

RESEARCH ARTICLE

Combining multiple data sources to estimate autumn migration timing and hunting exposure of woodcocks in Central Europe

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Abstract

1. During migration, individuals of migratory species occurring in a specific area can include a mixture of local breeding birds and migratory conspecifics from distant populations. In birds that are legally hunted during migration, the unknown extent of mixing between populations can be problematic for management.
2. The Eurasian woodcock (*Scolopax rusticola*) is a forest-dwelling wader with a wide Palearctic distribution, where migratory individuals from north-eastern Europe mix with central European birds during autumn and winter. Because woodcocks are hunted in autumn and winter in Central Europe, poor knowledge of the timing of autumn migration complicates an assessment of to what extent hunting affects local breeding populations.
3. Here, we quantified the timing of autumn migration of woodcocks breeding in a fully migratory population in Switzerland using ringing and tracking data ($n=110$ bird-years). Additionally, we estimated the proportion of non-local woodcocks shot in Switzerland using stable hydrogen isotopes ($\delta^2\text{H}$) in flight feathers of 842 individuals. We used a multistate mark-resight model to estimate the weekly probability of migration departure from late July until the end of December, and developed a hierarchical assignment model to estimate the probability of shot woodcocks to be of non-local origin, accounting for date and location of the harvest.
4. We found that 95% of the local Swiss population had departed by 7 December (95% credible interval 28 Nov–18 Dec), but that >50% of local woodcocks were exposed to hunting pressure during the legal hunting period in October and November. We estimated that 90.2% (48.8%–99.8%) of shot woodcocks were of non-local origin, but assigning individuals to an origin was highly uncertain.

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5. *Practical implication.* The late autumn migration departure in Switzerland exposes many locally breeding woodcocks to hunting pressure, and the proportion of local birds being shot was mostly determined by the dilution of local birds by more numerous migrants. A delay of the hunting season after November may further reduce the probability of shooting local birds, but to ensure the viability of migratory populations the hunting effort should be coordinated along the entire flyway.

KEYWORDS

assignment, flyway, gamebird, harvest management, migration, stable isotopes, telemetry, woodcock

1 | INTRODUCTION

Every autumn, millions of birds in the northern hemisphere migrate between breeding and non-breeding areas. This migratory behaviour varies among individuals or populations of a given species (Phipps et al., 2019; Shamoun-Baranes et al., 2017; Tedeschi et al., 2019), with early migration in more seasonal environments and late migration or year-round residency in more benign environments (Alerstam, 1990; Neufeld et al., 2021; Newton, 2023). The between-population variation in the timing of departure leads to frequent mixing of early and late departing populations during the migration period. Because populations breeding at higher latitudes often start migrating earlier than populations breeding at lower latitudes (but see Briedis et al., 2016), individuals from several populations can simultaneously co-occur at lower latitude breeding grounds. This temporary mixing of populations can have important ramifications for disease transmission and complicate management and conservation of local populations (Kucia et al., 2023; Risely et al., 2018; Turjeman et al., 2020; Waldenström et al., 2002; Webster & Marra, 2005).

Management of wild bird species should ensure that populations can sustain any mortality induced by human activities (Riley et al., 2002; Sinclair, 1991). Such management requires a good understanding of the source populations from which individuals are removed by targeted harvest, and the viability of those populations. For migratory species, the individuals that are removed by hunting may originate from different populations depending on the time of hunting (Gomez et al., 2026; Lindberg & Malecki, 1994; Marx et al., 2016). In areas where migratory individuals from distant origins and local breeding individuals of the same species co-occur, it is therefore imperative to understand the timing of migratory movements to assess what proportion of the local breeding population is affected by hunting at a given time.

The Eurasian woodcock (*Scolopax rusticola*) is a secretive forest bird that breeds across the Palearctic and migrates from breeding areas in Scandinavia and eastern Europe to south-western European and Mediterranean wintering areas (Bauthian et al., 2007; Guzmán et al., 2011; Schenk, 1925). This widespread species is considered a 'gamebird' that is hunted across its range, and hunting mortality appears to limit the growth rate of some populations (Duriez, Eraud,

et al., 2005; Kalchreuter, 1975; Péron et al., 2011a). To reduce the population impact of hunting, regionally varying regulations are in place that limit the hunting periods and the quantity of woodcocks that can be taken by hunters (McNicol et al., 2024). Typical hunting seasons in most countries are in autumn and winter, when migratory birds from higher latitude breeding areas mix with local breeding populations (McNicol et al., 2024). However, there is large variation in migration strategies between populations (Le Rest et al., 2019; Tedeschi et al., 2019) that leads to a diffuse mixing of different populations during migration. While the seasonal influx of migratory individuals provides a larger number of birds that can be harvested, the mixing of many local and non-local populations complicates the assessment of which population is affected by hunting mortality (Gomez et al., 2026; Lindberg & Malecki, 1994; Marx et al., 2016).

As a small central European country, Switzerland hosts both breeding and distant-origin migratory woodcocks. Because the lowland breeding population of woodcocks has decreased in Switzerland by approximately 10%–12% since 1993 (Knaus et al., 2018), local regulations aim to reduce hunting pressure on local breeding birds via temporal restrictions when woodcocks can be hunted (Andrist et al., 2022). The intended purpose of these regulations is to allow hunting at times when local birds have departed from their breeding grounds, but whether these restrictions are effective is unclear because the timing of autumn migration of local woodcocks is poorly understood (Kalchreuter, 1975). Therefore, a better understanding of the migration phenology of local breeders is required. In addition, knowing the origin of woodcocks that are hunted in Switzerland would be useful to assess how many local woodcocks fall victim to local hunting pressure (Bohnenstengel et al., 2021; Keller et al., 2020; Mollet, 2015).

