

Combining $\delta^2\text{H}$ and $\delta^{34}\text{S}$ stable isotopes identifies diverse moult strategies in a short-distance migratory bird

ELZA MARIJA ZACMANE,^{*1,2}  IVO DINSBERGS,¹  STEFFEN HAHN,^{1,3}  MĀRIS JAUNZEMIS,¹ 
 VALTS JAUNZEMIS,¹  OSKARS KEIŠS,¹  ANCE PRIEDNIECE,¹  VIESTURS VĪGANTS¹  &
 MARTINS BRIEDIS^{1,2} 

¹Laboratory of Ornithology, Institute of Biology, Faculty of Medicine and Life Sciences, University of Latvia, Riga, Latvia

²Unit of Bird Migration, Swiss Ornithological Institute, Sempach, Switzerland

³Department of Research, Conservation & Monitoring, National Park Harz, Wernigerode, Germany

Moult strategies in birds can vary considerably even within a single species, particularly in terms of where moulting takes place. Yet, the factors underlying this variation and its consistency across years and individuals remain poorly understood. One such strategy, moult migration, involves individuals moving to a specific moulting location amid migration to complete feather moult before continuing to their wintering grounds. Here, we used stable isotope analysis of hydrogen ($\delta^2\text{H}$) and sulphur ($\delta^{34}\text{S}$) in feathers from 291 Common Starlings *Sturnus vulgaris* to estimate the prevalence of moult migration among birds breeding in the Baltics, where some individuals are known to perform moult migration to north-central Europe. To establish isotopic baselines, we included reference samples from Common Starlings with known moult locations either close to the breeding sites in Latvia ($n = 24$) or near expected moulting sites in Germany ($n = 53$). Additionally, we tracked migration of a subset of individuals by using multi-sensor geolocators to integrate isotopic and movement data for a comprehensive assessment of moult migration patterns and validation of isotope assignment accuracy. Feather stable isotope values differed significantly between Common Starlings breeding in the Baltic region and those breeding in north-central Europe. Assignments indicated that 86.2% of Latvian Common Starlings moulted near their breeding sites, while 4.5% undertook moult migration (9.3% remained unassigned). Both isotopes contributed substantially to the assignment accuracy, with their combined use improving the best discrimination between moulting regions. The isotope-based method correctly classified five of seven geocator-tracked Common Starlings, with no incorrect assignments. Moult strategies did not differ between adults and juveniles, and repeated sampling of individuals showed consistent strategies across years. Our findings demonstrate that integrating $\delta^2\text{H}$ and $\delta^{34}\text{S}$, especially with reference samples, provides a reliable approach for identifying moult strategies even at small spatial scales, and highlight the promise of $\delta^{34}\text{S}$ as an emerging tracer in avian movement ecology.

Keywords: geocator, moult migration, stable isotopes, *Sturnus vulgaris*.

INTRODUCTION

The annual cycle of migratory birds typically comprises three major energy-demanding stages:

breeding, moult and migration (Newton 2011). While breeding and migration have received considerable attention in ornithological research, moult is an equally important but less understood stage that strongly influences various aspects of

*Corresponding author.
 Email: elza.zacmane@lu.lv

bird biology (Kiat 2023). Feather quality can influence flight efficiency (Matyjasiak *et al.* 2018, Hedenström 2023), plays a key role in thermoregulation (Crandell *et al.* 2025) and can also function in visual communication (Jukema & Piersma 2000). Once formed, feathers are inert structures that cannot be repaired if damaged. Over time, they gradually deteriorate as a result of mechanical wear and exposure to ultraviolet (UV) radiation, as well as feather-degrading mites and bacteria, and must therefore be replaced periodically (Newton 2011). Birds adopt diverse strategies regarding the timing and location of moult, which can vary between species and within species (Pageau *et al.* 2020). For example, differences in moult strategies often have been shown to be sex- and age-related (Delhey *et al.* 2020, Jenni & Winkler 2020, Mumme *et al.* 2025). However, the ecological drivers of intraspecific variation in moult strategies, as well as its consequences, remain poorly understood (Pyle *et al.* 2018).

Moult migration is a strategy in which migrants temporarily relocate to specific areas to moult before continuing to their wintering grounds (Jenni & Winkler 2020). This behaviour enables individuals to exploit favourable conditions, such as enhanced food and nutrient availability, reduced thermoregulatory costs or predation risk during the energetically demanding feather growth (Ramenofsky & Wingfield 2006). Several hypotheses have been proposed to explain the ecological and evolutionary drivers of moult migration. While the 'push-pull' hypothesis, where unfavourable conditions 'push' birds to leave their breeding grounds and favourable conditions 'pull' them to suitable moulting sites, has often been tested to explain moult migration in North American species (Pyle *et al.* 2009, Pageau *et al.* 2020), potential drivers in European passerines remain less clear. Similar mechanisms may operate, with unfavourable post-breeding conditions in northern or continental regions prompting departure. At the same time, predictable, spatially discrete resource peaks driven by regional environmental processes may attract individuals to suitable moulting areas. The expression of moult migration is nevertheless likely to be constrained by substantial costs. Migrating with worn feathers can increase flight costs and reduce performance through feather wear, reduced structural integrity and altered aerodynamics (Hedenström 2023), potentially selecting against long pre-moult movements, particularly

when moulting sites are distant from breeding areas. In addition to ecological factors, genetic predisposition (Contina *et al.* 2023) and behavioural learning (Sokolovskis *et al.* 2025) are likely to influence moult migration strategies, although these mechanisms remain largely untested.

Individual strategies of moult migration can be studied in detail using modern tracking technologies, such as GPS transmitters (Lewis *et al.* 2010) or archival tags such as geolocators (Vigants *et al.* 2023). Archival tags provide precise information on the timing and location of annual cycle events, including moult, in small-bodied species, yet their use is constrained by several factors – mainly the need to recover the tags for data retrieval and limitations in device size and mass, which restrict the range of species that can be studied (Bridge *et al.* 2013, Brlík *et al.* 2020). Moreover, data obtained from tracked individuals typically represent only a fraction of the population. To overcome these challenges, complementary approaches such as stable isotope analysis of feathers or other tissues offer valuable insights into moult and movement of many individuals.

