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Short Communication

Stable isotope evidence for suspended moult and age-related differences in moult location in the trans-Saharan migratory Alpine Swift

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Stable isotope analysis has been used extensively in migratory bird studies to provide ecological insights that may otherwise be difficult to obtain. However, an understanding of moult is critical for appropriate feather sampling, and here we make the first assessment of its relevance for examining the non-breeding ecology of the Alpine Swift *Tachymarptis melba*, a long-distance Afro-Palaearctic migrant. We sampled three feather types from birds found dead after their return from migration and investigated variability in δ^{13}C, δ^{15}N and δ^{2}H within and among feathers and between age classes. We found isotopic evidence supporting an interrupted primary moult in adults, with the innermost primary of adults (known to be moulted on the breeding grounds) significantly depleted in ^{13}C and ^{2}H compared with either the outermost primary or outermost tail feather, both of which were representative of sub-Saharan non-breeding areas. In contrast, the absence of significant differences in immature birds suggests the probable existence of a non-migratory strategy within this age class. These isotopic insights into moult and life history highlight the potential for stable isotope analysis as a tool for investigating non-breeding strategies in the Alpine Swift.

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Migration is a common strategy that allows species to persist and reproduce in environments where resources fluctuate seasonally (Winger *et al.* 2019). Migratory birds can travel great distances between breeding and non-breeding areas during their annual cycle, and where and when they moult can offer insights into their ecology and the physiological trade-offs they experience (Kjellén 1994, Kiat *et al.* 2019). Indeed, moult and migration, together with reproduction, are the three most energy-intensive stages of a bird's annual cycle (Newton 2009). For migratory species, the timing of moult can be complex as there is often insufficient time to complete moult before migration (Kiat *et al.* 2019). Migratory species, therefore, have varied moult strategies because of these temporal trade-offs (Jenni & Winkler 1994). These strategies can also vary by age class because of different energetic and temporal trade-offs (Newton 2011, Evans *et al.* 2012). An interrupted moult strategy is commonly found in long-distance migrants (Kiat & Izhaki 2021), with adult primary (wing) moult commencing on the breeding grounds, suspended during migration and completed in non-breeding destinations.

European swift species show a range of moult patterns that align with their movement ecology and contrasting reproductive strategies. The non-migratory Little Swift *Apus affinis* has a moult duration that can extend for up to half of the entire annual cycle (Kiat & Bloch 2023). Common Swifts *Apus apus* are single-brooded and only moult up to two primaries before leaving the breeding grounds (Boano *et al.* 2021), while Pallid Swifts *Apus pallidus* moult up to six primaries during the rearing of their second brood (Boano *et al.* 2015). The Alpine Swift *Tachymarptis melba* is described as having a moult schedule that partially overlaps the breeding season, termed a 'split moult pattern' (Newton 2009). Like other swift species, it then spends the non-breeding season almost entirely airborne (Liechti *et al.* 2013, Hedenström *et al.* 2016), which presents challenges to studying its non-breeding ecology.

Following bird movements with biologging devices has provided insights into movement strategies in many species (McKinnon & Love 2018). However, despite continued advances in tracking technology, using biologging devices is still relatively costly, both financially and in terms of compromising individual welfare, both of which typically restrict sample sizes (Rutz & Hays 2009, Bodey *et al.* 2018). Stable isotope analysis (SIA) of animal tissues offers one alternative approach, providing spatial and trophic insights into the ecology of animals that may otherwise be difficult to obtain (Atkinson *et al.* 2005, Inger & Bearhop 2008). For migratory species, this can be especially powerful when combined with predictable geographical isotopic patterns ('isoscapes') that facilitate the location assignment of animal tissue isotopic values (Hobson *et al.* 2012b, Franzoi *et al.* 2020). While combining this approach with biologging is preferable for the ground-truthing of geographical assignments to enhance geographical precision (Oppel *et al.* 2011, Seifert *et al.* 2018), SIA offers a less invasive and cheaper method than biologging to connect environmental and ecological processes to physiology (Inger & Bearhop 2008, Hobson *et al.* 2012a).