In this study, we combine ringing, tracking and stable isotope data to estimate when the breeding population of Switzerland departs in autumn, and to determine the proportion of shot individuals that are non-local breeding birds. According to federal law, woodcocks in Switzerland are subject to hunting from 16 September until 14 December. Our goal was therefore to estimate the proportion of birds of Swiss origin still residing in Swiss forests at several key dates when hunting is permitted. We then assigned origins of harvested woodcocks by using hydrogen stable isotopes in wing feathers (Hobson et al., 2004; Hobson, Van Wilgenburg, Ferrand, et al., 2013)

to estimate the combined probability of non-local origin for all sampled woodcocks depending on when and where they were shot. Together, the timing of autumn migration of local birds and the estimates of the proportion of shot woodcocks that are of non-local origin allow an assessment of the likely effectiveness of Swiss hunting regulations in protecting the local breeding populations of woodcock.

2 | MATERIALS AND METHODS

2.1 | Species and study area

The Eurasian woodcock is a medium-sized (300g) migratory wader that is largely nocturnal and breeds in forests with a well-developed shrub layer, clearings, and a high abundance of earthworms (Glutz von Blotzheim et al., 1986; Sládeček et al., 2023). While considered 'Least Concern' globally due to its huge geographic range and large global population (BirdLife International, 2021), breeding populations in western Europe are decreasing (Heward et al., 2024; Keller et al., 2020). In Switzerland, woodcocks breed in forests ranging from 400 to 2200m a.s.l. (Knaus et al., 2018), and the species is classified as 'Vulnerable' on the Swiss Red List of threatened birds (Knaus et al., 2021).

Woodcocks that breed in Switzerland depart from breeding grounds after September, and local hunting regulations reflect the desire to protect local breeding birds (Andrist et al., 2022). Most Swiss cantons have specific hunting seasons and regulate daily or annual harvest limits (Bohnenstengel et al., 2021). At the time of our study, regulations permitted hunting from 16 September through 14 December at the federal level with regionally varying start dates between mid-September and mid-October in different cantons (16 September in Jura and Neuchâtel, 1 October in Bern and Valais, 15 October in Fribourg since 2009, Ticino and Vaud since 2014, Figure 1). Note that cantonal hunting regulations can change annually, and hunting season dates reflected the regulations during the years of our study.

Our study area was in the Swiss Jura mountains, a core area of woodcock distribution in Switzerland, including the western part of the canton of Neuchâtel and a small part of the northern canton of Vaud (46.92°N, 6.58°E). The area covered approximately 225km² and was characterized by porous limestone soils with forest dominated by spruce (*Picea abies*), beech (*Fagus sylvatica*) and silver fir (*Abies alba*) at an elevation range from 700 to 1600m a.s.l.

2.2 | Woodcock capture and marking

From April to November 2005 to 2021, 472 woodcocks were captured by us (393 birds) and volunteer ringers (79 birds) either with mist-nets in the forest or with hand nets in open fields at 18 locations (Tables S1 and S2). Locations with displaying males were initially identified through the bird observation database of the Swiss Ornithological Institute (www.ornitho.ch) and expanded based on our own field observations. Mist-nets were fixed between poles up to 12m high, placed at points in the forest where displaying males

were regularly observed, and used during the displaying season from late April to early July. Visual (plastic woodcock imitations) and acoustic ('Firestorm', Foxpro Inc., Lewistown, USA) decoys lured displaying males to lower flight altitudes and into the nets. Hand nets were used before the breeding season in April and after the breeding season from mid-July to November. At these times of the year, woodcocks are regularly found on open pastures and meadows (Ferrand et al., 2008), where they can be dazzled with a spotlight and captured by hand net.

All captured birds were marked with a uniquely numbered metal ring, weighed to the nearest 1g using an electronic scale, aged by moult status as either first-year birds or adults, and genetically sexed using body feathers (Aradis et al., 2015; Han et al., 2009; Vali & Elts, 2002). Between 2016 and 2018, 58 birds caught in spring or summer that were suspected to be local breeding birds were additionally equipped with VHF radio transmitters (TW3, Biotrack or own construction; Naef-Daenzer et al., 2005), and 30 were equipped with solar-powered satellite transmitters (solar-powered PTT-1005 beacons, Microwave Telemetry Inc., Table S1). Transmitters weighed 9–10g and thus approximately 3% of male body mass. VHF transmitters had an estimated battery lifespan of 18 months, while satellite transmitters were configured to transmit for 7 h and recharge for 45h between 1 April and 31 January, which allowed for one or more locations every 2 days under optimal conditions. VHF tags were fitted with an elastic harness using the leg-loop method (Kenward, 2001; Le Rest et al., 2019), while PTT tags were fitted with a backpack-harness made of Kevlar-ribbon similar to other studies on woodcock (Clements et al., 2024; Moore et al., 2021; Tedeschi et al., 2019). Birds were released immediately after handling at the location where they were captured.

All capturing, sampling, ringing and marking was permitted by the Swiss Federal Office for the Environment (FOEN, permit numbers F044-0799 and 0274-1038) and the Service Faune, Forêt et Nature du canton de Neuchâtel (permit numbers FS7/2017 and FS9/2018).

2.3 | Resighting and recapturing

Recaptures occurred during capturing efforts, and dead recoveries were reported by hunters. Radio-tagged birds were located at least twice a week during the day between 7:00 and 20:00h local time between April and early December using the 'homing in' method (Kenward, 2001) with handheld antennas and vehicles. We focused localizations on daylight hours because woodcocks are primarily diurnal during breeding. The vehicles used for tracking were equipped with rotating directional antennas and searching by vehicle covered an expanded area including adjacent valleys to the south, east and north (France). Individuals were also recorded with five hand-operated rotating directional antennas mounted on 6m masts installed at various strategic hilltops that maximized the probability to receive VHF signals from individuals within the study area. PTT

localizations were received at irregular intervals depending on the power level of the transmitters. We summarized the effort to recapture marked woodcocks as the weekly sum of the lengths of all mist-nets multiplied by the amount of time these mist-nets were open and available to capture birds. Because the operation of mist-nets and the search for VHF-tracked birds coincided temporally, we used the net operation duration also as a proxy for the search effort to detect VHF-tracked birds, which was not independently recorded. For weeks in which no formal record existed about the observation effort (113 out of 312 weeks in the study period), we interpolated the observation effort from a linear regression relating the number of woodcock records to the recorded effort in those weeks when data were available.