Isotopic values differ among tissues and provide insights into diet over distinct time periods, depending on their metabolic activity and growth rate. Metabolically active tissues, such as blood plasma and erythrocytes, regenerate rapidly, and thus reflect the diet of the preceding days or weeks (Hahn *et al.* 2012). In contrast, metabolically inert tissues retain their isotopic composition once formed and, thus, provide insights into diet and environmental conditions experienced during the specific period when these tissues were grown. Continuously growing structures, such as hair, nails or horns, can therefore provide records of dietary inputs over extended time spans (Hahn *et al.* 2014, Kruszynski *et al.* 2021). In birds, the isotopic composition of feather keratin reflects diet and environmental conditions specifically during feather growth (Rubenstein & Hobson 2004). Consequently, the link between stable isotope values and food intake can also be used to infer the spatial movements of animals over time, particularly in migratory species (Hobson 2003).

Differences in the spatial distribution of stable isotopes in the environment allow the creation of isoscapes which can be used to infer torigin of where the tissue was grown. It has been shown as a useful tool in determining non-breeding locations

of migratory birds (Milano *et al.* 2021) as well as natal origins in birds and mammals (Hobson & Wassenaar 1996, Procházka *et al.* 2013, Kruszynski *et al.* 2021, Dufour *et al.* 2025). However, the reliability of this method depends on well-established spatial variation in isotope values, which is often lacking at fine spatial scales in many regions (Seifert *et al.* 2018). Moreover, isoscapes are typically derived from reference samples of animals with known geographical origins at the time of tissue formation, and they are frequently constructed for a single species but then applied across others, despite potential differences in, for example, diet and foraging behaviour.

Among the natural stable isotopes, hydrogen ^2H (i.e. deuterium) is one of the frequently used tracers for determining the geographical origins of birds. The distribution of stable hydrogen isotope ($\delta^2\text{H}$) values in precipitation follows general geographical and climatic patterns. Values are typically higher near the equator and decrease toward the poles, with similarly lower values at higher elevations and in continental interiors compared to coastal areas (Niewodniczanski *et al.* 1981, West *et al.* 2006, Winnick *et al.* 2014). Seasonal variation is also evident, with precipitation enriched in deuterium during warmer months (Xia *et al.* 2022). Because tissue $\delta^2\text{H}$ values correlate with local precipitation during growth, they can be used to infer geographical origins (Hobson & Wassenaar 1996).

Similarly, stable sulphur isotopes ^{34}S have been proposed as a useful tool to infer geographical origins of birds and other animals (Lott *et al.* 2003, Zazzo *et al.* 2011, Brlík *et al.* 2023). However, because this method is relatively new, knowledge about the geographical distribution of $\delta^{34}\text{S}$ remains limited (Kabalika *et al.* 2024). At the same time, the isotopic offset between the environment and organic tissues is typically low for $\delta^{34}\text{S}$ (Florin *et al.* 2011), potentially allowing a single $\delta^{34}\text{S}$ isoscape to be applied across a broad range of taxa. The first $\delta^{34}\text{S}$ isoscape for Europe, based on feather values, revealed high $\delta^{34}\text{S}$ levels in coastal areas and a weak gradient decreasing southward from central Europe. While coastal regions tend to show stable values, inland areas exhibit greater variation (Brlík *et al.* 2024). Even so, $\delta^{34}\text{S}$ has already been applied successfully to identify migratory phenotypes of Reed Warblers *Acrocephalus scirpaceus* with different non-breeding grounds in sub-Saharan Africa (Brlík *et al.* 2023).

In this study, we used hydrogen ($\delta^2\text{H}$) and sulphur ($\delta^{34}\text{S}$) stable isotopes in feathers to determine moult migration strategies of a short-distance migratory passerine, the Common Starling *Sturnus vulgaris*. We validated our results with multi-sensor geolocator data and isotope reference samples from individuals known to breed and moult in northern Germany, near expected moulting sites of individuals undertaking moult migration. Common Starlings undergo a complete post-breeding moult every year and both juvenile and adult birds follow the same sequence of feather replacement (Rothery *et al.* 2001). Birds breeding in the Baltics have been shown to use two distinct migration strategies – one involving moult migration, where individuals migrate to moulting sites in north-central Europe (i.e. Germany or Denmark) in summer, and another where birds moult near their breeding grounds and then migrate to their wintering sites, mainly in the British Isles, in autumn with a single continuous migration (Vigants *et al.* 2023). However, the limited sample size of geolocator-tracked birds leaves the true prevalence of each strategy in Baltic Common Starlings uncertain. In addition, archival tags cannot be reliably used on first-year birds owing to their low return rates, meaning that the occurrence of moult migration in different age-classes or its within-individual consistency across years remains unclear.

Here, we aim to quantify the proportion of Baltic birds that engage in moult migration through isotopic assignment of a large number of individuals. We expect that a larger proportion of Common Starlings from eastern Latvia will exhibit moult migration compared to birds breeding in western Latvia (Vigants *et al.* 2023). Second, we predict that moult migration will be more prevalent in juvenile compared to adult birds (Svårdson 1953) and, consequently, we expect moult migration to be a plastic age-dependent behavioural trait that changes within an individual's lifetime. Finally, we expect that the dual-isotope approach combining $\delta^2\text{H}$ and $\delta^{34}\text{S}$ can reliably identify isotopic signatures consistent with different moult regions in short-distance migrants even on a relatively small geographical scale.

MATERIALS AND METHODS

To investigate moult migration strategies for Latvian-breeding Common Starlings, we established three study populations in 2020, consisting

of 100 nestboxes each. Two of these were located in the western part of the country – Krievrags (57.29°N, 23.06°E) and Berzciems (57.25°N, 23.17°E) – and one in the east at Zeltaleja (57.19°N, 26.86°E).

Nestboxes were monitored regularly throughout the breeding season, and adult birds were captured at nests once chicks had reached at least 10 days of age to minimize the risk of nest abandonment. Between 2022 and 2024, we collected contour (breast) feathers from breeding adult birds for stable isotope analysis. These feathers are grown during the post-breeding moult which Common Starlings undergo during summer before the onset of autumn migration, with complete moult lasting approximately 100 days (Rothery *et al.* 2001). The moult follows a well-defined sequence that is generally consistent among individuals (Jenni & Winkler 2020).