Moulted feathers lend themselves to chemical analysis because, once grown, a feather's keratin is metabolically inert and offers a temporal snapshot of the nutritional and environmental conditions during the period of growth (Bearhop *et al.* 2002, Hobson 2005). However, to infer geographical information from feathers, a sound understanding of their growth (moult) schedule is required. Here, we provide insights into the moult schedule and potential for use of feather tract samples for SIA for the Alpine Swift, a species with incomplete information on its moult, which can therefore benefit from this technique. First, we aim to test for isotopic evidence of interrupted primary moult and to identify appropriate feather tracts for sampling breeding and non-breeding locations and conditions. We then assess the extent of isotopic variation within individual feathers. Finally, we use isotopic information to confirm differences in movement patterns between age categories. We predict that if Alpine Swifts show interrupted moult, then the isotopic signature of a feather known to be grown on the European breeding grounds will be depleted in ^{13}C (Neto *et al.* 2006, Evans *et al.* 2012) compared with feathers of unknown growth location, but that all feathers will exhibit differences between their tip and base because of the extended growing time of long feathers. Finally, we predict that isotopic values will differ between immature and adult age classes because immature swifts are rarely captured at breeding colonies until they return as breeding adults of 2–4 years of age (Tettamanti *et al.* 2012). However, we cannot predict directionality because of a lack of knowledge on age-related dietary or movement variation.

METHODS

Study species and site

Alpine Swifts are long-distance migrants that breed colonially from May to August in Europe before migrating to sub-Saharan West Africa in mid/late September and returning to Europe in early/mid-April (Liechti *et al.* 2013, Meier *et al.* 2020). Our study colonies in urban Switzerland (Fig. 1) are part of a multi-decadal longitudinal life-history study where individuals are captured on a regular basis throughout the season (Moullec *et al.* 2023).

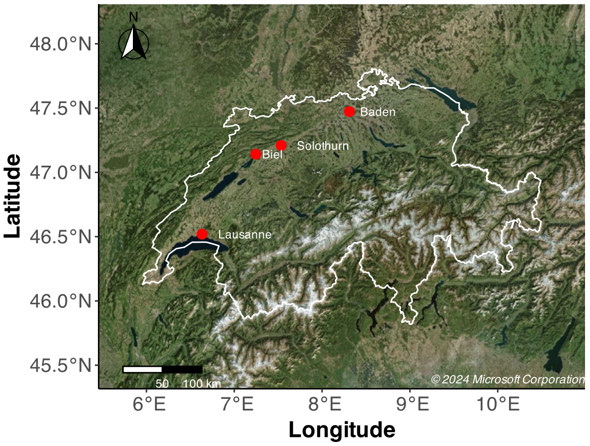

Figure 1. Map of Switzerland showing four focal study colonies.

Alpine Swifts begin their primary moult during breeding, with the most advanced moult observed before departure reaching the eighth primary and a mean moult of four primaries (P. Bize pers. comm.; Fig. S1). Tail (rectrix) feather moult has never been recorded at breeding colonies in over 25 years of monitoring (P. Bize pers. comm.), and this is mirrored in other swift species including the Common Swift (Boano *et al.* 2021). We therefore hypothesize that, in contrast to the innermost primaries that we see moulted on the breeding grounds, the outermost primaries and tail feathers are grown in sub-Saharan Africa.

Sample collection

To study moult patterns, we collected 12 dead Alpine Swifts found in the breeding colonies of Solothurn ($n = 3$), Biel ($n = 4$), Baden ($n = 4$) and Lausanne ($n = 1$) between 2014 and 2021. Birds were preserved at −20°C for later laboratory analysis. We collected three whole feathers from the bird's right side: the innermost primary (P1), the outermost primary (P10) and outer rectrix (R5) (Fig. 2d). Sampled feathers were analysed blind to the age of birds. However, 11 individuals were ringed (on capture as nestlings or as adults) and so could be assigned ages for subsequent analyses, namely adult (≥3 years old, $n = 8$) and immature (2 years old, $n = 3$), with one unknown (unringed disperser, $n = 1$; Table S1). Here, nestlings are assigned as <1 year old if captured during the year they fledged, 1 year old if captured the year after fledging and so on.

