

RESEARCH ARTICLE

Adult body mass is heritable, positively genetically correlated and under selection of differing shapes between the sexes in a bird with little apparent sexual dimorphism

Michela N. Dumas¹  | Sophia St. Lawrence¹  | Giulia Masoero^{1,2}  | Pierre Bize²  | Julien G. A. Martin¹ 

¹Department of Biology, University of Ottawa, Ottawa, Ontario, Canada

²Swiss Ornithological Institute, Sempach, Switzerland

Correspondence

Michela N. Dumas

Email: mduma060@uottawa.ca

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Abstract

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

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Pierre Bize and Julien G. A. Martin share senior authorship.

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selection on females and males respectively in relation to the weighted proportion of surviving fledglings.

5. Overall, these results suggest that while body mass may be able to respond to environmental conditions and evolve, genetic constraints would result in similar changes in both sexes or an overall absence of response to selection. It remains unclear whether the weak (1%) dimorphism in Alpine swift body mass we report is simply a result of the similar fitness peaks between the sexes or of genetic constraints.

KEYWORDS

alpine swift *Tachymarptis (Apus) melba*, cross-sex genetic correlation, environmental effects, quantitative genetics, sexual conflict, sexual dimorphism, sexually antagonistic selection

1 | INTRODUCTION

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

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

Furthermore, energy allocation and trade-offs may differ between the sexes, resulting in sex-specific phenotypic optima. Sexual size dimorphism (SSD), a difference in the mean body size and/or mass of males and females, has been extensively studied and varies dramatically within and between taxa. In birds and mammals, males are often larger than females, while in reptiles and fish, females are generally larger than males (Fairbairn, 2007). Nonetheless, within taxa, some species can present the opposite trend (reverse SSD). For example, in seabirds and raptors, females are often larger and heavier than males (Krüger, 2005; Székely et al., 2007). These differences between the sexes can reflect sex-specific natural and sexual selection. For instance, in the context of sexual selection, intra-sexual competition for mates could result in different optimal sizes for males and females. Male northern elephant seals *Mirounga angustirostris* compete over access to harems of females with body size as a sexually selected weapon (Lloyd et al., 2020). As a result, they can be 3.5 times heavier than females (Salogni et al., 2019). Conversely, in species where males compete aerially for mates, males may be lighter than females to increase their agility (Székely et al., 2007). Natural selection may also be responsible for these pronounced differences as a result of males and females specializing on different food sources (i.e. to lessen inter-sexual foraging competition through niche segregation; Krüger, 2005), different parental roles, and differences in fecundity selection (Székely et al., 2007). Given these sex-specific ecological roles, SSD is often considered to be adaptive (Fairbairn, 2007).

In species with little apparent dimorphism, the evolution of SSD may be potentially constrained by a shared genetic architecture between the sexes (Bonduriansky & Chenoweth, 2009; Poissant et al., 2010). This can be estimated through the cross-sex genetic correlation (r_{MF} ; Lande, 1980). A r_{MF} different from zero suggests the presence of shared genetic architecture between the sexes, meaning that selection acting on one sex could constrain the evolution of the other (Bonduriansky & Chenoweth, 2009). In cases where a negative r_{MF} is coupled with sexually concordant selection, the evolution of SSD will not be favoured, though the mean value of the trait may evolve in both sexes. In cases where a positive r_{MF} is coupled with sexually antagonistic selection the evolution of SSD may likewise be

constrained (Kruuk et al., 2008). This could lead to intra-locus sexual conflict (broadly defined as sex-specific fitness optima for a shared trait; Parker, 1979), studies of which are rare in natural populations. Of those studies, most focus on highly dimorphic species (Poissant et al., 2010) and present differing results. For example, intra-locus sexual conflict over body mass has been reported in mountain goats *Oreamnus americanus* (Mainguy et al., 2009) but not in bighorn sheep *Ovis canadensis* (Poissant et al., 2008). Given that SSD may represent a resolution to an intra-locus sexual conflict, this conflict should be especially strong in species with weak sexual dimorphisms.

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

2 | MATERIALS AND METHODS

2.1 | Study species and site

The Alpine swift is a long-lived migratory bird, with a median lifespan of 7 years (maximum: 26 years; Bize et al., 2009). They live a highly aerial lifestyle, remaining in flight for over 6 months at a time (Liechti et al., 2013) and landing only during the reproductive period. Colonies of a few to a hundred pairs will nest on cliffs or in the roof spaces of tall buildings. Alpine swifts nest from May to August, with both parents incubating their 1–4 eggs for approximately 18 days (Bize et al., 2004). Chicks take approximately 50–70 days from hatching to fledging, during which time both parents will brood and feed them (Bize et al., 2004). As such, males and females are expected to have similar parental allocation into reproduction (with the exception of

egg-laying costs exclusive to females). Further, since adults return to the same breeding site throughout their life, and the probability of recapturing breeders is virtually 1 (Bize, Gasparini, et al., 2006), we can adequately estimate the annual survival of adults through the records of captures from year to year. In addition, weather during the breeding period can be highly variable, resulting in important yearly variations in egg-laying dates (de Villemereuil et al., 2020) as well as fluctuations in prey availability and hence mass (Bize et al., 2007; Bize, Metcalfe, et al., 2006).

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

2.2 | Statistical analyses

All statistical analyses were conducted in R version 4.2.0 (R Core Team, 2022). Throughout the analyses, linear and quadratic effects were calculated using orthogonal polynomials. When included in the analyses, the effects of mass, age, day of capture, hour of capture, rainfall and temperature were mean-centred and scaled to a variance of 1.

For all analyses (Environmental effects, Quantitative Genetic and Selection analyses), models were also run with the inclusion of sternum length as a fixed effect to correct for skeletal size differences. The results obtained were qualitatively similar and are presented only in the appendix (Tables S1, S5 and S6).