To enable comparison of feather stable isotope values between Latvian-breeding Common Starlings that moult locally and those that undergo moult migration (i.e. moult in north-central Europe; Vīgants *et al.* 2023), we collected additional reference samples in 2023 and 2024 from breeding Common Starlings at three sites in northern Germany: Dedelow (53.36°N, 13.80°E), Bahnitz (52.49°N, 12.40°E) and Oberthau (51.39°N, 12.14°E), where moult near breeding sites is well-documented (Hug 2019, Rost 2021).

Alongside feather sampling, we deployed multi-sensor geolocators (GDL3-PAM, Swiss Ornithological Institute; Liechti *et al.* 2018) on a subset of Common Starlings breeding in Latvia. Devices were attached using leg-loop harnesses and weighed 1.95 ± 0.07 g ($n = 308$), representing 2.4% of the mean adult body-mass (79.8 ± 4.3 g, $n = 297$). Between 2020 and 2023, we deployed 308 geolocators, of which 45 (14.6%) were recovered. Moult regions for tagged birds were determined through full migration track reconstruction using the 'GeoPressureR' R-package (Vīgants *et al.* 2023, Nussbaumer *et al.* 2023a, 2023b). In short, we first manually identified migratory flights in the recorded logger data using the TRAINSET tool (<https://trainset.rafaelnussbaumer.com/>) based on sustained high dynamic body acceleration and concurrent rapid changes in pressure. Then, 'GeoPressureR' estimates bird positions across the annual cycle by aligning logger-measured pressure data with global weather reference data (ERA5 hourly surface-level pressure) to generate a

likelihood map for each stationary period. Light-level data were then processed with the threshold method to build likelihood maps for each twilight event, further refining spatial estimates derived from pressure. Next, transition probabilities between consecutive stationary sites were estimated through a movement model incorporating birds' airspeed during flight and contemporaneous wind conditions (ERA5 hourly pressure-level data) at the recorded flight altitudes. The final 'GeoPressureR' track thus represents the most probable route connecting stationary locations, constrained by both pressure- and light-based likelihoods and the birds' ground-speed distribution. Finally, we extracted moult locations from the resulting tracks based on the known moult timing of Starlings (c. mid-June until mid-September; Rothery *et al.* 2001).

Of 45 devices retrieved, data from 31 geolocators met both criteria to be included in this study: (a) moulting location could be determined based on the timings or migratory flights and stationary periods; and (b) feather sample was collected when the tag was retrieved and later tested for both $\delta^2\text{H}$ and $\delta^{34}\text{S}$.

Stable isotope analysis

Analyses were performed in two batches: the first at Iso-Analytical Ltd and the second at Sercon Analytical Ltd. However, both laboratories operated with the exact same equipment and analytical protocols, ensuring full comparability of results.

Feathers were washed in 0.25 M sodium hydroxide, rinsed twice in purified water, dried overnight at 60°C and homogenized by finely cutting with surgical scissors. Subsamples of 0.75 ± 0.1 mg were weighed into silver capsules for hydrogen isotope analysis, and 1.0 ± 0.1 mg into tin capsules with 5 mg of vanadium pentoxide for sulphur isotope analysis.

Stable isotope ratios are expressed in δ notation (‰) relative to Vienna Standard Mean Ocean Water (V-SMOW) for hydrogen and Vienna-Canyon Diablo Troilite (V-CDT) for sulphur.

Hydrogen isotope ratios ($\delta^2\text{H}$) were determined using elemental analyser–isotope ratio mass spectrometry (EA–IRMS). Samples were equilibrated with laboratory air moisture before analysis to account for exchangeable hydrogen. Non-exchangeable $\delta^2\text{H}$ values were calibrated using

USGS42, USGS43, USGS CBS and USGS KHS reference materials. A three-point linear calibration based on USGS43, CBS and KHS was applied, with USGS42 analysed as a quality control check. Internal laboratory standards, calibrated against internationally recognized reference materials (e.g. NBS-22, IAEA-CH-7), were analysed alongside samples to ensure accuracy and comparability.

Sulphur isotope ratios ($\delta^{34}\text{S}$) were also determined using EA-IRMS. For calibration, in-house standards IA-R061, IA-R025 and IA-R026 (traceable to NBS-127 and IAEA-S-1) were analysed together with samples. Quality control was verified with IA-R061, IAEA-SO-5, IA-R068 and IA-R069, the latter two calibrated against NBS-127 and IAEA-SO-5. Reference materials were included within each analytical batch to ensure accuracy and consistency with internationally accepted $\delta^{34}\text{S}$ values.

Replicated measurements spread every 10 samples provided standard deviations of $\pm 1.9\text{‰}$ for $\delta^2\text{H}$ and $\pm 0.1\text{‰}$ for $\delta^{34}\text{S}$.

In total, we obtained both $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values from 368 samples, while an additional 37 samples were analysed only for $\delta^{34}\text{S}$ owing to insufficient material being available for hydrogen isotope analysis. Of those, 69 were repeated samples from the same individual of feathers collected in different years. Thus, in total 315 feather samples from Latvia were tested for $\delta^2\text{H}$ (102 collected in 2022, 103 in 2023, 110 in 2024) and 351 for $\delta^{34}\text{S}$ (104 collected in 2022, 124 in 2023, 123 in 2024); and from Germany 53 were tested for $\delta^2\text{H}$ (31 collected in 2023 and 22 in 2024) and 54 for $\delta^{34}\text{S}$ (32 collected in 2023 and 22 in 2024).

Classifying moult locations based on stable isotopes

To determine the factors that influence stable isotope values and should be considered in further analysis, we fitted linear mixed-effects models for $\delta^2\text{H}$ and $\delta^{34}\text{S}$ with sex, year and site as fixed effects and ring number (individual id) as a random effect. To test if there were broad regional differences between $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values in Starling feathers, we fitted an additional reduced model for each element including only sampling country (Latvia vs Germany) as a fixed effect. All models were fitted in the R package 'lme4' (Bates *et al.* 2015), and *P*-values for fixed effects were obtained with 'lmerTest' (Kuznetsova *et al.* 2017).