2.4 | Ringing and tracking data processing

We were interested in quantifying the autumn departure date of woodcocks, and therefore focused on resighting and recoveries during the period of autumn migration from late July until the end of December (Bohnenstengel et al., 2021). We estimated the probability of survival and migration in weekly encounter occasions, and selected data from week 31 (~late July) to week 52 (end of December).

Most ringed birds ($n=390$) were either never observed during the breeding season, or never located within the study area between late July and January, and were therefore excluded from the analysis of departure time because they provided no relevant information on departure timing of confirmed local breeders (an analysis including those birds yielded almost identical results). To allow independent estimation of autumn departure for birds recorded in multiple years, we split the encounter history of individuals into bird-years and used each bird-year as data point to estimate the probability of migration in each week (17 individuals provided data in 2 years, 2 in 3 years, 1 in 4 years and 1 in 5 years). For three individuals that were recovered dead within our study area in autumn, but were last recorded alive in June or July (i.e., prior to the start of our first autumn occasion), we moved their last live encounter to week 31 to facilitate their inclusion in the study, which is unlikely to bias the estimates of migration departure (O'Brien et al., 2005).

2.5 | Estimating departure timing

To estimate the timing of departure of woodcocks from the Swiss study area we used data from both ringed individuals and those equipped with either a VHF tag or a satellite transmitter. Because birds could only be recorded if they were either caught or shot, or if there was a location signal of either the VHF or satellite transmitter, we estimated the timing of departure with a multistate capture–recapture model (Kendall & Nichols, 2002; Schaub et al., 2004; Schwarz et al., 1993) that accounted for uncertainty in the true state of the individual during weeks when it was not observed.

This model used weekly encounter occasions to estimate whether marked individuals were in one of four true states, namely, (1) alive inside the study area, (2) dead inside the study area, (3) alive outside the study area after migration, or (4) dead outside the study area after migration. These true states were informed by the available data in five observable states, which could either indicate that an individual was re-captured or recorded in the study area, whether transmitter signals were received from a live individual outside the study area, or whether the individual was found dead inside or outside of the study area. We included an observation state when no data were received from an individual in a week, and when the true state of this individual was therefore unknown for this week (labelled 'not observed', see [Supporting Information](#) for detailed state transition and observation probability matrices).

The probability of an individual to be in any of the four latent true states given that it was observed in one of the five observation states was modelled based on the probability to receive data from or directly observe an individual, and the probability to find a dead individual once it died. The model estimated weekly survival, migration and observation probabilities, where survival was assumed to be constant over the period analysed (August–December), while the probability to depart the study area from one week to the next (migration probability) was assumed to increase linearly through the autumn period. Given that our data were accumulated over a time span of 13 years, we accounted for the possibility of temporal variation in survival and detection probabilities by allowing survival and detection probabilities to vary in each year (Péron et al., 2011b), but the probability to migrate in a given week was held constant across years. We also explored a model that allowed survival probability to vary over weeks within each year, but we found no support for such a parameter, presumably because the temporally variable hunting mortality did not have a measurable effect on our population of marked individuals (Péron et al., 2011a). We included an individual random effect on the weekly migration probability to account for some individuals contributing >1 year of data.

The probability of recovering the carcass of a dead individual in each week was modelled as a function of a temporally constant intercept and an additive effect specifying whether the individual was inside or outside the study area. The much higher observer density and reporting rate inside the study area made it more likely that dead individuals would be recovered inside than outside the study area. The probability to observe a live individual inside the study area was assumed to depend on the amount of observation effort in each week (standardized weekly sum of observation and recapturing effort), and additionally on whether an individual was equipped with a transmitter, because the probability to receive data from a bird with a transmitter was greater than the probability to observe or recapture a bird only equipped with a ring. Outside the study area, the probability of detection depended also on whether an individual was equipped with a transmitter, and on the type of transmitter because birds equipped with a satellite transmitter could be detected over a larger geographic area than birds equipped with VHF transmitters.

We used a Bayesian framework for inference and parameter estimation, with weakly informative priors for the weekly survival probability (beta distribution with $\alpha=35$ and $\beta=1$, based on typical annual survival probabilities; Tavecchia et al., 2002), and resighting and recovery probabilities outside our study area (beta distribution with $\alpha=1$ and $\beta=15$). Because we expected migration probability to increase over time, we chose a positive prior (normal with mean=1 and standard deviation=2) for the coefficient of the linear relationship affecting weekly migration probability. Similarly, we expected resighting probability to increase with observation effort and to be higher for individuals marked with a satellite transmitter, and therefore chose positive priors for those two parameters (normal with mean=1 and standard deviation=2). We used mildly informative priors (beta distribution with $\alpha=1$ and $\beta=50$) for the intercept of resighting and recovery probabilities within our study area. We fit the multistate model in the program Nimble (de Valpine et al., 2016) with a customized marginalized likelihood function appropriate for combined resighting and recovery models (Schaub & Badia-Boher, 2025). We ran four Markov chains for 50,000 iterations each, discarded the first 25,000 iterations, and used every fourth iteration for inference. Convergence of the four chains for all monitored parameters was visually inspected using trace plots and tested using the Gelman-Rubin diagnostic with an R-hat threshold of 1.05 (Brooks & Gelman, 1998).