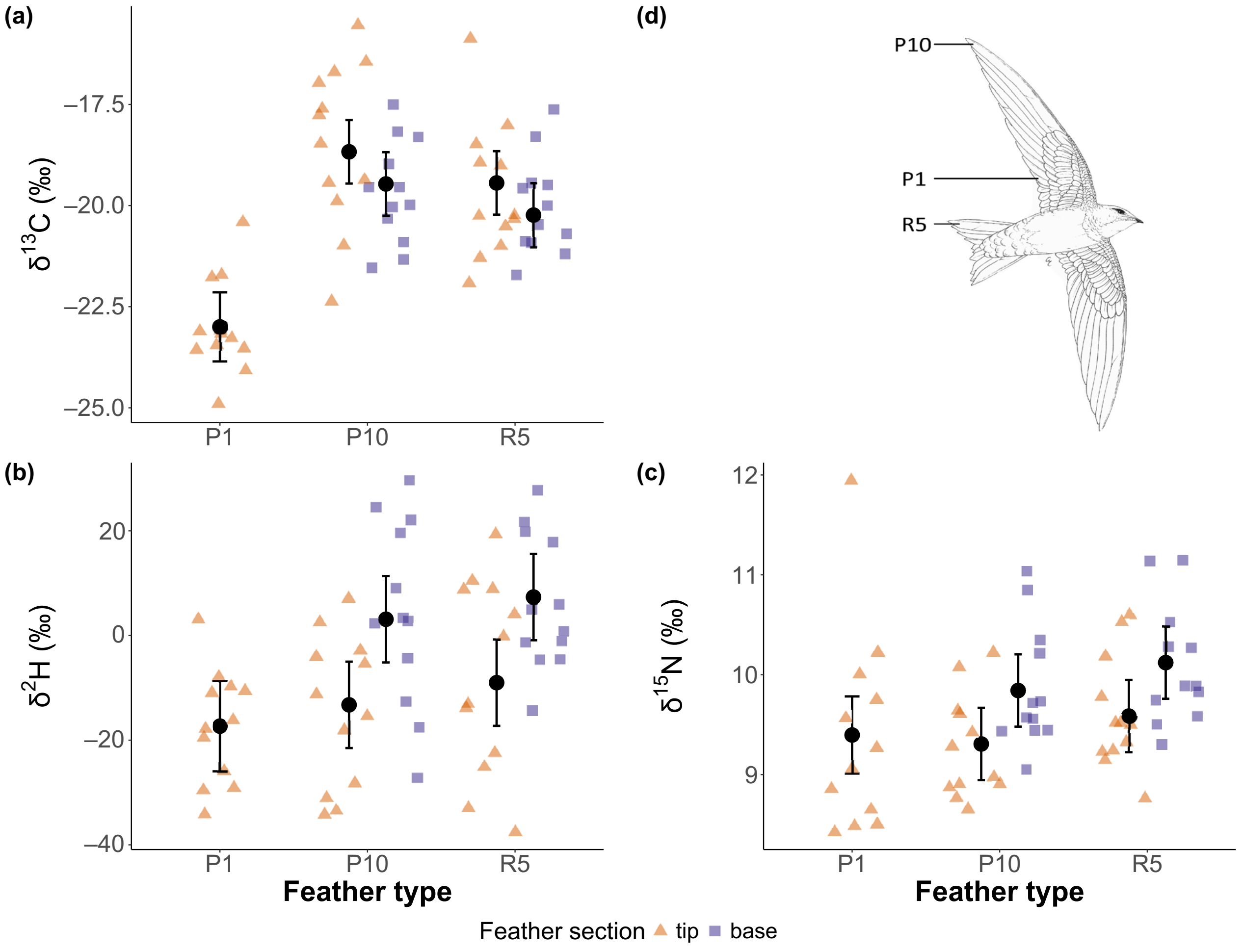

Figure 2. Variation in isotopic values for each feather type (inner primary P1 or outer P10 and outermost tail (R5)) split by feather section (tip or base). Black circles are estimated marginal means from a linear mixed model with 95% confidence interval error bars, coloured points are raw values with shapes denoting feather section for (a) carbon δ^{13}C, (b) hydrogen δ^{2}H and (c) nitrogen δ^{15}N and (d) drawing showing the feathers sampled from Alpine Swift for stable isotope analysis.

Sample preparation and isotopic analysis

Tip (distal) and base (proximal) sections of vane, omitting the central rachis, were cut from P10 and R5 using dissection scissors (sterilized between feathers in 90% ethanol) as was the tip section of P1. Feather sections of approximately 3 cm were placed into individual 30-mL screw-top, glass vials and washed in 15 mL of diethyl ether-methanol 2:1 in a sonicator (Decon Ultrasonics Ltd FS 100 1.5 L, 100 W, 45 kHz) for three cycles of 60 s (Bontempo *et al.* 2014). Samples were then air-dried in a fume cupboard for 2 h before being transferred to a drying oven (40°C for 48 h), after which samples reached a constant weight. Individual feather sections were then cut into fragments with dissection scissors, and subsamples of c. 0.7 mg were weighed into tin cups for SIA of combined carbon (δ^{13}C) and nitrogen (δ^{15}N), and of c. 0.2 mg into silver cups for hydrogen (δ^{2}H).

Continuous-flow isotope ratio mass spectrometry (IRMS) was conducted by the National Environmental Isotope Facility Stable Isotope Ecology Laboratory, SUERC, East Kilbride, UK. δ^{13}C and δ^{15}N were analysed using a Thermo Fisher (Bremen, Germany) Delta XP Plus IRMS device from sample combustion in an Elementar vario Pyrocube elemental analyser (Elementar UK Ltd, Cheadle Hulme, UK). Reference materials with known isotopic values from internal laboratory standards (gelatine, glycine and alanine mixtures, see Jones *et al.