We developed a method to classify moult locations of Common Starlings based on stable isotope values ($\delta^2\text{H}$ and $\delta^{34}\text{S}$) measured in feathers. Because some birds that leave the breeding sites shortly after breeding moult in nearby regions (e.g. other parts of Latvia or Lithuania; Priedniece 2024), their isotope values were expected to be similar to those from Latvian study sites. Other birds, however, were expected to moult farther away, in regions geographically closer to the German sampling sites (Vigants *et al.* 2023). Classification was therefore based on the assumption that part of the population moults near the breeding sites, while the rest perform moult migration and moult in areas close to the German sampling sites.

For the analysis, we defined a reference group consisting of birds sampled in the German sites ($n = 53$) and individuals breeding in Latvia known from geolocator data to have moulted at breeding sites ($n = 24$). The classification group comprised the remaining samples for which both $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values were available ($n = 291$, all from Latvia). Among these were seven geolocator-tracked birds with known moult locations in the Baltic region or northern Germany, which were later used for validation and interpretation of classification outcomes.

To account for interannual variation in stable isotope values, we first fitted linear models including collection year as a predictor ($\delta^2\text{H} \sim \text{year}$; $\delta^{34}\text{S} \sim \text{year}$). The residuals of these models, representing relative isotope values corrected for year, were used in the classification.

Moult location classification for each bird with unknown moult site, as well as for the validation group (seven geolocator-tracked birds that did not moult on breeding sites), was performed using maximum *a posteriori* (MAP) estimation implemented in the R package 'mvtnorm' (Genz & Bretz 2009) using the function *dmvnorm*. A prior probability of 0.2 for moulting near Germany was chosen based on geolocator data from Latvian-breeding Common Starlings, where approximately one in five birds moulted in north-central Europe (Priedniece 2024). A probability threshold of 0.8 was set for assignment to one of the groups. A higher threshold was not applied, as Latvian-breeding Common Starlings were not expected to moult directly at the German sampling sites but rather within a broader regional context (the same reasoning applied to birds moulting near Latvia).

To assess whether a combined use of both stable isotopes improved the classification, we repeated the MAP estimation separately for $\delta^2\text{H}$ and $\delta^{34}\text{S}$ residuals and compared assignment outcomes to the bivariate ($\delta^2\text{H} + \delta^{34}\text{S}$) model. All models used identical reference data, prior probabilities and thresholds, allowing direct comparison of assignment proportions and classification confidence. To statistically compare assignment outcomes among isotope models ($\delta^2\text{H}$ -only, $\delta^{34}\text{S}$ -only and $\delta^2\text{H} + \delta^{34}\text{S}$), we tested differences in the proportion of individuals assigned using a chi-square test of proportions, followed by pairwise proportion tests with Holm correction for multiple comparisons.

Analyses were conducted in R v.4.4.2 (R Core Team 2024).

RESULTS

Feather stable isotope values of $\delta^2\text{H}$ and $\delta^{34}\text{S}$ differed among the six breeding sites included in the study (Fig. 1). Latvian sites (Berzciems, Krievrags, Zeltaleja) clustered closely together, while German sites (Bahnitz, Dedelow, Oberthau) formed a separate group with generally disparate $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values compared to the Latvian samples.

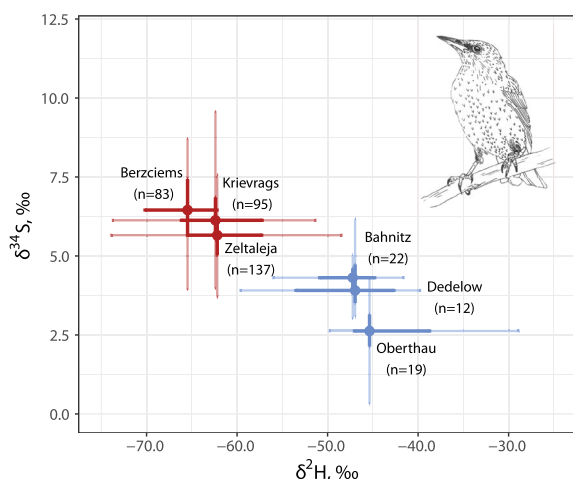


Figure 1. Common Starling *Sturnus vulgaris* feather stable isotope $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values across birds breeding at Baltic (Latvia, red) and north-central European breeding sites (northern Germany, blue). Only samples with results from both elements are shown. Each point represents the median values for a site. Thick bars indicate the 25th and 75th percentiles, while the thinner bars represent the 2.5th and 97.5th percentiles.

We did not find an effect of sex on either $\delta^2\text{H}$ ($\beta = 0.47$, 95% CI: -0.87 to 1.82 , $P = 0.489$) or $\delta^{34}\text{S}$ ($\beta = 0.04$, 95% CI: -0.10 to 0.29 , $P = 0.745$). Sampling year significantly influenced $\delta^2\text{H}$, with lower values in 2023 ($\beta = -2.01$, 95% CI: -3.63 to -0.39 , $P = 0.015$) and 2024 ($\beta = -2.66$, 95% CI: -4.29 to -1.03 , $P = 0.001$) compared to 2022. In contrast, $\delta^{34}\text{S}$ values were consistent across years (2023 vs 2022: $\beta = 0.01$, 95% CI: -0.29 to 0.32 , $P = 0.931$; 2024 vs 2022: $\beta = 0.19$, 95% CI: -0.12 to 0.50 , $P = 0.224$). Comparisons between regions showed strong isotopic differentiation, with German birds having significantly higher $\delta^2\text{H}$ ($\beta = -16.78$, 95% CI: -18.73 to -14.82 , $P < 0.001$) and lower $\delta^{34}\text{S}$ ($\beta = 2.41$, 95% CI: 2.03 to 2.79 , $P < 0.001$) values relative to Latvian birds. Full model outputs are provided in Tables S1 and S2.

Assignment and validation of individual moulting areas

Stable isotope values of birds with known moulting sites used as the reference groups for classification showed generally good separation between birds from the Baltic and north-central Europe with minimal overlap in both elements (Fig. 2).