2.3 | Environmental effects on body mass

Environmental conditions are expected to affect body mass in swifts since insect prey availability is highly dependent on weather (Grüebler et al., 2008). To determine the weather time period(s) that

best explained variation in body mass, we used a sliding window approach fitted with the function `slidingwin` from the R package *climwin* (Bailey & van de Pol, 2016; van de Pol et al., 2016). The sliding window approach allows the user to simultaneously test for critical periods as well as descriptive metrics (i.e. mean, sum) and functions (i.e. linear, quadratic) that best describe the relationship between weather and biological data. We used a relative window which opened 105 days before each mass measurement and closed the day of mass measurement. We chose this opening date to include the full duration of the breeding season (May–August) for those weights taken at the end of the breeding season (e.g. for a weight on August 10th, the opening date corresponded to April 27th and hence immediately preceded the first egg laid). Adults were captured and weighed between 08:00 and 20:00h, from May 1st to August 10th (1999–2021). Given that swifts can travel great distances within a day, we estimated daily weather data as the average of daily rainfall and daily temperature across five Swiss Meteorological Stations surrounding the colonies (Bern-Zollikofen, Cressier, Grenchen, Koppigen, Wynau). We averaged these measurements to account for daily variations across stations (e.g. strong local precipitation recorded by one of the stations).

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

2.4 | Quantitative genetic analyses

A detailed social pedigree has been constructed over the years of the study based on behavioural observations (parents are caught at the nest while brooding the eggs or chicks, and later feeding the chicks). Extra-pair paternity (the proportion of a female's clutch sired by a male other than her social partner, EPP) approaches zero in this Alpine swift population (C. M. Meier & P. Bize, personal comm.). A molecular analysis of another Swiss colony of Alpine swifts nesting in

Baden (50 breeding pairs) shows little evidence of EPP (C. M. Meier and P. Bize, manuscript in preparation). Likewise, low incidences of EPP are reported for the common swift *Apus apus*, which has similar ecology to the Alpine swift (Martins et al., 2002). Hence, behavioural observations are suitable to construct a social pedigree in the Alpine swift. Furthermore, frequent natal dispersal (10%) coupled with no breeding dispersal (Bize et al., 2017) ensures gene flow between the two colonies. Previous analyses including genetic groups have shown no heterogeneity in additive genetic variance between colonies. As such, the two colonies are treated in the analyses as a single population. The pruned social pedigree used in this study is five generations deep and includes data on 1159 individuals, with 533 maternities and 516 paternities (Table S3). In our data set, individuals from Biel with at least one parent from Solothurn accounted for 5.9% of the colony, while individuals from Solothurn with at least one parent from Biel accounted for 11.8% of the colony (Table S4). The social pedigree statistics were determined using the R package *pedantics* (Morrissey, 2018).

Using the R package *MCMCglmm* (Hadfield, 2010), we fitted body mass as a function of sex, hour and day of capture (linear and quadratic effects), colony as well as the weather signals (daily mean rainfall and temperature; linear and quadratic effects) extracted from the best *climwin* model detailed above (rainfall window: 6–0 days before weighing; temperature window: 1–0 days before weighing). We also included an interaction term between sex and day of capture (linear and quadratic) to assess sex differences in these terms. We also tested for an interaction between sex and colony; as this interaction was not statistically significant, it was dropped from the model (Table S2).

We estimated the following sex-specific variance components: additive genetic variance (individual identity linked to the pedigree), permanent environment variance (individual identity), yearly variance (year of observation) and residual variance. In addition, we estimated the cross-sex genetic and yearly covariances and correlations. We did not include parental effects in the model for two reasons. First, we are studying mass in adults and parental (maternal or paternal) effects on mass are often found to become negligible at adulthood (e.g. Vedder et al., 2023). Second, including parental identity in the model would result in a strong reduction in sample size due to the incomplete maternities and paternities of individuals in the first years of the study and of immigrants. Variance parameters were estimated as the posterior mode and reported with their 95% highest posterior density intervals (HPDI). Variance ratio estimates were calculated as the proportion of total phenotypic variation explained by the given variance parameter, that is heritability conditioned on the fixed effects was estimated as the sex-specific additive genetic variance divided by the total phenotypic variance, while evolvability was estimated as the additive genetic variance divided by the squared mean of the population. For the residuals and the permanent environment effect, for which cross-sex correlations cannot be estimated, we used standard priors with $V = \text{diag}(2)$, $\nu = 1.002$. For the additive genetic and year effects, we used expanded priors, adapted for models estimating cross-sex correlations (i.e. $V = \text{diag}(2)$

* 0.02, $\nu=3$, $\alpha.\mu=\text{rep}(0, 2)$, and $\alpha.V=\text{diag}(2) * 1000$). The model had a burn-in period of 50,000 iterations and was sampled every 2000 iterations for a total effective sample size of 1500. Plot traces were visually assessed, and absolute autocorrelation values were verified to be <0.1 . We verified chain convergence for each parameter using the Heidelberg and Welch's convergence diagnostic (`heidel.diag` function) as recommended by Hadfield (2010).

2.5 | Adjusting mass for selection analyses

Body mass is a highly labile trait in the Alpine swift, and highly sensitive to short-term climatic variability. As individuals are not captured on the same days or at the same time, we needed to account for this additional source of between and within individual variation before fitting selection models. To do so, we adjusted mass estimates for each individual each year for the average weather within a year, at a specific time of day for a given date. We used 14:00h which is the median capture time. For the date, we adjusted body mass to two different dates; (1) on June 13th ('June mass'), which corresponds to the median capture date and is representative of mean hatching throughout the study (range: June 2nd to June 28th) and may reflect how much energy is available for reproduction; (2) August 8th ('August mass'), possibly reflecting the energy available at the end of the breeding season when chicks are approaching fledging, but prior to migration. The adjusted body mass estimates for each individual each year were obtained as predictions of a linear mixed model including fixed effects of the hour of capture (linear and quadratic), date of capture (linear and quadratic), rainfall (linear and quadratic), temperature (linear and quadratic), individual age (linear and quadratic), sternum length and colony. The model also included random intercepts for the year of measurement and for individual identity, as well as random slopes of the date of capture (linear and quadratic) at the individual level within each year. We fit one model for females (Figure S3) and a second for males (Figure S4). Models were fitted using the R package *MCMCglmm* (Hadfield, 2010) with 1000 iterations in the final posterior output. Mass predictions conditional on random effects were obtained using the `predict.MCMCglmm` function using 14:00h for the time of capture, average rainfall and temperature for the given year and a specific date to get either June or August mass. Year-specific measurements of age, sternum length and colony for each individual were also used for the predictions. Predictions were done for each iteration of the model; thus, we obtained a set of 1000 individual-year-specific estimates.