We present posterior estimates with 95% credible intervals for the weekly migration and survival probability, including the slope parameter (β) for the weekly increase in migration probability on the logit scale. Note that our weekly survival estimates are conditional on a bird being observed during the autumn migration period at least once, thus excluding birds that died or emigrated between their initial capture and before the end of July.

To facilitate interpretation of migration departure timing of the population, we extrapolated our weekly migration probabilities over the second half of the year (from late July to the end of December) with a cumulative distribution function and estimated what proportion of the woodcock population would remain in the study area at the beginning of each week. For each posterior MCMC sample, we generated a starting population of 1000 woodcocks, and then used the estimate of weekly migration probability to randomly draw the number of woodcocks that would have migrated every week from a binomial distribution. We used this extrapolation to derive the date when 95% of the simulated local woodcock population had departed the study area, and assumed that this timing was consistent across Switzerland (including cantons in which we did not track any individuals). We also provide the estimated proportion of local woodcocks remaining in the study area for several key dates that were valid at the time of our study, namely, the 16 September (beginning of hunting season by federal law, and in the cantons of Jura and Neuchâtel), 1 October (beginning of hunting season in Bern and Valais), 15 October (beginning of hunting season in Fribourg since 2009, Ticino and Vaud since 2014) and 15 November (by which time 95% of the annually reported hunting bag of woodcocks have been shot; Bohnenstengel et al., 2021). Note that cantonal hunting regulations

can change annually, and hunting season dates are indicative only and reflect the regulations during years of our study.

2.6 | Assessing origin of hunted woodcocks using feather hydrogen isotopes

To quantify what proportion of woodcocks shot in Switzerland were not from the local breeding population, we used the natural geographic variation in hydrogen isotope ratios (Bowen et al., 2005; Hobson et al., 2004). Between 2013 and 2018, we encouraged hunters to sample the first secondary feather of each shot woodcock. Adult woodcocks generally moult secondary feathers on their breeding grounds in July and August, and young birds do not moult their secondary feathers until they breed; hence these feathers of young birds were grown at the place where the birds hatched (Glutz von Blotzheim et al., 1986). The isotopic composition of the first secondary feather should therefore reflect the environment in the breeding area of the sampled bird (Hobson, Van Wilgenburg, Ferrand, et al., 2013; Hobson, Van Wilgenburg, Guzmán, & Arroyo, 2013; Powell et al., 2026). For calibration purposes, we additionally sampled 207 feathers from known-origin birds caught during the breeding season between 2002 and 2018 at 29 breeding locations across Norway, Sweden, Finland, Estonia, Latvia, Belarus, Russia, Germany, Switzerland, Spain and the UK (Figure S3, Powell et al., 2026). These feathers included both innermost primaries and first secondaries, but were all likely grown in the region where the bird was captured and thus provided isotope samples of 'known origin'.

Collected feathers were stored individually in a dry envelope and analysed for hydrogen isotope measurements ($\delta^2\text{H}$) at the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. We removed contaminants from feathers by soaking samples in a 2:1 chloroform:methanol solution and dried for at least 10 days under a fume hood (Bowen et al., 2005). We weighed similar masses of feather samples and reference materials in silver capsules, which were then pyrolysed at 1350°C in a high-temperature elemental analyser (HTO Elementaranalysator HEKAtech GmbH Analysentechnik, Wegberg, Germany) containing a silicon carbide (SiC) tube with glassy carbon chips. The resolved H_2 sample gas, separated from N_2 and CO using a GC column at 80°C, was introduced into the isotope ratio mass spectrometer (Delta V Advantage IRMS, ThermoFisher Scientific, Bremen, Germany). Stable hydrogen isotope values were expressed in the delta notation as per mil (‰) deviations from the international standard Vienna Standard Mean Ocean Water (VSMOW). Using in-house keratin reference materials (RMs) with assigned stable isotope values of the non-exchangeable portion of hydrogen, we report stable isotope values of the non-exchangeable hydrogen in fur keratin via the comparative equilibration method (Wassenaar et al., 2023). The assigned $\delta^2\text{H}$ values of these keratin RMs were normalized against the recent values for USGS42 (−72.9‰), CBS (−157.0‰) and KHS (−35.3‰) RMs (Coplen & Qi, 2016; Soto et al., 2017; Wassenaar et al., 2023). $\delta^2\text{H}$ values of in-house RMs averaged −111.7‰

(SWE-SHE), -61.5‰ (ESP-SHE) and -26.4‰ (AFR-GOA). Analytical precision based on the repeated analyses of keratin RMs was better than 2‰ (1 SD).

Details on the preparation of the in-house keratin RMs are described in Popa-Lisseanu et al. (2012) and Voigt and Lehnert (2019). Feather $\delta^2\text{H}$ data from known-origin samples were extracted from Powell et al. (2026), analysed at the Natural Environment Research Council Life Sciences Mass Spectrometry Facility, East Kilbride, UK. All datasets from both labs were adjusted to current 'assigned' keratin isotope values of the RMs with the following equation (Soto et al., 2017): revised $\delta^2\text{H} = 10.774 + 0.852 \times \delta^2\text{H}_{\text{previous_data}}$.

We used the feather hydrogen isotope values to estimate the probability that shot woodcocks may have represented local birds. Because Switzerland is a topographically diverse country and hydrogen isotope values in rainwater decrease with both elevation and latitude, certain hydrogen isotope values in woodcock feathers could reflect origin areas either in Switzerland or in north-eastern Europe (Bowen et al., 2005; Hobson et al., 2004; Hobson, Van Wilgenburg, Ferrand, et al., 2013). We therefore constructed a model that estimated the probability of a shot woodcock to be of non-local origin, while accounting for uncertainty in isotopic measurements, the relationship between hydrogen isotope values measured in rainfall and in woodcock feathers (Hobson, Van Wilgenburg, Ferrand, et al., 2013; Hobson, Van Wilgenburg, Guzmán, & Arroyo, 2013; Powell et al., 2026), and the timing and location where a woodcock was shot.