Based on the combined $\delta^2\text{H}$ and $\delta^{34}\text{S}$ model assignment, 86.2% ($n = 251$) of the Latvian breeding Common Starlings (not included in the

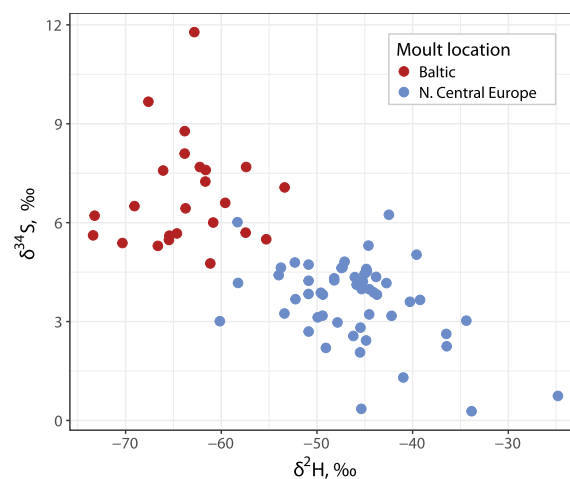


Figure 2. Stable isotope values ($\delta^2\text{H}$ and $\delta^{34}\text{S}$) of feathers from Common Starlings *Sturnus vulgaris* in the training dataset used for maximum *a posteriori* (MAP) estimation. Only birds with known moulting locations are included.

reference dataset) were predicted to moult in the Baltics (Fig. 3a). Only 4.5% ($n = 13$) of individuals were assigned to north-central European moulting sites and thus conforming to a long post-breeding moult migration. The remaining 9.3% ($n = 27$) could not be confidently assigned to either moult region at 0.8 confidence threshold.

Of the seven birds equipped with geolocators, five were correctly classified: three individuals that moulted in Lithuania were assigned to the Baltic group, and two that moulted in Germany were assigned to the north-central European group (Fig. 3b). One bird that moulted in Germany and one that moulted in Lithuania were classified as undetermined. None of the individuals with known moult sites were misclassified.

Among the three study sites in Latvia, the distribution of classified moult regions did not differ significantly (Fisher's exact test, $P = 0.376$). Similarly, we did not find any differences among age-classes with both yearlings and adults primarily moulting near the breeding sites with only a few

individuals from each age group conforming to moult migration (Fisher's exact test, $P = 0.608$).

To evaluate how the choice of isotopic marker influenced assignment results, we compared the proportion of birds assigned to the Baltics, north-central Europe or remaining unclassified across three isotope-based approaches: $\delta^2\text{H} + \delta^{34}\text{S}$ (combined), $\delta^2\text{H}$ -only and $\delta^{34}\text{S}$ -only. The distribution of assignment categories differed significantly among the three methods ($\chi^2 = 37.79$, $\text{df} = 4$, $P < 0.001$). The combined $\delta^2\text{H} + \delta^{34}\text{S}$ model assigned 90.7% of birds to one of the two regions with 9.3% remaining unclassified. The $\delta^2\text{H}$ -only model assigned 86.6% of birds (Baltics: 245, north-central Europe: seven), while the $\delta^{34}\text{S}$ -only model assigned only 73.2% (Baltics: 207, north-central Europe: six). Pairwise comparisons of the proportion of assigned individuals with high posterior probability (≥ 0.8) indicated that both the $\delta^2\text{H}$ -only and combined $\delta^2\text{H} + \delta^{34}\text{S}$ models classified significantly more birds than the $\delta^{34}\text{S}$ -only model ($P < 0.001$), whereas the difference

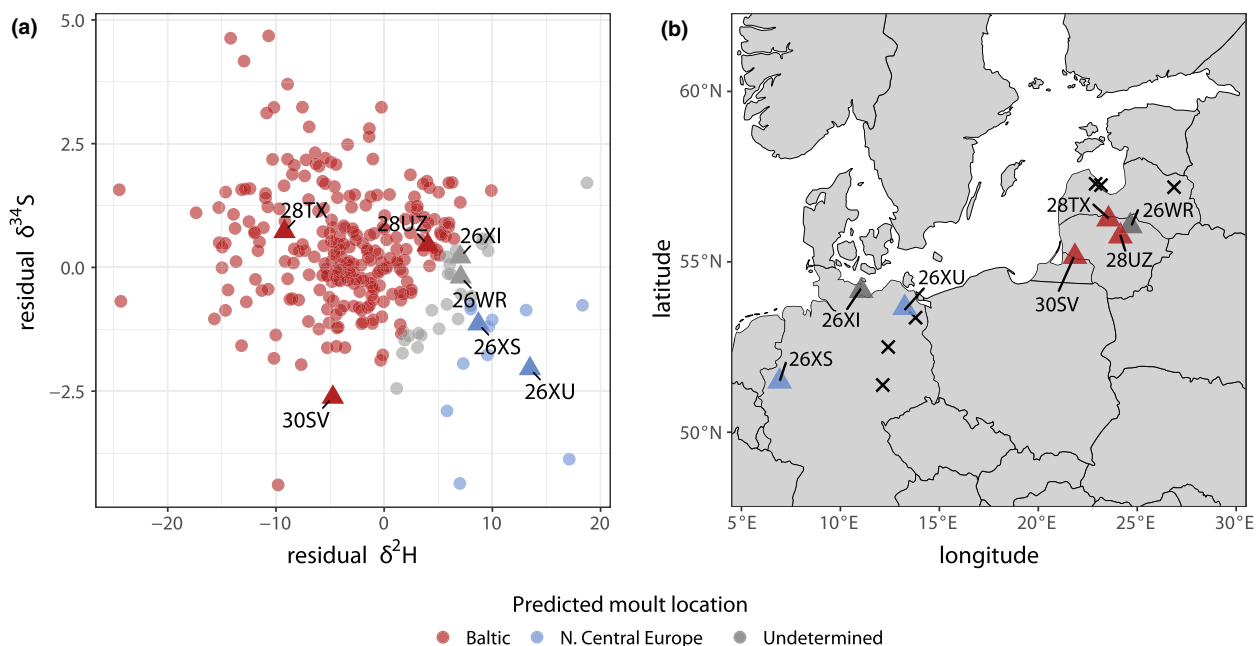


Figure 3. Inferred moult locations of Common Starlings *Sturnus vulgaris* breeding in Latvia based on feather stable isotope $\delta^2\text{H}$ and $\delta^{34}\text{S}$ values: (a) all classified individuals and (b) subset of individuals with geolocator-confirmed moult sites used to validate isotopic assignments. Colours indicate assigned moult origins by maximum *a posteriori* estimation: Baltic region (red), north-central Europe (blue) and undetermined region (grey). Coloured assignments represent posterior probabilities ≥ 0.8 ; grey indicates posterior probabilities < 0.8 . Triangles represent geolocator-tracked individuals with known moult locations, which are shown here as part of the classification (i.e. treated as unknown during analysis) and labelled with individual geolocator IDs. Breeding sites in Latvia and Germany are marked with an x in the map.

between the combined and $\delta^2\text{H}$ -only models was not statistically different ($P = 0.15$). For the validation group of seven geolocator-tracked birds, $\delta^2\text{H}$ correctly assigned four individuals and left three undetermined. For $\delta^{34}\text{S}$, three were correctly assigned, two were misclassified and two remained undetermined.