2.6 | Selection analyses

We used the R package *lmerTest* (Kuznetsova et al., 2017) to investigate selection for adjusted June and August mass based on measures of reproductive success and overwinter survival. June mass was used for the reproductive success models, while August mass was used for the overwinter survival model. To carry forward the error

from the mass adjustment detailed above, we ran each selection model using each of the 1000 set of mass estimates in a Bayesian-like approach. We obtained a posterior distribution for every statistic from the selection models, and report the posterior mode, 95% HPDI and posterior mode of the associated p -value.

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

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

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

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

survival), we extended Morrissey and Goudie (2022) approach with methodology from Janzen and Stern (1998) to approximate average selection gradients (see appendix for details of the method).

2.7 | Ethical note

Adult swifts were caught at the nest between 08:00 and 20:00h (usually between 09:00 and 18:00h) to avoid disturbing the adults during periods of intense social activity (dawn and dusk) (Meier et al., 2018). We minimized the number of captures and disturbances during severe weather events to avoid extra stress to the birds. To further limit stress to the birds, swifts were placed in cloth bags and handled quickly, typically 5–15 min depending on data collection. All individuals were released at the colony site. All handlers were trained by PB or senior members of the field team. All work was conducted in accordance with international standards on animal welfare and in compliance with Swiss local and national regulations (ringing permit 2235 & project 72 delivered to Pierre Bize by the Swiss Federal Office for the Environment).

3 | RESULTS

3.1 | Environmental variation in adult swift body mass

There was an effect of meteorological factors on mass (Figure 1). For daily rainfall, the climatic window that best explained the variation in body mass included the 6 days just before mass measurement

(window started 6 days before the mass measurement was taken and closed the day of the measurement; Figure S1). For daily mean temperature, the best-supported climatic window included the day before and the day of mass measurement (Figure S1). In both cases, the best descriptive metric was mean, and the best function was quadratic, based on the delta AICc of each model. For temperature, the delta AICc of the quadratic function model was 109.17 units lower than that of the linear function model. For rainfall, the delta AICc of the quadratic function model was 66.73 units lower than that of the linear function model. Body mass decreased non-linearly with increasing average rainfall over the 6 days before the measurement, with an attenuation of this effect at high levels of rainfall. Body mass increased non-linearly with increasing average ambient temperature in the ~36 h before the measurement, with an attenuation of this effect at high temperatures.

In addition, this population of Alpine swifts showed minor sexual dimorphism in body mass, with females being on average 1% heavier than males (Table 1). Average body mass was 98.9 g (SD: 8.0 g) for females and 98.0 g (SD: 7.7 g) for males based on the raw data. When including sternum length into the model to correct for skeletal size, females were on average 1.7% of higher body condition than males, and individuals of both sexes with longer sternums were heavier than those with shorter sternums (Table S1). This sexual dimorphism was most apparent earlier in the season, as females lost more mass than males between the start and the end of the breeding period (significant sex by day of capture interaction, Table 1). Despite this steeper decline of mass in females than in males, mass decreased non-linearly with the day of capture in both sexes (Table 1, Figure S2a). Mass increased non-linearly with the hour of capture (Table 1, Figure S2b) and age in both sexes (Table 1, Figure S2c).

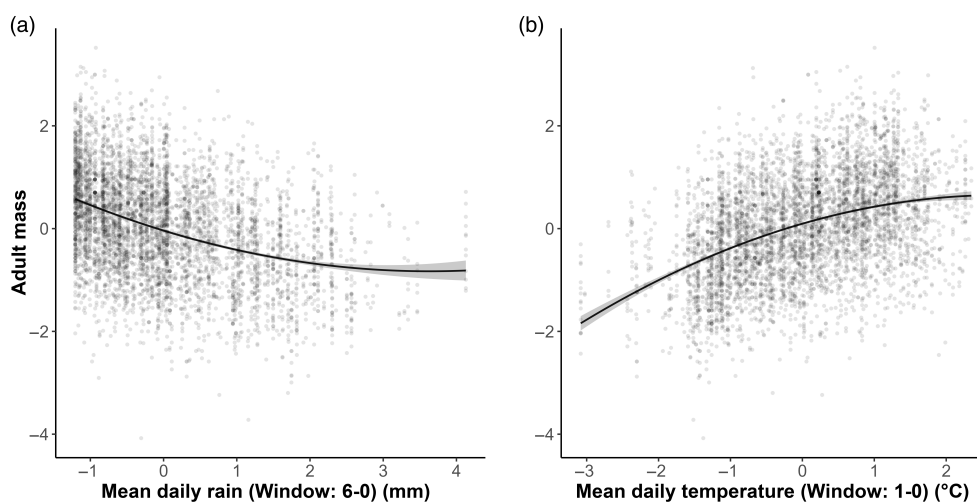


FIGURE 1 Association between adult body mass and (a) mean daily rainfall (mm) and (b) mean daily temperature (°C) in Alpine swifts. Points are raw data and the line with the grey polygon represents the prediction from the models with 95% HPDI. The daily weather records were obtained by averaging observations from five Swiss Meteorological Stations (Bern-Zollikofen, Cressier, Grenchen, Koppigen, Wynau) to reflect regional weather. The data span 1999–2021. The mean daily rainfall was estimated as the average rainfall in the period from 0 to 6 days before the measurement was taken, while for temperature the daily mean was estimated over the ~36 hours prior to measurement (Figure S1). Number of individuals: 1079; number of observations: 5387.