This model first estimated an age-dependent linear relationship between hydrogen isotope values in woodcock feathers and the average annual rainfall isotope values at the location where woodcocks of known origin were sampled ($n=207$). We used the R package IsoriX (Courtiol et al., 2019) to generate annual rainfall hydrogen isoscapes across Europe (Figure S3) based on measured hydrogen isotope values in rainfall obtained from the Global Network of Isotopes in Precipitation (GNIP) of the International Atomic Energy Agency (IAEA/WMO 2025, <https://www.iaea.org/services/networks/gnip>, accessed 12 October 2025). We then related the measured hydrogen isotope values in woodcock feathers to the rainfall hydrogen isotope values at the location where, and in the year when, a woodcock was sampled, using a simple linear model with a Gaussian error distribution, while accounting for the age of the bird (adult or juvenile).

To assess whether shot birds of unknown origin could have come from the local population, we used the location where each bird was shot and generated a plausible feather hydrogen isotope value distribution for that location. This distribution was based on the average annual rainfall hydrogen isotope value at that location in that year, and on the above calibration equation. Similarly, we generated a feather isotope value distribution for the entire breeding range of woodcocks in north-eastern Europe in the same year following the approach of Hobson, Van Wilgenburg, Ferrand, et al. (2013). We overlaid a global forest cover map (ESA & UCL, 2011) with the polygons of countries where woodcocks occur (BirdLife International, 2021),

extracted the average annual rainfall hydrogen isotope values across all suitable forest areas from where woodcocks could have originated (to the N and E of Switzerland, below elevations of 2200m a.s.l., Figure S4), calculated the mean and standard deviation of these values and then applied the above calibration equation to obtain a feather isotope value distribution for adult and for juvenile woodcocks from across Europe. We then estimated the probability of a shot woodcock to be derived from either the general European distribution (hereafter referred to as 'non-local') or the local population, based on the measured feather isotope value of the shot woodcock and the two isotope value distributions (local and non-local) specified above.

We used a Bayesian framework for parameter estimation and inference to facilitate the inclusion of different prior information about the potential origin of shot woodcocks. We explored three sets of prior information in three separate assignment analyses, where the probability of non-local origin was informed for each shot woodcock by (1) the empirically estimated migration phenology (hereafter 'migration prior'); (2) the maximum of the estimated migration phenology and an abundance index-derived probability (hereafter 'abundance prior'), and (3) by using an uninformative vague prior (beta distribution with $\alpha=2$ and $\beta=2$) for each age group per canton (hereafter 'null prior'). The prior of migration phenology was based on the probability for local birds to have departed on migration at the time of harvest derived from our migration departure model (see Section 2.5 above). The prior abundance probability was based on the fact that the probability to shoot a woodcock of local origin will decline over the course of a season when many migratory birds arrive and the number of local birds is diluted by the influx of migrants (Royle & Rubenstein, 2004; Figure S5). To account for this dilution effect, we used the phenological abundance distribution of woodcocks in Switzerland derived from citizen-science observations and robust abundance indices available for 5-day periods (Korner-Nievergelt et al., 2022; O'Reilly et al., 2025; Strebel et al., 2022). We fit a generalized linear model to this abundance index over the time frame of the hunting period, and used the predicted response divided by the maximum predicted response as the prior probability of non-local origin for each shot woodcock derived from the day it was shot.

The first analysis ignores overall abundance of woodcocks in Swiss forests, and results from this analysis are therefore conservative because they do not account for the dilution effect, while the second analysis makes the most use of independent information about the abundance and migration phenology. The third analysis is only informed by feather isotope values and therefore forms a baseline assignment in the absence of any prior information. In addition to the priors for the probability of non-local origin, we also used informative priors for the intercept (normal with mean = -13 and standard deviation = 20), age effect (normal with mean = -24 and standard deviation = 35) and rain effect (normal with mean = 0.2 and standard deviation = 1) for the linear calibration model relating rainfall to feather isotope values from

a similar calibration of woodcock feathers in NW Europe (Powell et al., 2026).

We fit these three assignment models in Nimble (de Valpine et al., 2016) with the same MCMC specifications as for the multistate model above, and used all posterior estimates for our assessment of the geographic origin of shot birds of unknown origin, thus ensuring adequate error propagation that ultimately affects the estimated certainty of origin. We summarized the proportion of birds of non-local origin by age group (adult and juvenile) and by the six cantons in which woodcocks were shot in this study. For each group we present median posterior estimates with 95% credible intervals for the probability to be of non-local origin, and we caution that this probability is conservative: areas in Europe that have similar rainfall hydrogen isotope values as the local area where a bird was shot cannot be distinguished based on feather isotope values, and birds originating from such regions would therefore contribute to the probability to be of local origin (Figure S4). However, the advantage of our models is that all uncertainty (in calibration, timing and origin) is accounted for and therefore evident in the resulting probability estimates. All code and data to replicate the analyses are available online (Oppel et al., 2026).

3 | RESULTS

We marked 472 individual woodcocks in the study area between 2005 and 2018, of which 18 were recovered dead inside the study area (8 of which had been shot) and 89 were recovered dead (all shot) outside the study area (Table S1).

3.1 | Departure timing

For the analysis of migration timing, we retained data from 82 individuals marked during the breeding season and recorded at least once during the migration season, which yielded 110 woodcock-years of data. The last confirmed location when these individuals were observed alive in the study area ranged from 1 August to 22 November (Figure S1).