Between-year individual consistency of moult strategy

For individuals sampled in consecutive years, mean $\delta^2\text{H}$ values changed on average by $-3.88\text{‰} \pm 9.88\text{‰}$ sd between 2022 and 2023 and by $-0.32\text{‰} \pm 5.63\text{‰}$ between 2023 and 2024. Correspondingly, $\delta^{34}\text{S}$ values changed by $0.33\text{‰} \pm 1.72\text{‰}$ and $0.14\text{‰} \pm 1.78\text{‰}$, respectively (Fig. 4). Among repeatedly sampled individuals, moult origin assignment was generally consistent across years with only a few individuals shifting between being confidently assigned to one or the other region in one year and remaining unclassified in another year ($n = 7$). Thus, we found no evidence for individuals switching from moulting near the breeding grounds in one year to undertaking moult migration in another year or vice versa.

DISCUSSION

We demonstrated that stable isotopes of hydrogen ($\delta^2\text{H}$) and sulphur ($\delta^{34}\text{S}$) in feathers can be used to distinguish between alternative moult regions in a European short-distance migratory bird on a relatively small geographical scale. Both isotopes contributed substantially to differentiating moult-related migration strategies, showing that this dual-isotope approach is a powerful tool for identifying isotopic patterns consistent with different moulting regions. By assigning moult strategies to more than 250 individuals, we were able to show an overall low prevalence of moult migration in our study populations without differences between East and West Latvian Starling populations. Moreover, both juvenile and adult birds showed a similar low prevalence of moult migration, with its occurrence remaining consistent within individuals across years. These findings contribute to our understanding of moult migration and provide a useful basis for future studies exploring how and why this strategy may vary among individuals and populations.

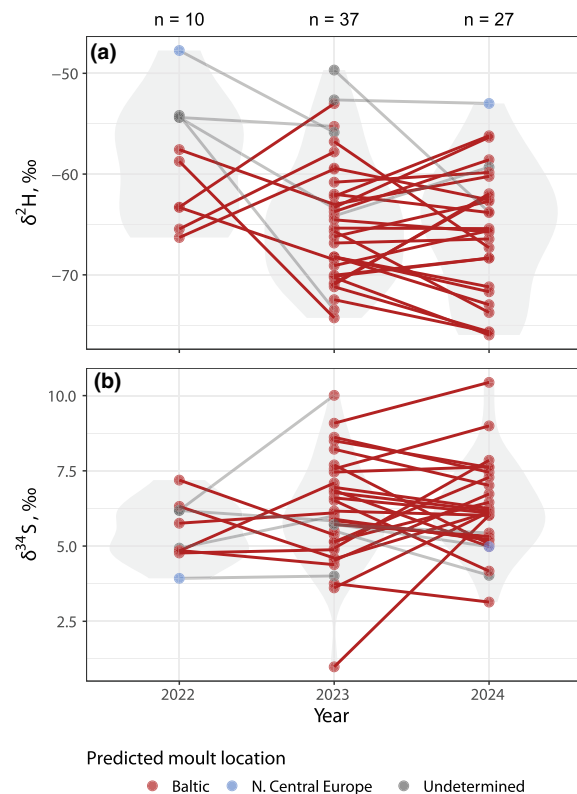


Figure 4. Comparison of Common Starling *Sturnus vulgaris* feather (a) $\delta^2\text{H}$ and (b) $\delta^{34}\text{S}$ values across sampling years, showing only individuals sampled in consecutive years (lines connect individual level data). Colours correspond to moult region assignment by maximum *a posteriori* estimation: Baltic region (red), north-central Europe (blue) and undetermined region (grey). Connecting lines match point colour when assignments were consistent; grey lines indicate at least one year with uncertain assignment.

Moult region assignment using a dual-isotope approach

Stable hydrogen isotopes ($\delta^2\text{H}$) are widely used to infer the origins of migratory animals in North America, where strong continental gradients in precipitation $\delta^2\text{H}$ provide high spatial resolution (Hobson *et al.* 2012). In Europe, however, the isotope distribution is more constrained, and consequently $\delta^2\text{H}$ has been less informative for animal tracking at regional scales. For instance, Tonra *et al.* (2015) found that using hydrogen isotopes alone provided poor assignment precision when determining the breeding origin of a European passerine species. Similarly, Kruszynski *et al.* (2021) showed that hydrogen-based origin assignments for

migratory bats were refined after incorporating strontium isotope data, as $^{87}\text{Sr}/^{86}\text{Sr}$ signatures – reflecting underlying geology – were inconsistent with some regions suggested by $\delta^2\text{H}$ alone, thereby excluding them as likely origins.

In our study, $\delta^2\text{H}$ nevertheless captured meaningful spatial resolution. We found that values varied among sites, but these patterns were best explained when sites were grouped into broader regions, with Baltic populations showing significantly lower $\delta^2\text{H}$ values than those in northern Germany (Table S2). Variation between years was also evident (Table S1), consistent with the known temporal instability of precipitation $\delta^2\text{H}$ (Hobson *et al.* 2012, Tonra *et al.* 2015, Nordell *et al.* 2016). This annual variation can be accounted for statistically, as we did here, by analysing model residuals adjusted for year of sample collection. While this approach helps control for baseline shifts among years, it may also reduce signals associated with true spatial changes if such shifts coincide with strong year-to-year variation in baseline $\delta^2\text{H}$ values. We therefore interpret our results primarily at the level of inferred moult strategy rather than absolute or fine-scale changes in isotope values. Conversely, we detected no effect of sex (Table S1), which is expected given the lack of evidence for sex-specific migration patterns in Common Starlings (Dolbeer 1982, Werner *et al.* 2020).