TABLE 1 Estimates (posterior mode) and 95% HDP intervals (Bayesian model fit using the R package *MCMCglmm*) for the relationships between body mass and fixed effects for male and female Alpine swifts measured over the May–August breeding period (1999–2021). Estimates with 95% HPD intervals that exclude 0 were deemed statistically significantly different from zero and bolded. Female is the reference level for sex. Biel is the reference level for colony.

	Estimate	Lower 95% HPDI	Upper 95% HPDI
Intercept	0.051	−0.034	0.143
Sex [M]	−0.098	−0.181	−0.015
Colony [Solothurn]	−0.027	−0.108	0.058
Age	4.519	2.722	6.283
Age ²	−5.694	−7.041	−4.360
Rain signal	−9.020	−10.706	−7.432
Rain signal ²	3.089	1.802	4.370
Temperature signal	38.905	37.285	40.543
Temperature signal ²	−7.774	−9.131	−6.639
Hour of capture	10.585	9.306	11.760
Hour of capture ²	−1.859	−3.173	−0.634
Day of capture	−31.015	−32.855	−29.029
Day of capture ²	7.472	5.748	9.248
Sex [M] * Day of capture	5.591	3.380	8.210
Sex [M] * Day of capture ²	−3.134	−5.475	−0.587

TABLE 2 Variance component and ratio estimates (posterior mode) along with their 95% HDP intervals for adult body mass in female and male Alpine swifts. Variance component estimates: additive genetic variance, permanent environment, year and residual variance. Variance ratios: heritability, evolvability, permanent environment and year effects. Evolvability is expressed as a percentage. Given that variance components are bounded to zero, components for which the lower 95% HPDI was higher than 0.01 were deemed statistically significant and bolded. The cross-sex covariances and correlations are estimated as between the sexes and hence displayed in the table only once.

	Females	Males
Variance component estimates		
Additive genetic variance	0.154 [0.0863–0.218]	0.169 [0.1–0.239]
Permanent environment	0.105 [0.0602–0.165]	0.098 [0.0575–0.171]
Year	0.0162 [0.00769–0.0361]	0.0185 [0.00993–0.041]
Residual	0.316 [0.299–0.338]	0.299 [0.281–0.318]
Variance ratio estimates		
Heritability	0.265 [0.146–0.346]	0.299 [0.168–0.377]
Evolvability	0.147 [0.0904–0.191]	0.166 [0.111–0.206]
Permanent environment	0.183 [0.0974–0.271]	0.17 [0.0928–0.28]
Year	0.0261 [0.0128–0.0584]	0.0305 [0.0179–0.0681]
Cross-sex covariances		
Genetic	0.0998 [0.0361–0.157]	—
Yearly	0.0168 [0.00699–0.0338]	—
Cross-sex correlations		
Genetic	0.702 [0.264–0.933]	—
Yearly	0.914 [0.688–0.996]	—

3.2 | Heritability and cross-sex genetic correlation of adult swift body mass

We report additive genetic variance in both sexes, accounting for 15.4% [8.63, 21.8] (posterior mode [95% HPDI]) of the variance in females and 16.9% [10, 23.9] of the variance in males (Table 2). Heritability was of 0.265 [0.146–0.346] in females and 0.299 [0.168–0.377] in males, while evolvability was of 0.147% [0.0904–0.191] in females and 0.166% [0.111–0.206] in males. The permanent environment explained 18.3% [9.74, 27.1] of variance in female and 17.0% [9.28, 28.0] of variance in male body mass (Table 2). The year effect explained only a small proportion of variance in body mass (2.61% [1.28, 5.84] in females and 3.05% [1.79, 6.81] in males), and residual variance remained relatively high in both sexes. There was a positive cross-sex genetic correlation in body mass of 0.702 [0.264, 0.933], as well as a positive cross-sex yearly correlation in body mass of 0.914 [0.688; 0.996] (Table 2, Figure 2). Results were qualitatively similar when correcting for skeletal size (Table S5).

3.3 | Sex-specific selection over body mass in adult swifts

There was a negative effect of female and male June mass on laying date, with heavier parents laying their clutches sooner than lighter ones (Table 3, Figure 3a,b). The effects of maternal or paternal June mass on clutch size, brood size at hatching and brood

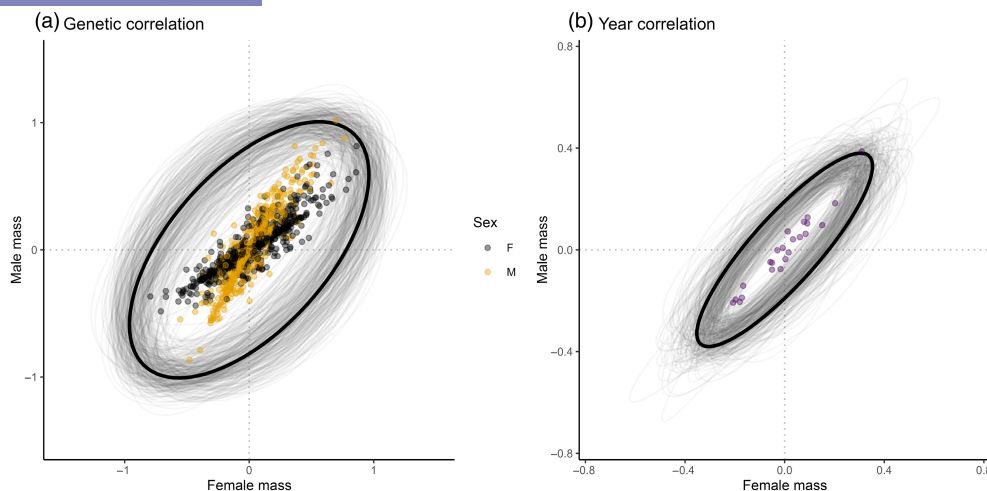


FIGURE 2 Cross-sex (a) genetic and (b) yearly correlations in Alpine swift adult body mass. The points represent the posterior mode of the best linear unbiased predictors (BLUPs) from the MCMCglmm model. For the genetic correlation plot, points in black are females and yellow are males, while for the yearly correlation plot, points in purple correspond to each year (1999–2021). Ellipses represent the correlation estimate. The bold ellipses were estimated from the posterior mode while the grey ellipses represent the uncertainty (300 randomly selected estimates from the posterior distribution).