* (2020) and Table S2)) were interspersed between samples to correct raw delta values for instrumental drift and linearity. δ^2H was analysed using a high-temperature thermal conversion elemental analyser (Thermo Fisher Scientific) interfaced with a Thermo Fisher Scientific Delta V IRMS device.

We report stable isotope values using the δ notation expressing the deviations from primary international standards in per mil (‰) following the equation: δ sample = [(R sample/R standard) − 1] (McKinney *et al.* 1950), where R is the ratio of heavy (^{13}C, ^{15}N, ^{2}H) to light (^{12}C, ^{14}N, ^{1}H) isotope in the sample versus the standard. The standards in the δ equation are Vienna Pee Dee Belemnite for δ^{13}C, atmospheric N_2 (air) for δ^{15}N and Vienna Standard Ocean Water for δ^2H. Measurement precision was ±0.17 ‰ for δ^{13}C and ±0.18 ‰ for δ^{15}N, based on the standard deviation of the most common laboratory standard used (gelatine; Table S2) and for δ^2H was determined to be ±1.69 ‰ (Arctic Willow Grouse *Lagopus lagopus* feather; Table S3).

Statistical analysis

To test for differences in isotopic signatures among and within feathers, we ran three separate linear mixed models (one model per isotope: δ^{13}C, δ^{15}N and δ^2H) with feather type and feather section as explanatory factors on the full dataset (n = 12 individuals) and bird identity included as a random effect (Table S4a). We did not include year within these models because of limited inter-annual isotopic variation and the small number of individuals analysed.