The use of sulphur isotopes ($\delta^{34}\text{S}$) in avian migration studies is relatively new. Sulphur isoscapes have been developed in several parts of the world, including Europe (Brlík *et al.* 2024) and suggest that spatial variation in $\delta^{34}\text{S}$ is largely driven by distance to the sea, bedrock age and soil composition (Brlík *et al.* 2024). Distance to saltwater may therefore also influence $\delta^{34}\text{S}$ values in our study system, with coastal areas being more enriched in sulphur isotopes (Zazzo *et al.* 2011). However, because the expected moulting locations in both regional groups span a range of distances from coastal systems, and because $\delta^{34}\text{S}$ was used only in combination with $\delta^2\text{H}$, we consider our approach appropriate for capturing this known source of variation. Additionally, a probabilistic assignment framework also accommodates small-scale spatial heterogeneity in isotope values. Because these underlying factors are stable over time, $\delta^{34}\text{S}$ is expected to show less interannual variability than $\delta^2\text{H}$. Our results supported this expectation: we found no evidence for annual

effects on $\delta^{34}\text{S}$ values (Table S1). Nor did we detect differences between sexes (Table S1). Instead, spatial differences were the primary driver of variation, with Baltic populations again showing significantly higher $\delta^{34}\text{S}$ values compared to northern Germany (Table S2).

In our study, for both isotopes a subset of individuals fell into intermediate isotopic space between the Baltics and north-central Europe, creating a ‘grey zone’ that limited confident assignments (Fig. 2). To address this, we adopted an approach that defined broader regional groups and treated assignments probabilistically. This framework accounts for small-scale spatial variation in both $\delta^2\text{H}$ and $\delta^{34}\text{S}$ while still providing a robust basis for distinguishing between regions. With this structure, the reference dataset was sufficiently reliable to support regional assignments and to evaluate moult strategies in a large sample of untracked birds. These findings highlight the importance of robust reference datasets, as well as the benefit of combining multiple isotopic markers. However, some limitations must be acknowledged. For the German reference group in particular, we cannot entirely rule out the possibility of short-distance movements before or during moult in some individuals. Ring recoveries and previous studies suggest that such movements are rare and usually limited to only tens of kilometres (Hug 2019, Rost 2021), but they may still introduce additional isotopic noise. We also cannot definitively state that all Latvian birds moult exclusively in either of these two regions; instead, a few individuals may do so somewhere in between or in other locations. Similarly, isotopic values can be influenced by local factors such as diet composition and fine-scale environmental heterogeneity, leading to variation even among individuals originating from nearby locations (Nordell *et al.* 2016, Brlík *et al.* 2024). Finally, we acknowledge that interpreting isotopic differences as reflecting geographical differences may not always be precise, because similar isotopic values can occur in multiple regions.

Nevertheless, the joint use of $\delta^2\text{H}$ and $\delta^{34}\text{S}$ increased the proportion of individuals that could be assigned above the confidence threshold compared with either isotope alone. Sulphur isotopes on their own showed relatively low assignment precision, with fewer than three-quarters of individuals classified with confidence and had two cases of misclassifications in the validation group

from geolocator-tracked birds. Although the difference in the proportion of confidently classified individuals between the combined and $\delta^2\text{H}$ -only approaches was not statistically significant, using both isotopes still allowed a greater number of individuals to be assigned to one or the other moult region. Additionally, one individual from the validation group that was assigned correctly when using the combined approach fell below the threshold when using hydrogen alone. This indicates that $\delta^2\text{H}$ provides the primary discriminatory signal, while $\delta^{34}\text{S}$ contributes to improving assignment confidence when used in combination with hydrogen. Future work could explore the potential inclusion of other stable isotopes, for example ^{13}C , ^{15}N , $^{87}\text{Sr}/^{86}\text{Sr}$ and ^{18}O , which might in some cases help strengthen classification, but their utility would probably depend on the study system and geographical context, and should be evaluated beforehand.

Prevalence of moult migration in Baltic Common Starlings

Applying our dual-isotope classification approach, we were able to assign moult strategies to the majority of Latvian-breeding Common Starlings tested. Most individuals were classified as moulting within the Baltic region (Fig. 3a), with only a small proportion identified as moult migrants. This demonstrates that the method can provide clear insights into moult strategies at the population level, even in a short-distance migrant where the distance between regions of interest is relatively small (a few hundred kilometres). Using a similar approach Dingle *et al.* (2025) showed that in the East Asian–Australasian Flyway in White-shouldered Starlings *Sturnia sinensis* stable isotopes of $\delta^2\text{H}$ and $\delta^{34}\text{S}$ differed between birds with alternative migration strategies.

The reliability of our results was further supported by the geolocator-tracked validation group. For these birds, isotope-based assignments were largely consistent with the independent tracking data, showing that the method can correctly distinguish between regional strategies (Fig. 3b). Two individuals, however, could not be confidently classified, which is likely to be a consequence of individual variation in isotope composition. During moult, Common Starlings consume both invertebrates and plant material (Feare 1984), and the relative proportion of these food sources is likely

to vary among individuals. Additionally, Common Starlings frequently forage in anthropogenic habitats, such as cattle farms, where they take cattle feed and thus may ingest plant material originating from distant locations (Feare & Swannack 1978, Glahn *et al.* 1983). Such food items could carry isotopic signatures that do not reflect the local environment, introducing further variability into feather isotope values. Together, these findings highlight both the potential and the limitations of the isotope-based classification approach: it can assign most individuals with high confidence while also identifying cases where isotopic variability or incomplete reference coverage reduce certainty. It is also important to consider that moult strategies may occur along a displacement distance continuum rather than as a strict dichotomy, with individuals moulting at multiple sites or shifting strategies across years (Jenni & Winkler 2020), which could account for unclassified individuals.