The probability to depart the study area increased with every week ($\beta=0.400$, 95% credible interval 0.299–0.511), and 95% of the population had departed the study area by 7 December (28 Nov–18 Dec). The proportion of the local population that remained inside the study area on 16 September was 97% (93%–99%), on 1 October 93% (86%–97%), on 15 October 86% (76%–93%), and on 15 November 36% (22%–51%; Figure 1). Thus, >50% of local woodcocks were exposed

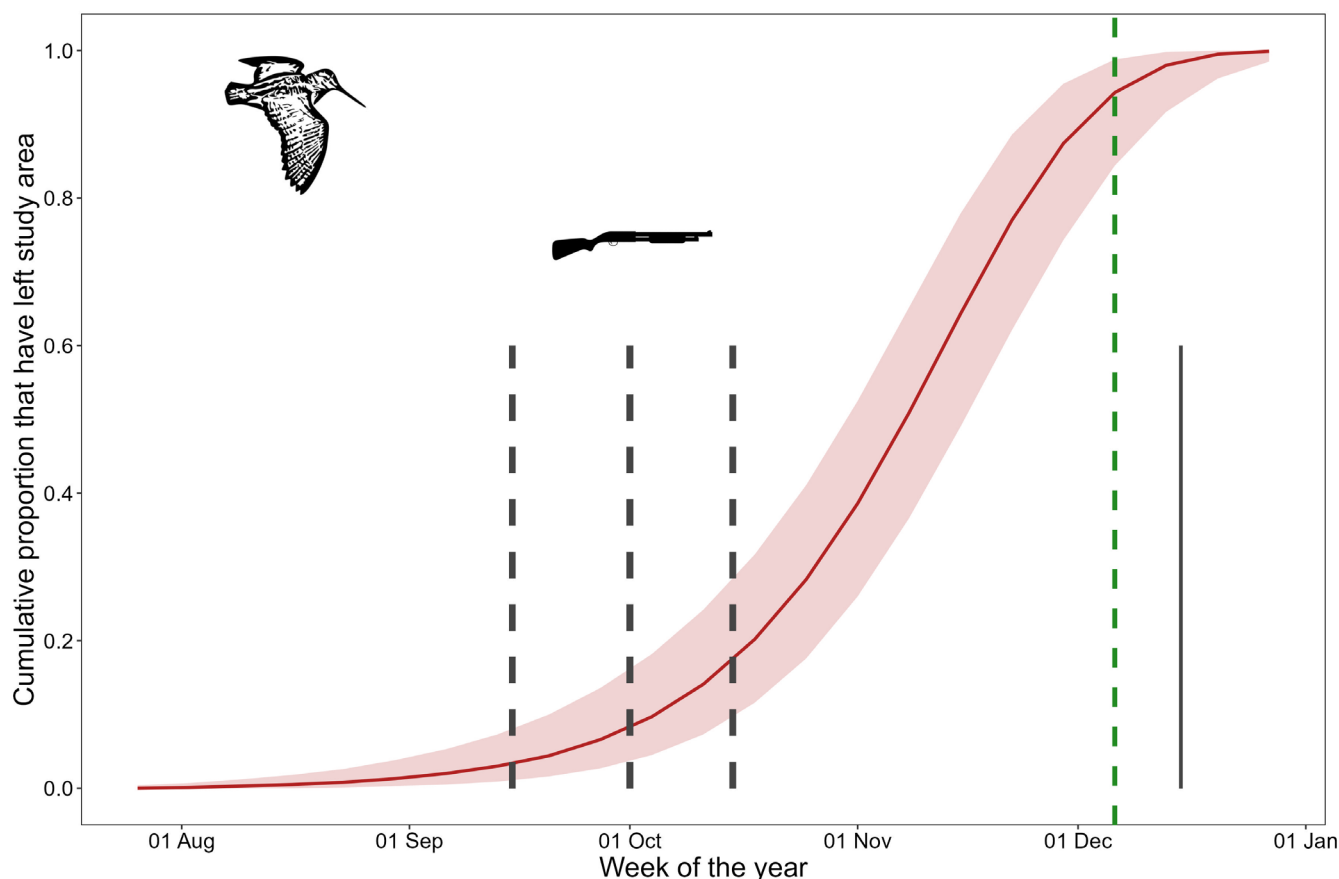


FIGURE 1 Predicted proportion of woodcocks that had departed our study area in Switzerland per given week of the year based on estimates of a multistate model taking detection probability, survival and state uncertainty into account ($N = 110$ woodcock-years). Dashed black vertical lines indicate the beginning of the hunting seasons in different administrative regions (16 September, 1 October, 15 October), which ends on 14 December (solid grey line). The green dashed line indicates the time when 95% of the local breeding population had departed the study area (7 December).

to hunting pressure during the legal hunting season applied in all cantons between 15 October and 15 November.

Our model estimated that weekly survival probabilities varied between 0.971 (0.954–0.986) and 0.994 (0.985–1) among years of our study.

3.2 | Probability of origin

We sampled feathers from 72 woodcocks of known origin (61 adults, 11 juveniles) in NW Switzerland, and stable hydrogen isotope values in these feathers ranged from -53.2‰ to $+2.0\text{‰}$, with a mean of -15.9‰ . The stable hydrogen isotope values in secondary feathers of 842 shot woodcocks of unknown origin (187 adults, 645 juveniles) ranged from -94.3‰ to -3.0‰ , with a mean of -54.9‰ (Figure S2). These birds represented 8.7% of the woodcocks shot by hunters in Switzerland between 2013 and 2017 ($n=9681$, www.jagdstatistik.ch). These woodcocks were mostly shot at elevations around 1000m, with a range from 358 to 2596m a.s.l. (only two birds were shot above 2200m).

