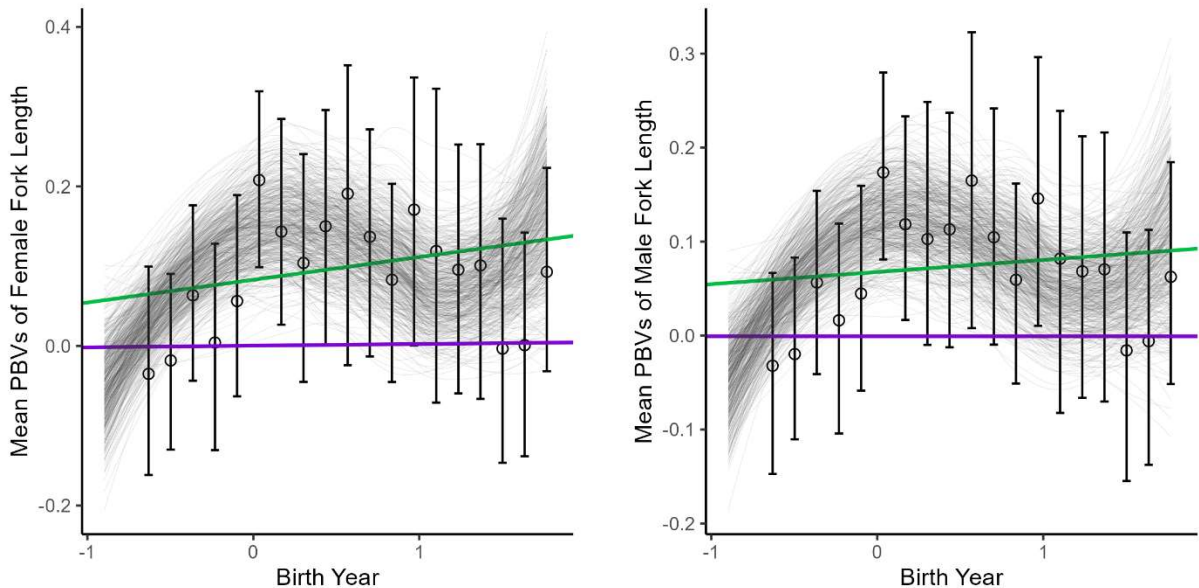342   represent the uncertainty (300 randomly selected estimates from the posterior distribution).

343

344   Figure 3. Changes in average female-trait (left) and male-trait (right) predicted breeding values for

345   Alpine swifts in relation to their year of birth as of 1999. The green lines represent the posterior median

346   of predicted changes from linear regressions, while the purple lines represent the changes as expected

347   from genetic drift alone. The circles are the medial of the PBVs per birth year and the bars are the

348   associated 95% HDP intervals. The thin grey lines are a loess fit on a random draw of 500 iterations (out

349   of 1500) from the posterior distribution of female-trait and male-trait average PBVs per birth year. The

350   intercept for the predicted PBVs (green line) does not cross zero likely partially because individuals with

351   birth years prior to 1999 were not removed from the data set and pedigree when running the animal

352   model from which the PBVs were estimated.

353

354   DISCUSSION

355   In this study, we investigated the predictors and fitness consequences of tail fork length in both

356   sexes of a Swiss population of Alpine swifts. Fork length showed moderate sexually dimorphism, with

357   males displaying tails with longer forks than females. In line with the expectation that forked tails are a

358   sexually selected signal in males, males with longer forks had greater reproductive success than those

359   with shorter forks. Females with longer forks produced larger eggs, suggesting a greater allocation into

360   reproduction than females with shorter forks, and that fork length may be a positively selected trait in

361   both sexes. Contrary to our expectations, longer forks did not appear to incur survival costs for either

362   sex. Finally, the length of the fork was heritable and positively genetically correlated between the sexes,

363   with effectively the same genetic architecture in males and females.