size at fledgling were not significantly different from zero, but estimates suggest stabilizing selection on females and disruptive selection on males (Table 3). For the weighted proportion of surviving fledglings, there was evidence of stabilizing selection on female June mass, and diversifying selection on male June mass, with a negative and positive quadratic effect, respectively (Table 3, Figure 3c,d). For females, threshold regression estimates showed that the weighted proportion of surviving fledglings increased with increasing June mass until a maximum was reached, followed by a decrease, though this decrease was not statistically different from zero (Table 4). For males, threshold regression estimates showed that the weighted proportion of surviving fledglings decreased with increasing June mass until a minimum was reached, followed by an increase, though this increase was not statistically different from zero (Table 4). The masses providing maximum fitness for females and minimum fitness for males were similar and close to the average mass of both sexes (females: 102.5 g; males: 101.8 g). Selection gradients estimated using the extended Morrissey and Goudie (2022) and Janzen and Stern (1998) approach for the weighted proportion of surviving fledglings model likewise reflects these trends with stabilizing selection for females and diversifying selection for males (Table 5). For all models except clutch size, we report a statistically significant effect of colony (Table 3). Laying dates were on average earlier in Solothurn than in Biel, and reproductive success (brood size at hatching and fledging, weighted proportion of surviving fledglings) and overwinter survival were higher in Solothurn than in Biel (Table 3). There were no sex differences in overwinter survival, and there was a two-way interaction between August mass and breeding status (Table 3, Figure 4). Non-breeding individuals that were heavier in August had higher overwinter survival than lighter non-breeding individuals, whereas August mass did not affect the survival probability of breeding individuals. Estimated

average selection gradients likewise reflect these trends (Table 5), and similar conclusions were drawn when correcting for skeletal size (Table S6).

4 | DISCUSSION

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

Body mass presented comparable and non-zero additive genetic variance and heritability in both sexes (Table 2). This suggests that body mass has the potential to evolve in response to selection at the same rate in both sexes. Evolvability was nonetheless low, suggesting that the magnitude of any change would be small even with strong selection. However, as the Alpine swift is a highly aerial avian species which can fly non-stop for up to 200 days (Liechti et al., 2013) even a small change in mass would be biologically relevant. Furthermore, we found a moderately positive cross-sex genetic correlation (Table 2) indicating that the sexes would be positively correlated in any evolutionary response. Positive cross-sex genetic correlations in body mass have been found in many other species (see review by

TABLE 3 Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between body mass and laying date (gaussian distribution), clutch size (Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), the weighted proportion of surviving fledglings (binomial distribution) and overwinter survival (binomial distribution). Models were fitted on the 1000 sets of estimated mass from a Bayesian model. We report the posterior mode with 95% HPDI for each parameter. Post *p*-value is the posterior mode of the *p*-values. Statistically significant estimates (Post *p*-value <0.05) were bolded. The reference levels are as follows: Biel for colony, females for sex and non-breeders for breeding status. Data span from 1999 to 2021.

	Estimate	Lower 95% HPDI	Upper 95% HPDI	Post. <i>p</i> -value
<i>Laying date</i>				
Number of observations: 1328; Number of females: 464; Number of males: 427; Number of years: 23				
Intercept	0.204	0.193	0.209	0.175
Female mass	-3.862	-5.352	-2.735	<0.001
Female mass ²	0.124	-0.848	1.084	0.765
Male mass	-2.490	-3.341	-1.381	0.004
Male mass ²	-0.309	-1.116	0.500	0.619
Colony	-0.325	-0.334	-0.313	<0.001
<i>Clutch size</i>				
Number of observations: 1334; Number of females: 470; Number of males: 432; Number of years: 23				
Intercept	0.985	0.985	0.986	<0.001
Female mass	-0.187	-0.408	-0.021	0.767
Female mass ²	-0.143	-0.385	0.046	0.693
Male mass	0.148	-0.044	0.304	0.815
Male mass ²	0.149	-0.051	0.293	0.804
Colony	0.059	0.058	0.060	0.076
<i>Brood size at hatching</i>				
Number of observations: 1332; Number of females: 465; Number of males: 428; Number of years: 23				
Intercept	0.684	0.682	0.685	<0.001
Female mass	0.078	-0.390	0.471	0.918
Female mass ²	0.082	-0.360	0.607	0.946
Male mass	-0.248	-0.670	0.216	0.870
Male mass ²	0.616	0.121	1.085	0.281
Colony	0.164	0.162	0.166	<0.001
<i>Brood size at fledgling</i>				
Number of observations: 1330; Number of females: 465; Number of males: 428; Number of years: 23				
Intercept	0.451	0.448	0.454	<0.001
Female mass	0.557	0.109	1.271	0.320
Female mass ²	-0.323	-1.023	0.255	0.680
Male mass	-0.427	-1.062	0.069	0.440
Male mass ²	1.241	0.563	1.643	0.090
Colony	0.173	0.170	0.178	<0.001
<i>Weighted proportion of surviving fledglings</i>				
Number of observations: 1323; Number of females: 464; Number of males: 428; Number of years: 23				
Intercept	0.425	0.413	0.438	0.010
Female mass	2.074	0.091	4.310	0.224
Female mass ²	-3.238	-5.502	-1.315	0.005
Male mass	-3.919	-5.318	-1.086	0.124
Male mass ²	5.266	2.904	7.207	0.001
Colony	0.338	0.319	0.353	0.014

(Continues)

TABLE 3 (Continued)