Initial data visualization suggested a difference in the isotopic signature of P1 feathers of three individuals, which ringing records confirmed were immature birds. Hence, to further investigate differences in moulting patterns between immature and adult birds, we ran an additional linear model per isotope on P1 data using birds of known age (three immatures and eight adults) with age class as the categorical two-level predictor (Table S4b). Because immature birds are rarely seen at breeding colonies, we compared isotope ratios from immature P1 tips with adult R5 and P10 tips (only comparing tips because we only took tip samples from P1 feathers, assuming the moult origin of all birds in adult plumage) using pairwise Mann–Whitney U tests performed in R using the pairwise_wilcox_test() function from the Rstatix package (Kassambara 2023). To test our hypothesis that immature birds moulted all their feathers outside the breeding grounds, we used a Kruskal–Wallis test to compare variances of all three immature feathers.

We did not investigate potential sex differences as this information was lacking for five birds, and previous data from a much larger cohort of birds equipped with geolocators revealed no sex-based differences in non-breeding locations (C. Meier unpubl. data) at scales relevant to isotopic variation. All statistical analyses were conducted in R version 4.3.1 (R Core Team 2023). We used Satterthwaite approximations of degrees of freedom for final t-tests with the lmerTest R package (Kuznetsova *et al.* 2017) with statistics reported as mean (95% CI).

RESULTS

We found significant isotopic differences in carbon and hydrogen between the feather known to be grown on the breeding grounds (P1) and feathers hypothesized to be grown elsewhere (P10 and R5). Compared with P1, feathers grown elsewhere were significantly enriched in ^{13}C: P10 (β = +4.33 ‰, 95% CI 3.42–5.24, $t(54)$ = 9.50, $P < 0.001$) and R5 (β = +3.56 ‰, 95% CI 2.65–4.47, $t(54)$ = 7.81, $P < 0.001$; Fig. 2a). Compared with P1, only R5 was significantly enriched in ^{2}H, (β = +8.31 ‰, 95% CI 1.45–15.18, $t(54)$ = 2.43, P = 0.019; Fig. 2b), and for δ^{15}N, we found no significant differences between feathers (P10; P = 0.611 and R5; P = 0.286; Fig. 2c). When P10 was used as the intercept in the models, R5 was significantly different and depleted in ^{13}C (β = −0.77 ‰, 95% CI −1.46 to −0.08, $t(54)$ = −2.23, P = 0.030; Fig. 2a) and also significantly enriched in ^{15}N (β = +0.28 ‰, 95% CI 4.43e−03, −0.55, $t(54)$ = 2.04, P = 0.047; Fig. 2c). In δ^2H, however, we found no significant differences between P10 and R5 (P = 0.107; Fig. 2b).

There were significant differences between base and tip sections for all three isotopes. Compared with the tip of the feather, samples from the base were significantly enriched in ^{2}H (β = +16.36 ‰, 95% CI 11.17–21.55, $t(54)$ = 6.32, $P < 0.001$) and ^{15}N (β = +0.54 ‰, 95% CI 0.27–0.80, $t(54)$ = 4.03, $P < 0.001$; Fig. 2b,c, respectively) but significantly depleted in ^{13}C (β = −0.79 ‰, 95% CI −1.48 to −0.10, $t(54)$ = −2.31, P = 0.025; Fig. 2a).

Age class significantly explained differences in both δ^{13}C and δ^{15}N values of P1 feathers (Fig. 3a,c, respectively). Immature P1 were enriched in ^{13}C (β = +2.11 ‰, 95% CI 1.40–2.82, $t(9)$ = 6.75, $P < 0.001$) and in ^{15}N (β = +1.63 ‰, 95% CI 0.52–2.74, $t(9)$ = 3.33, P = 0.009), but there was no difference in δ^2H (β = +4.07 ‰, 95% CI −2.80 to 10.93, P = 0.153; Fig. 3b). In pairwise comparisons of feather tips of immature P1 to both adult R5 and adult P10 tips (Table S5), we found no differences in any of the three isotopes (Fig. S2). We also found no differences among the immature feather types when tip sections were compared in δ^{13}C (Kruskal–Wallis $\chi^2_{(2,N=9)}$ = 5.956, P = 0.051), δ^2H (χ^2 = 1.422, P = 0.491) and δ^{15}N (χ^2 = 5.956, P = 0.587).