When considering only Latvian-breeding Common Starlings, our classification results did not reveal significant differences in the proportion of moult strategies between study sites. Birds from eastern and western Latvia showed similar prevalence in moulting locally versus exhibiting moult migration. This finding contrasts with the results of Vīgants *et al.* (2023), who documented clear spatial variation in moult strategies within Latvia using geolocator tracking, with higher rates of moult migration in eastern Latvia. Differences in sampling years could partly explain the observed discrepancies, as Vīgants *et al.* (2023) analysed birds sampled in 2020 only, and potential year-to-year differences in environmental conditions – though not assessed in their study – could have influenced the prevalence of moult migration. Interannual variation in weather or food availability has been proposed to influence the prevalence of moult migration across years or regions (Pyle *et al.* 2009). Additionally, the relatively small sample size in Vīgants *et al.* (2023) (10 geolocator-tracked individuals) may have limited the representativeness of their estimates.

We found no significant differences in moult strategies between first-year birds and adults, contrasting with observational accounts of ‘summer migration’ reported mainly in juveniles from north-eastern Common Starling populations (Bulyuk *et al.* 2000). Instead, our findings suggest that both age groups follow broadly similar strategies, redefining moult migration in Common

Starlings as a population-wide rather than age-specific trait. Previous geolocator studies that cover moult migration in our study populations (Vigants *et al.* 2023) have focused exclusively on adults, as juvenile birds are generally rarely tagged with archival tracking devices owing to their low inter-annual return rates. Additionally, past observational studies may have introduced bias by monitoring primarily diurnal movements, based on the long-held assumption that Common Starlings are predominantly diurnal migrants (Thorup & Rabøl 2007). Recent studies have challenged this view, showing that many migrants, once considered predominantly diurnal, migrate primarily at night (e.g. Liechti *et al.* 2018, Briedis *et al.* 2020). The same has now been demonstrated in Common Starlings (Vigants *et al.* 2023). These findings raise the possibility that apparent age-related differences in moult migration reported in earlier studies may partly reflect this observational bias, as nocturnal movements could have gone undetected. To date, nocturnal migration has only been documented in adult Common Starlings, and whether juveniles exhibit similar nocturnal flight behaviour remains an open question.

Across our Latvian dataset, only 4.5% of individuals were classified as moult migrants. This proportion is considerably lower than estimates from earlier studies, which reported rates of 17% (Priedniece 2024) and 44% (Vigants *et al.* 2023). The same explanations as discussed above when explaining the spatial patterns of moult migration in Common Starlings could account for these differences. Alternatively, the discrepancy may reflect rapid evolution in moult strategies – moult migration might have been more prevalent in past decades but could have rapidly declined in these populations as a result of climate change or other external factors. For example, milder springs with fewer cold spells (Briedis *et al.* 2024) may decrease interannual variability in fruit and berry yield – a common food of Common Starlings during summer (Feare 1984) – at northern latitudes, decreasing selection pressure against moulting on the breeding sites. However, with no direct evidence, this alternative explanation should be viewed with caution. Additionally, it has been proposed that moult migration may be underestimated in other systems, such as in North American passerines, as a consequence of methodological or observational limitations (Pyle *et al.* 2018).

Furthermore, when assessing moult strategies of individuals sampled across multiple years, we found the strategy to be consistent within individuals: none of the recaptured birds switched between moulting locally or moulting abroad (Fig. 4). This includes a few repeatedly sampled individuals that were classified both as yearlings and adults. These results indicate that, at the individual level, moult strategy with respect to moulting location appears to be stable rather than annually adjusted or age dependent. At the same time, the coexistence of different strategies across individuals demonstrates that moult strategies vary on a population level. Such individual consistency may indicate a genetic basis (Contina *et al.* 2023), early-life imprinting or a learned behavioural component (Sokolovskis *et al.* 2025) that is maintained across years.

CONCLUSION

We believe that the combined use of $\delta^2\text{H}$ and $\delta^{34}\text{S}$ is effective in Common Starlings and could also hold considerable potential for application across other species. The method may be particularly valuable for short-distance European migrants, for which other tracking techniques either lack sufficient spatial resolution or cannot feasibly be applied to large sample sizes (e.g. geolocators or GPS tags). Nevertheless, careful consideration of moult patterns and the inclusion of appropriate reference samples remain crucial, as $\delta^2\text{H}$ values vary temporally with precipitation, while $\delta^{34}\text{S}$ can exhibit fine-scale spatial heterogeneity. Despite these limitations, the high assignment accuracy achieved within our study region highlights the power of this method and suggests further extensions to broader spatial scales, including studies of long-distance migrants. Integrating $\delta^{34}\text{S}$ with $\delta^2\text{H}$ assignments is expected to improve spatial precision further. For many long-distance migrants, where moulting and wintering sites often coincide, this combined isotope approach could enable more accurate identification of wintering areas than hydrogen isotopes alone, offering a valuable complement to conventional tracking techniques.

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AUTHOR CONTRIBUTIONS

Elza Marija Zacmane: Investigation; conceptualization; data curation; formal analysis; methodology; visualization; writing – review and editing; writing – original draft. **Ivo Dinsbergs:** Investigation; writing – review and editing. **Steffen Hahn:** Investigation; writing – review and editing. **Māris Jaunzemis:** Investigation; writing – review and editing. **Valts Jaunzemis:** Investigation; writing – review and editing. **Oskars KeiĶs:** Investigation; writing – review and editing; funding acquisition; project administration. **Ance Priedniece:** Investigation; writing – review and editing. **Viesturs Vīgants:** Investigation; writing – review and editing. **Martins Briedis:** Investigation; conceptualization; data curation; formal analysis; methodology; visualization; writing – review and editing; funding acquisition; supervision.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ETHICAL NOTE

This study was conducted under permits issued by the Nature Conservation Agency of Latvia (permit no. 155/2020 & 127/2022) and the Food and Veterinary Service of Latvia (experimental project permit no. 111 for animal use in research).

Data Availability Statement

The data and code used to generate these results are publicly available on Zenodo Open Repository: <https://doi.org/10.5281/zenodo.18339418>.

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SUPPORTING INFORMATION

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

Table S1. Linear mixed-effects model results for feather stable isotope values ($\delta^2\text{H}$ and $\delta^{34}\text{S}$) in Common Starlings *Sturnus vulgaris*, with sex, site and year as fixed effects and individual as a random effect.

Table S2. Linear mixed-effects model results for feather stable isotope values ($\delta^2\text{H}$ and $\delta^{34}\text{S}$) in Common Starlings *Sturnus vulgaris*, with country as a fixed effect and individual as a random effect.