The estimated proportion of non-local origin was largely dependent on whether the migration phenology was included in the prior probability of non-local origin. Most woodcocks were shot at a time when less than half of the tracked local birds had migrated (Figure S5), thus leading to maximum ambiguity about the origin of shot woodcocks (Figure 2). Our first analyses, which used only migration timing in the prior probability of non-local origin, estimated proportions of non-local origin of 14.9% of adults (1.6%–52.7%) and 15.5% of juveniles (1.9%–46.2%; Figure 2). Our second analysis that included local abundance phenology as prior information estimated that on average 88.9% of adults (95% credible interval 44.2%–99.8%) and 90.6% of juveniles (50.1%–99.8%) were of non-local origin (Figure 2), because non-local migrants greatly outnumber Swiss breeders in autumn (Figure S5). The third model, which did not use any prior timing information, estimated mean proportions of non-local origin of 84.9% of adults (19.4%–99.1%) and 59.2% of juveniles across all cantons (11.1%–96.6%; Figure 2).

4 | DISCUSSION

In areas where local and migratory woodcocks co-occur during migration, sustainable hunting management requires estimates about the origin of hunted individuals. Our study provides the first robust estimate of autumn migration timing for Swiss-breeding woodcocks and demonstrates that most local individuals are still present during the legal hunting season. Nonetheless, by integrating multiple sources of information, we estimated that >50% of the woodcocks shot in Switzerland were likely not of local origin, although this estimate was surrounded by considerable uncertainty that was introduced by the late departure of locally breeding woodcocks. The relatively low proportion of local birds shot is likely a fortuitous consequence of the dilution effect caused by the influx of more

numerous non-local individuals in autumn. However, we caution that assigning shot individuals to a specific origin based on feather hydrogen isotopes and timing was too uncertain in Switzerland to inform management decisions, and we suggest that protecting local individuals from hunting pressure is only possible by adequate curtailment of the hunting season.

Although our assignment probabilities are uncertain, the sheer quantity of birds that were shot in Switzerland renders it highly unlikely that most of the shot birds could originate from the rather small breeding population in Switzerland (Royle & Rubenstein, 2004). Our raw data show that only 2% of our individually marked birds were shot in Switzerland (Table S1), and that hydrogen isotope values of shot woodcocks of unknown origin were generally very depleted compared with sampled birds of known Swiss origin (Figure S2), which is therefore consistent with the estimated small proportion. Previous attempts to assign shot woodcocks in France, Spain, and the UK to their origin based on $\delta^2\text{H}$ in feathers appeared more precise due to lower levels of variation in the relationship between rainfall and feathers (Hobson, Van Wilgenburg, Ferrand, et al., 2013; Hobson, Van Wilgenburg, Guzmán, & Arroyo, 2013; Powell et al., 2026). By accounting for the topographic complexity in Switzerland and the associated uncertainties, we found the isotopic assignment approach to be less certain. Large areas outside Switzerland where woodcocks breed have similar rainfall hydrogen isotope values as some of the higher elevation breeding areas within Switzerland (Figure S4). Our estimate of 'local origin' is therefore conservative in that not all birds with feather isotope values that reflect the local rainfall isotope values necessarily bred in Swiss forests. The high variability in average annual rainfall hydrogen isotope values across the elevational gradient of woodcock habitats in Switzerland renders the geographic assignment of woodcocks shot in Switzerland based on feather hydrogen isotope values extremely challenging, and additional markers or samples of known origin from high elevation forests would be necessary to more reliably assign shot individuals to their origin.

By contrast, our estimate of migration timing was precise (Figure 1) and consistent with the known migratory behaviour of woodcocks (Clements et al., 2024; Coon et al., 1976; Tedeschi et al., 2019). Woodcocks in Switzerland started to migrate in early September, but a large part of the population remained in the breeding areas until early November. In Mediterranean countries and Great Britain, most woodcocks arrive in November or December (Birtsas et al., 2013; Duriez, Fritz, et al., 2005; Guzmán et al., 2017; Hoodless et al., 2020; Hoodless & Heward, 2019), and this timing matches with our estimated peak departure time of late October and early November. Thus, at the time when woodcock hunting is permitted, more than half of the locally breeding woodcocks were still present on their breeding grounds. Based on the timing of migration of our marked birds, any woodcock hunting in Switzerland prior to 15 November exposes a considerable proportion of local woodcocks to hunting pressure. A further delay of the hunting season to winter (mid-December to January), as is the case in other countries