364   On average, males had forks which were 7% longer than those of females (raw data). This sexual

365   dimorphism was driven primarily by sex differences in the outer tail feather length, as the inner tail

366   feather was effectively of the same lengths in both sexes (Table S1). It was therefore unsurprising for

367   analyses on the absolute and the relative fork depth (fork / outer tail feather length and fork / inner tail

368   feather length) to be qualitatively similar. Although most swifts have historically been considered to be

369   monomorphic, sexual dimorphism in fork length has also been reported in the Common swifts (3-7%;

370   Jukema *et al.,* 2023), the Plain swift (4%; Garcia-Del-Rey *et al.,* 2008) and the Black swift *Cypseloides*

371   *niger borealis* (83%; Gunn *et al.,* 2018), suggesting sexual dimorphism in this trait may be more

372   widespread than previously reported. That said, sexual dimorphism in fork length in this population has

373   decreased over the course of study, being of 8% in the first decade and 6% in the second decade (Dumas

374   *et al.,* in prep). Sexual dimorphism in outer tail feather length has likewise decreased by 1.6% over the

375   course of the study (Masoero *et al.,* in prep).

376   We report that males with longer forks had greater reproductive success than those with less

377   deeply forked tails. Males with longer forks had larger brood sizes at hatching and fledgling as well as a

378   greater weighted proportion of surviving fledglings than males with shorter forks. This is consistent with

379   the expectation for fork length to be a sexually selected trait in male swifts (Hasegawa & Arai, 2020).

380   Males with more deeply forked tails likewise are reported to have greater reproductive success than

381   those with less deeply forked tails in the barn swallow (Møller *et al.*, 1998), with the length of the fork

382   possibly acting as a reliable signal of offspring longevity (Møller, 1994). Thought little is known about the

383   behaviours of swifts outside of the breeding period, they likely engage in aerial courtship displays, and

384   possibly also aerial threat displays, as has been suggested in Common swifts (Lack, 1956) and Chimney

385   swifts *Chaetura pelagica* (Fischer, 1958). Indeed, birds of many species use their tails in agonistic and/or

386   sexual displays (Fitzpatrick, 1998). Males with more deeply forked tails may also have greater foraging

387   success than those with less deeply forked tails, potentially specializing on different prey, and hence

388   may be better able to provision their offspring. Male pallid swifts have been found to consume larger

389   prey than females (Fernandez et al., 2023), suggesting that dietary niche segregation between the sexes

390   could also be possible in the Alpine swift.

391   Females with longer forks produced larger eggs—and hence, had greater energetic investment

392   into reproduction—than females with shorter forks. This is contrary to what previous studied have

393   identified in other species, with a possible trade off between deeply forked tails and egg size in swifts

394   and swallows (Hasegawa & Arai, 2017, 2018). Females with longer forks may, like their male

395   counterparts, have greater foraging success than those with shorter forks, perhaps as a result of the

396   prey species available in these regions. However, although numerous studies have shown that larger

397   eggs give rise to larger hatchlings that grow faster and are more likely to survive up to fledging (Bize et

398   al., 2002), there was no detectable effect of female fork length on more direct measures of

399   reproductive success (clutch size, brood size at hatching and fledgling, weighted proportion of surviving

400   fledglings). This suggests that the previous benefit of larger eggs do not translate into higher

401   reproductive success, and thus that longer forks may still be costly to bear for females.

402   Beyond serving as a possible signal of individual quality in both sexes, the length of the fork may

403   potentially also serve as an indication of age and therefore experience. A general tendency for flight

404   feathers to become longer with age has been reported, and tail feather length have also been shown to

405   increase with age (*e.g.,* older birds had longer tail feathers than younger birds in the Sand Martin *Riparia*

406   *riparia*, Szép *et al.,* 2019). Fork depth has also been shown to increase with age in barn swallows, as the

407   combined result of both outer tail feather lengthening and inner tail feather shortening with age

408   (Adamkova et al., 2022). Older birds are generally considered to be more experience than younger birds

409   and may be more skilled when it comes to migration (*e.g.,* older Whooping cranes *Grus americana*

410   deviate less from a straight-line migration path then younger birds, Muller *et al.,* 2013) and breeding

411   behaviours (*e.g.,* older mute swans *Cygnus olor* lay earlier and have larger clutches than younger birds,

412   McCleery *et al.,* 2008). In our population, fork length has been shown to increase in early life in both

413   sexes (Moullec *et al.,* 2023; present study, Table S6), while remaining relatively stable from

414   approximately 5 years of age onwards. As such, it is unlikely that our results are simply a reflection of

415   age effects on reproduction.