Figure 3. Variation in isotopic values for inner primary (P1) feathers split by age class (immature or adult). Black boxes are estimated marginal means from a linear model with 95% confidence interval error bars. Coloured points are raw values with shapes denoting age class for (a) carbon δ^{13}C, (b) hydrogen δ^{2}H and (c) nitrogen δ^{15}N.

DISCUSSION

To search for potential isotopic signature differences between European breeding grounds and sub-Saharan Africa non-breeding grounds, we compared the stable isotope compositions of different types and sections of feathers in Alpine Swifts that had died soon after their return to their Swiss breeding colonies. Feathers of hypothesized non-breeding moult origin (P10 and R5) were found to be consistently enriched in ^{13}C and ^{2}H compared with the P1 feather known to be moulted on the breeding grounds, which is the first empirical evidence for a hypothesized interrupted moult strategy in Alpine Swifts. We also found age-related differences in the isotopic signature of P1 feathers, suggesting behavioural variation and therefore different growth locations of the P1 feather depending on age class.

Feather type

There were significant differences between P1 and R5 for both δ^{13}C and δ^{2}H, and with P10 also significantly differing from P1 in δ^{13}C. This provides empirical evidence, albeit from a small sample size, that adult primary moult is suspended until reaching non-breeding areas, adding to visual observations of retained, old, outer primaries on the breeding grounds. It also confirms that rectrices are moulted away from the breeding grounds. The enrichment in the heavier isotopes in P10 and R5 aligns with geographical isoscape predictions and other studies of Afro-Palaearctic migrants (Neto *et al.* 2006, Szép *et al.* 2009, Hobson *et al.* 2012a). While acknowledging potential minor isotopic baseline differences across years (which we do not have the statistical power to investigate), our results offer the first evidence that SIA is a viable geolocational technique for Alpine Swifts, with the combined use of δ^{13}C and δ^{2}H presenting an effective locational representation of the non-breeding grounds of this species. It should be noted that sampling of R5 is preferable to P10 from live birds to reduce impacts on flight performance.

Feather section

The significant differences found across all three isotopes between samples within individual feathers have also been found in other species; for example, in the Antarctic Prion *Pachyptila desolata*, tip sections of feathers were found to be depleted in ^{15}N compared with the base (Grecian *et al.* 2015). Although this highlights the importance of consistency in sections sampled, there is limited biological insight gained from some statistically significant differences, with the average difference we found of $+0.54$ ‰ between base and tip in δ^{15}N being far lower than the accepted thresholds appropriate for differentiating trophic levels (typically between 2 and 5 ‰ (Post 2002, Authier *et al.* 2012)). Therefore, this difference is probably due to the time taken to fully grow the new feather. In nestling Alpine Swifts, P10 grows approximately 5 mm per day (P. Bize pers. comm.), so for an adult P10 with length around 200 mm, this suggests a growth period of 40 days. This is probably sufficient to incorporate minor dietary or habitat variation on the non-breeding grounds given that Alpine Swifts take only around 7 days to complete their migration (Meier *et al.* 2020).

Immatures versus adults

The significant difference in δ^{13}C values between adult and immature P1 feathers provides evidence for a previously unsupported hypothesis that immature Alpine Swift migratory patterns differ from those of adults. We found immature Alpine Swift P1 feathers to be similar to adult R5, with both enriched in ^{13}C compared with adult P1, which therefore suggests that, unlike adults, these three immature swifts moulted their P1 feathers in sub-Saharan Africa. Hence, immature Alpine Swifts are either returning much later than adults to the breeding grounds or spend their first summer resident in sub-Saharan Africa.