	Estimate	Lower 95% HPDI	Upper 95% HPDI	Post. p-value
<i>Overwinter survival</i>				
Number of observations: 4111; Number of individuals: 1072; Number of years: 23				
Intercept	0.905	0.888	0.934	0.005
Sex	0.063	0.043	0.075	0.418
August mass	0.147	0.056	0.276	0.094
Colony	0.515	0.512	0.520	<0.001
Breeding status	0.031	0.005	0.054	0.804
August mass: breeding status	−0.190	−0.324	−0.091	0.031

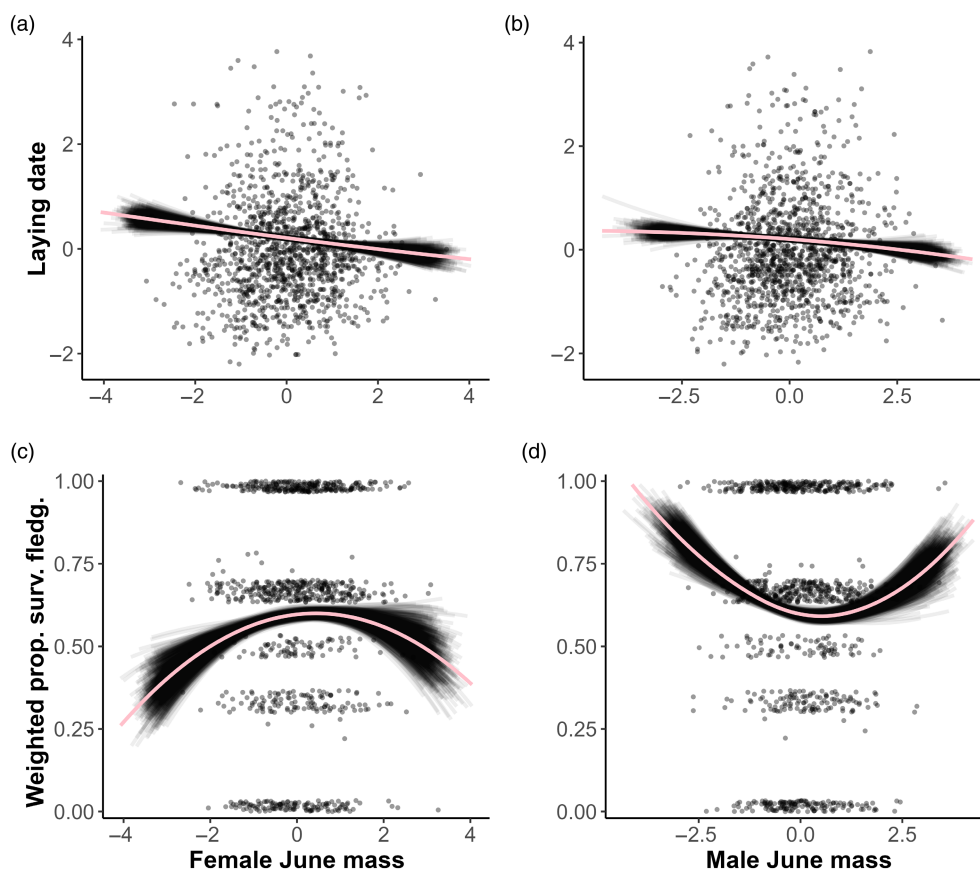


FIGURE 3 Association between female (left) and male (right) June mass and laying date (panels a and b) as well as the weighted proportion of surviving fledglings (panels c and d) in a Swiss population of Alpine swifts (data spans 1999–2021). The pink lines are the mean response across all Bayesian models while the black lines are associated with each individual model and hence reflect the error around adjusted June mass. The data points correspond to the raw data.

Kruuk et al., 2008), as have positive correlations between mass and fitness (e.g. snow voles *Chionomys nivalis*; Bonnet et al., 2017).

When evaluating sex-specific selection for body mass in relation to the weighted proportion of surviving fledglings, we found indications of stabilizing selection for female, but diversifying selection for male June mass based on statistically significant negative and positive quadratic effects, respectively (Table 3). This difference in the shape of selection between the sexes could potentially result in a difference in the variance but not the mean value of the trait. Thus, we would not expect the evolution of more pronounced sexual

dimorphism. However, this would help to maintain genetic diversity in the population. Coefficient of variations for males and females were similar, suggesting that either the differences in the shape of selection are weak or that the shape of selection are not truly stabilizing and disruptive. Follow-up analyses using threshold regression models revealed that female reproductive success increased linearly with June mass until a maximum was reached close to the average female mass, while for males, reproductive success decreased linearly with June mass until the minimum was reached close to the average male mass (Table 4). This suggests the possibility of sexually

TABLE 4 Threshold regression model assessing the association between body mass and the weighted proportion of surviving fledglings (binomial distribution). A single breakpoint was used at the stationary point (minimum or maximum). The model was run using the 1000 sets of mass estimates to obtain the posterior mode (estimate) with 95% HPDI and the posterior mode of *p*-values (Post. *p*-value). Posterior mode of *p*-values lower than 0.05 were deemed statistically significant and bolded. The reference level for colony is Biel. Data span from 1999 to 2021.

	Estimate	Lower 95% HPDI	Upper 95% HPDI	Post. <i>p</i> -value
Intercept	0.376	0.227	0.475	0.054
Female mass (left)	0.173	0.071	0.268	0.015
Female mass (right)	-0.171	-0.294	0.018	0.114
Male mass (left)	-0.274	-0.361	-0.151	0.001
Male mass (right)	0.211	0.048	0.312	0.101
Colony	0.332	0.316	0.351	0.015

TABLE 5 Selection gradients calculated using the Morrissey and Goudie (2022) method for log-link models (clutch size) as well as the extended Morrissey and Goudie (2022) and Janzen and Stern (1998) approach for logit-link models (weighted proportion of surviving fledglings and overwinter survival).