416   Contrary to our expectations, we report no selection on fork length in relation to overwinter

417   survival in either sex, suggesting that deeply forked tails did not hamper overwinter survival for either

418   sex. However, overwinter survival may not accurately reflect the costs of deeply forked tails. Rather,

419   fork length may incur costs during incubation or chick provisioning in terms of increased effort (e.g.,

420   increased energetic expenditure or foraging time) which will need to be investigated in future studies.

421   Thought our study was unable to detect costs of fork length in either sex, deeply forked tails in barn

422   swallows have been associated with increased oxidative damage (Vitousek et al., 2016), which can

423   impair survival (Bize et al., 2014). As these costs should be especially apparent during and following

424   migration, which represents a period of high exertion and risk, individuals with less deeply forked tails

425   (and hence less drag) should have a clear advantage. One possible future avenue of research in the

426   Alpine swift could then be to investigate the link between fork length and arrival to the breeding

427   grounds, with the expectation that those with longer forks would arrive later—should there be a cost

428   associated with deeply forked tails.

429   Furthermore, fork length presented comparable and moderate additive genetic variance and

430   heritability in both sexes. This suggests that fork length has the potential to evolve in response to

431   selection in both sexes. We found a strong positive cross-sex genetic correlation suggesting that females

432   and males would be positively correlated in any evolutionary response. Per the genetic correlation

433   hypothesis (Lande, 1980; Bonduriansky & Chenoweth, 2009; Poissant *et al.,* 2010), this strong cross-sex

434   genetic correlation could explain the presence of forked tails in females despite direct advantages of

435   more deeply forked tails only being found for males. However, male fork length has remained relatively

436   static over the course of the study, with female fork length increasing to more closely resemble that of

437   males. Given clear reproductive benefits for males with longer forks, the strong genetic correlation

438   across sexes, and no detected costs in either sex, we would have expected fork length to increase in a

439   similar way in both sexes. We found small (but not statistically significant) changes at the genetic level in

440   both sexes. As such, it is unlikely for the observed changes in fork length in this population to have

441   occurred as a result of selection and genetic constraints on fork length. Rather, this more rapid change

442   in female than male fork length could be due to as of yet unidentified environmental causes. Though

443   preliminary GPS data suggests that Alpine swifts forage mostly within a 15km radius surrounding the

444   colony during the breeding period (Brighten et al., pers. com.), it remains unknown whether males and

445   females forage in the same areas or on the same time, or if they specialize on the same insect prey.

446   Indeed, male Pallid swifts appear to prey on larger arthropods than females (Fernandez et al., 2023). It

447   would be interesting to look at links between fork size and foraging strategies using GPS loggers and diet

448   using metabarcoding. Female foraging habits may have changed over the last decades, perhaps as a

449   result of climate change, accelerating the changes in their fork length.

450   To conclude, fork length is a moderately sexual dimorphic trait likely to be under sexual

451 selection in the Alpine swift. Longer forks conferred reproductive benefits to females and males in terms

452 of reproductive allocation and success, respectively, suggesting that fork length has the potential to

453 signal aspects of individual condition in both sexes. The sexes effectively shared the same genetic

454 architecture for fork length, with relatively high heritability and a cross-sex genetic correlation

455 approximating one, indicating that males and females should share the same evolutionary trajectory. In

456 line with this, we identified a possible increase in breeding values in both sexes over the course of the

457 study. Though it remains unclear why female fork length increased while male fork length remained

458 relatively static over the course of the study and finer scale studies on male and female foraging

459 behaviour would be needed.

460

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