Differences in moult schedule between immature (sub-adult) and adult birds have been reported in several avian taxonomic groups including non-passerines, raptors and waders, especially where there is a non-breeding immature life stage (Newton 2011). In addition to the inherent stochasticity in a juvenile migratory bird's first migration (Cresswell 2014), differences in the movements of immature birds can result in different moult locations compared with adults. Western House Martins *Delichon urbicum* show isotopic differences between adults and juveniles, suggesting different age-related moult locations (Evans *et al.* 2012), as do adult and immature Black-throated Blue Warblers *Setophaga caerulescens* (Graves *et al.* 2002). In over 25 years, immature birds (especially 1-year-old birds) have very rarely been captured in our study colonies until they return as adults (P. Bize pers. comm.). This contrasts with other swift species; for example, immature Common Swifts have been found to be moulting their primaries on the breeding grounds in July (Jukema *et al.* 2015, Boano *et al.* 2021).

Our study provides the first evidence that immature Alpine Swifts complete a full moult away from the breeding grounds, confirming an important difference in movement strategy across life-history stages. The movements of immature birds are currently unknown as they have not previously been successfully equipped with biologgers due to the likelihood of tag loss from their substantially lower survival rates (Robinson *et al.* 2020). Our study confirms the potential for SIA to address this knowledge gap and advance our knowledge on the variation in non-breeding strategies of this Afro-Palaearctic migrant.

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AUTHOR CONTRIBUTIONS

Alexandra L. Brighten: Conceptualization; investigation; writing – original draft; methodology; writing – review and editing; visualization; formal analysis; data curation. **Pierre Bize:** Resources; supervision; data curation; project administration; methodology; conceptualization; funding acquisition; writing – review and editing. **Ana Payo-Payo:** Conceptualization; writing – review and editing; supervision. **Christoph M. Meier:** Data curation; resources; writing – review and editing. **Jason Newton:** Writing – review and editing; resources; validation; data curation. **Thomas W. Bodey:** Conceptualization; funding acquisition; writing – review and editing; methodology; project administration; supervision; resources.

ETHICAL NOTE

The procedures in this study were conducted under approval by the ethics board of the Swiss Ornithological Institute and feather samples were imported to the UK under Scottish Government regulations (EC) No. 1069/2009 and (EU) No. 142/2011. Ringing and sampling were conducted in accordance with National Animal Experimentation permit number 34497 granted by the Swiss Federal Office for the Environment.

CONFLICT OF INTEREST

The authors declare no commercial, financial or personal conflicts of interest in conducting this research.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

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

Figure S1. Moult scores of 1044 adult Alpine Swifts caught in post-breeding population census captures between 2000 and 2023 (390 individuals repeatedly captured in multiple years) with regression line showing the trend across capture days.

Figure S2. Raw isotopic values of feather tip sections only for each age class (adult $n = 8$, immature $n = 3$) split by feather type (inner primary P1 or outer P10 and outermost tail (R5)).

Table S1. Meta data of individual Alpine Swifts (dead) *Tachymarptis melba* sampled for stable isotope analysis.

Table S2. Isotopic values of reference materials for nitrogen (δ^{15}N) and carbon (δ^{13}C) stable isotope analysis from internal laboratory standards (gelatine, glycine and alanine mixtures).

Table S3. Isotopic values of hydrogen (δ^{2}H) reference materials from internal laboratory standards.

Table S4. Model selection tables arranged in order beginning with top candidate models showing number of parameters (K); Akaike Information Criterion for small sizes (AICc); AICc difference compared with the top model (ΔAICc); model weight (AICc weight) for: (a) linear mixed model per isotope with random effect of bird identity to investigate the effect of feather type (number: P1, P10, R5) and feather section (tip, base) in Alpine Swifts; and (b) linear model per isotope to investigate the effect of age class (adult, immature) on a single feather type (P1) in Alpine Swifts.

Table S5. Pairwise Mann–Whitney U tests between the tips of immature P1 (inner primary), adult P10 (outer primary) and R5 (outer tail) feathers.