	Mass	Mass ²
Clutch size		
Females	-0.00273	-0.209
Males	0.00159	0.319
Weighted proportion of surviving fledglings		
Females	0.0143	-0.0404
Males	-0.0233	0.0506
Overwinter survival		
Non-breeders	0.0330	—
Breeders	-0.00810	—

antagonistic selection with heavy mass favoured in females and light mass favoured in males. Taken together, the positive cross-sex genetic correlation coupled with this sexually antagonistic selection would suggest the possible presence of an intra-locus sexual conflict over body mass in the Alpine swift. Intra-locus sexual conflict has been shown in other species (e.g. conflict over tarsus length in the collared flycatcher *Ficedula albicollis*, Merilä et al., 1998).

The differing shape of selection between the sexes for June body mass in relation to the weighted proportion of surviving fledglings (Table 3) could be associated with sex-specific reproductive tactics. For females, fecundity selection may play a role: the costs of laying eggs may set a minimum viable mass, while the costs of being too heavy may likewise set an upper limit. In birds, the costs of being too large can stem from increased predation risk (e.g. increased exposure to predators due to increased foraging times; Lima, 1986) and physiological limitations (e.g. higher cost of flight; Pennycuik, 1978). In addition, heavier females may not only be able to produce more eggs than lighter females, but their eggs are also larger, allowing them to fledge more offspring (Bize et al., 2002). Indeed, larger eggs will typically lead to larger offspring, which are more likely to survive until fledgling and to be recruited into the

population (e.g. Dawson & Clarck, 2000). For males, intra-sexual competition potentially causing niche specialization may play a role. Light and heavy males may be specializing on different prey items, with both classes of male able to provide more resources to their young than average weight males. Light males may be more agile than average or heavy males and therefore able to catch faster prey. Heavy males may be targeting larger and slower flying insects than the light or average weight males and may monopolize access to these resources as a result of their greater mass. These results could potentially also arise as a result of size disassortative pairing, with light and heavy females pairing with average weight males and average weight females pairing with light and heavy males. Under size assortative mating, it is expected that the fitness function for body mass would be similar for males and females since within a pair both sexes share the exact same fitness value. The contrasted selection pattern for male and female mass thus suggests at least an absence of assortative mating and potentially disassortative mating. Further research on assortative or disassortative pairings will be required to better understand this result. Differences in the strength or shape of selection between the sexes for body mass is uncommon in wild populations, though numerous examples of sexually concordant selection for body mass can be found. For instance, while selection for larger body mass in the greater white-toothed shrew *Crocidura russula* may be sexually concordant, the magnitude of this selection is much larger in males than in females, resulting in heavier body mass in males than in females (Boutellier-Reuter & Perrin, 2005).

We found that females were heavier than males on average, with a 1% difference in mass between sexes (Table 1). This SSD is most apparent early in the season, when females are at their heaviest in preparation for egg laying. Females then decreased in mass more sharply than males over the course of the season (Table 1), likely reflecting their higher initial reproductive investment. Body mass further fluctuates in response to the time of capture, likely reflecting daily foraging patterns in both sexes (Table 1). During the breeding season, foraging is typically restricted to daylight hours, with swifts returning to the colony at dusk and fasting overnight. Body mass increases throughout the day as swifts resume foraging, with a maximum daily weight reached in the afternoon. Since foraging success may depend on individual experience, we also considered the effect

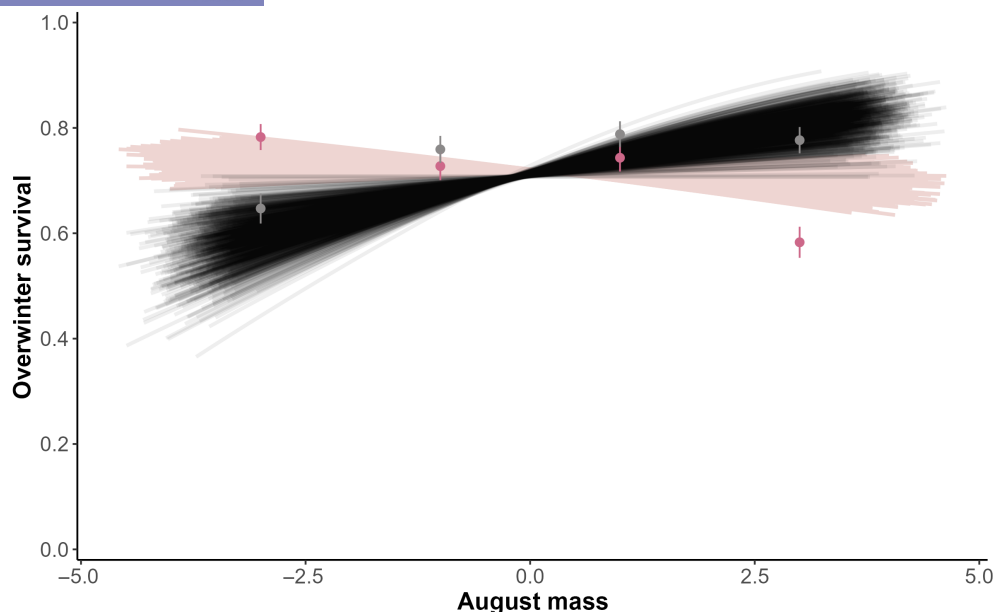


FIGURE 4 Association between August mass and survival of non-breeders (black) and breeders (pink) of Alpine swifts monitored in Switzerland between 1999 and 2021. Mean and confidence intervals per adjusted August mass interval are displayed (non-breeders: black; breeders: pink).

of age on body mass. We report a non-linear increase of mass with age in both sexes (Table 1), suggesting improvement in foraging abilities as an individual ages. This effect has been observed in many species including the Alpine swift (Moullec et al., 2023) and Adélie penguins *Pygoscelis adeliae* (Lescroël et al., 2019, 2021).

Heavier individuals tend to lay their eggs sooner than lighter ones, which may be explained through one of two mechanisms. First, migration to the breeding grounds may only occur after a certain weight has been reached. Consequently, heavier individuals may arrive to the breeding grounds earlier than lighter ones. This appears to be the case for the semipalmated sandpipers *Calidris pusilla*, which must weigh at least 25 g before migrating (Fedrizzi et al., 2004). However, this seems unlikely to explain our result as swifts arrive at the breeding ground several weeks before the breeding season begins, and hence arrival dates should not be strictly related to laying dates, though additional research is required. Second and more likely, larger energetic reserves may potentially allow heavier individuals to begin reproducing sooner after arriving at the breeding grounds than lighter ones. Indeed, there is strong selection on egg-laying date in the Alpine swift in relation to annual reproductive success (de Villemereuil et al., 2020). Alternatively, this result may be due to experience as older individuals tend to be heavier than lighter ones (Table 1). More experienced individuals may be able to reproduce right away as opposed to less experienced individuals that must spend more time preparing for reproduction (e.g. finding a partner and building their nest). For example, Australian magpie-larks *Grallina cyanoleuca* that had mated together previously were able to reproduce earlier than those pairs which had not (Hall, 1999).

Furthermore, we report directional selection on adult August mass in both sexes in relation to overwinter survival (Table 3). However, this result was only apparent for non-breeding

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

Adult body mass was strongly impacted by meteorological conditions. This was expected as previous studies showed that cold temperatures and high precipitations strongly affected the mass of nestling swifts (Alpine swift: Bize et al., 2007; common swift: Sicurella et al., 2015). In our study, adult body mass increased non-linearly with ambient temperature (Table 1), possibly stemming from increased insect availability during periods of warmer than colder temperatures. However, as temperatures continue to rise, swifts may be incurring higher metabolic costs, decelerating mass gain (Figure 1). Insect activity may also plateau with increasing temperatures, providing no additional mass gain. Ambrosini et al. (2006) report similar results in nestling barn swallows *Hirundo rustica* with a positive relationship between mass and temperature. Conversely, adult body mass in our study decreased non-linearly with increasing rainfall (Table 1), potentially stemming from decreased insect availability. In conditions of very high rainfall, adult swifts may be able to offset continuous mass loss by waiting out the rain or foraging elsewhere. In the first case, they may conserve their energy by not flying

in poor conditions, while in the second case they may be reaching new foraging opportunities in areas with better weather. These results are also supported by Cox et al. (2019) who found a negative relationship between body mass and precipitation in nestling tree swallows *Tachycineta bicolor*.

The permanent environment and year effects further accentuate the importance of short-term weather effects on adult body mass (Table 2). The permanent environment effect suggests that environmental conditions encountered in early life will have some carryover effects at adulthood, accounting for 17% and 18% of the variance in males and females, respectively. The small year effect suggests little inter-annual variation in body mass, explaining only 3% of the variance in both sexes. The strong cross-sex yearly correlation however indicates that the impact of year on body mass would be similar for both sexes. Such strong cross-sex yearly correlations have been reported in several species across a wide range of traits, such as for reproductive success in yellow-bellied marmots where in good years, individuals of both sexes will perform well (St. Lawrence et al., 2022). Body mass was also higher in Biel than in Solothurn, reflecting microenvironmental differences between these two colonies.

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

AUTHOR CONTRIBUTIONS

PB and GM collected the data. SSL and MND developed the idea of the study, with support from PB and JGAM. MND ran the analyses with support from JGAM and PB. MND and SSL wrote the first draft of the manuscript, and all authors revised the manuscript. MND and SSL had similar contributions to the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data and code for this study are available on OSF <https://doi.org/10.17605/OSF.IO/CD9GE> (Dumas et al., 2023).

ORCID

Michela N. Dumas  <https://orcid.org/0000-0003-2948-8751>

Sophia St. Lawrence  <https://orcid.org/0000-0002-6455-6249>

Giulia Masoero  <https://orcid.org/0000-0003-4429-7726>

Pierre Bize  <https://orcid.org/0000-0002-6759-4371>

Julien G. A. Martin  <https://orcid.org/0000-0001-7726-6809>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Output from the climwin model describing the effects of (a) rainfall and (b) ambient temperature on adult mass in the Alpine swift (models ran on 5387 weights from 1079 individuals measured between 1999 and 2021).

Figure S2. Association between (a) day and (b) hour of capture as well as (c) individual age and adult mass in two colonies of Alpine swifts captured between May 1st and August 10th from 1999 to 2021.

Figure S3. Adjusted June and August mass of adult female Alpine swifts using a frequentist approach. Relation between the (a) predicted and observed and (b) residual and predicted values of female mass. Distribution of (c) June and (d) August female mass, as well as (e) the spread of the data over the course of the season with June mass in red and August mass in green.

Figure S4. Adjusted June and August mass of adult male Alpine swifts using a frequentist approach. Relation between the (a) predicted and observed and (b) residual and predicted values of male mass. Distribution of (c) June and (d) August male mass, as well as (e) the spread of the data over the course of the season with June mass in red and August mass in green.

Table S1. Estimates (posterior mode) and 95% credible intervals (Bayesian model in the R package MCMCglmm) for the relationships between body condition (mass corrected for skeletal size) and fixed effects for adult male and female Alpine swifts measured over the May–August breeding period (1999–2021).

Table S2. Estimates (posterior mode) and 95% credible intervals (Bayesian model in the R package MCMCglmm) for the relationships

between mass and fixed effects for adult male and female Alpine swifts measured over the May–August breeding period (1999–2021) including the sex by colony interaction.

Table S3. Summary statistics of the pruned social pedigree used in the quantitative genetic analyses.

Table S4. Summary statistics of the colony specific social pedigree used in the quantitative genetic analyses.

Table S5. Variance component and ratio estimates (posterior mode) along with their 95% credible intervals for body condition (body mass corrected for skeletal size) in both adult female and male Alpine swifts.

Table S6. Linear (LMM) and generalized (GLMM) linear mixed-effects models assessing the association between body condition (mass corrected for size) and laying date (gaussian distribution), clutch size

(Poisson distribution), brood size at hatching (Poisson distribution) and at fledgling (Poisson distribution), and the weighted proportion of surviving fledglings (binomial distribution).

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