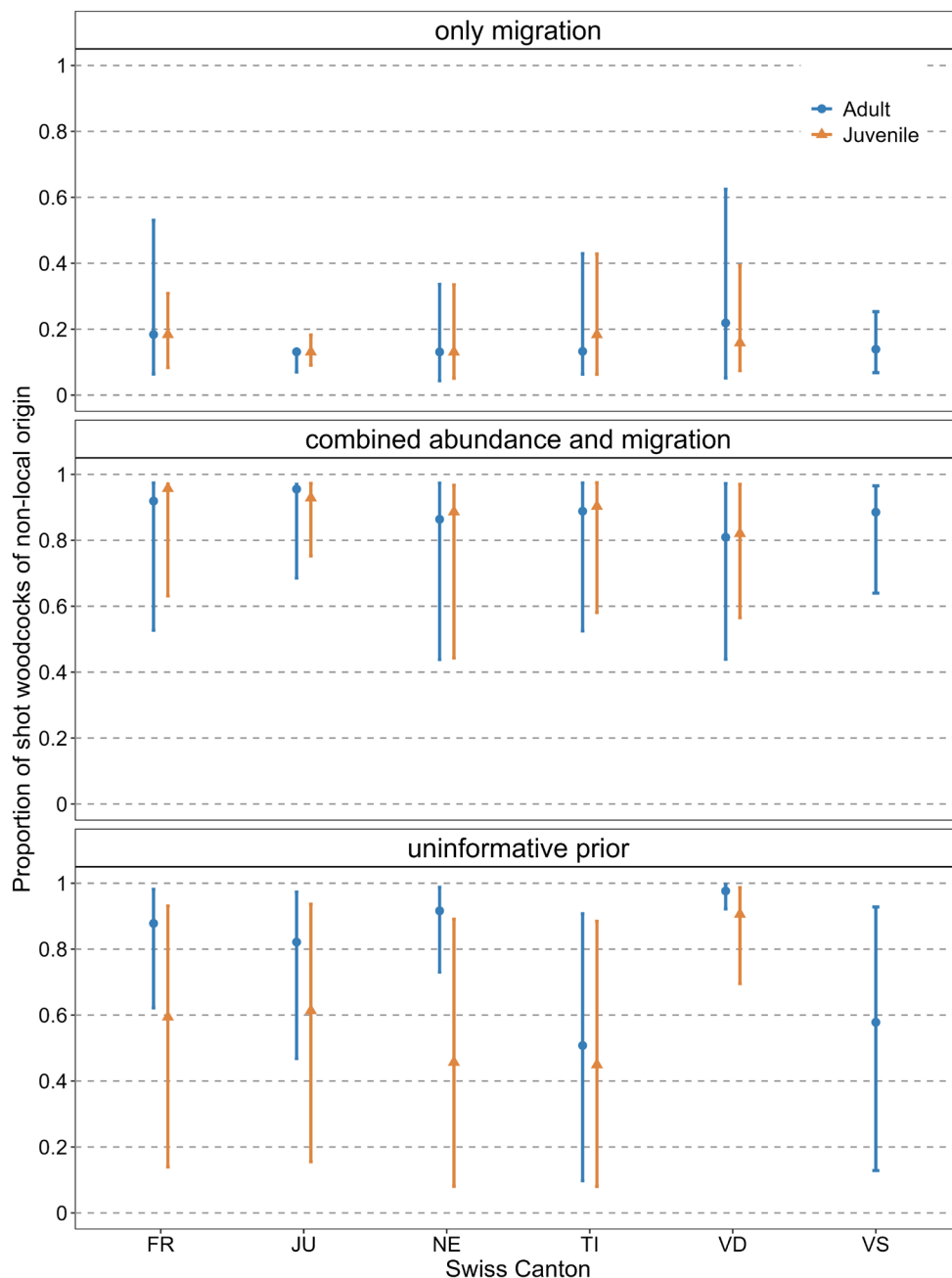


FIGURE 2 Estimated median ($\pm 95\%$ credible interval) proportion of shot woodcocks from a non-local origin across six Swiss cantons (JU=Jura, NE=Neuchatel; BE=Bern, VS=Valais, FR=Fribourg, TI=Ticino, VD=Vaud) for adult (blue) and juvenile (orange) age groups based on feather hydrogen isotope values and the location and time when each bird was shot. Top panel shows estimates when prior probability is only informed by migration timing (Figure 1), central panel shows estimates when prior probability is informed by both migration timing and general abundance phenology, and bottom panel shows estimates based solely on feather isotopes without informative prior. Note that the credible intervals encompass uncertainty in both the measurement and isotopic discrimination processes, as well as the similarity in rainfall hydrogen isotope values between each canton and other potential origin areas in Europe (Figure S4).

(McKinlay et al., 2026; McNicol et al., 2024), could reduce this exposure of Swiss woodcocks to hunting mortality in Switzerland.

While the late migration timing exposes Swiss-breeding woodcocks to hunting mortality in Switzerland, the impact of this local mortality on the breeding population is likely relatively small due to the influx of migratory individuals. For woodcocks, the mortality imposed by hunting is additive to natural mortality (Duriez, Eraud,

et al., 2005), and survival of woodcocks is often directly related to hunting effort (Bruggink et al., 2013; Péron et al., 2011a; Prieto et al., 2019). Across all years, 20% of our individually marked birds were reported shot, but >90% of the hunting mortality of our marked individuals occurred abroad (Table S1). This highlights the difficulty of protecting migratory species that are threatened by unsustainable hunting levels, where coordination along the flyway

is necessary to ensure viable populations (Carboneras et al., 2024; Lormée et al., 2020).

Swiss hunting regulations have been designed with the idea to reduce hunting pressure on local birds, and therefore implicitly consider the shooting of non-local 'migrants' as appropriate. If each country along the flyway implements hunting regulations that protect only local breeding birds, most breeding populations of a migratory species like the woodcock may be adversely affected by hunting mortality along the flyway (Andreotti et al., 2023). Targeting non-local birds along a flyway also means that no country has the agency to regulate the hunting mortality that affects its respective breeding population. Following our field investigation and an initial report (Bohnenstengel et al., 2021), the hunting regulations in several cantons of Switzerland were changed to postpone the beginning of the hunting season by 2–4 weeks to reduce the probability to shoot local woodcocks. While this may afford somewhat greater protection to Swiss woodcock populations, it does not reduce the hunting pressure on other populations, unless harvest limits are also revised (McNicol et al., 2024). Most of the hunting mortality of Swiss woodcocks occurred abroad in France and Spain, where Swiss woodcocks are considered 'migrants'. If hunting mortality affects the viability of Swiss woodcock populations, some international collaboration with these countries would be required. This collaboration is unlikely to materialize if one country that allows hunting of non-local migrants expects other countries to protect non-local migrants. Coordination of hunting regulations along the flyway can be highly effective, as is demonstrated by the rapid recovery of another hunted migratory bird species (European Turtle-dove *Streptopelia turtur*) following a flyway-level moratorium (Carboneras et al., 2024).

5 | CONCLUSIONS

The influx of many non-local-origin woodcocks into Swiss forests after September likely reduces the probability that a woodcock shot at that time is of local Swiss origin. However, the determination of the origin of shot woodcocks based on timing and feather hydrogen isotope values is surrounded by large uncertainty unless additional markers could be used or known-origin samples from high elevation forests were available. Therefore, the proportion of shot birds that are of non-local origin cannot be reliably quantified to evaluate whether hunting mortality in Switzerland affects the sustainability of local breeding populations. We recommend that our estimates of migration timing are considered when setting the dates during which woodcock hunting in Switzerland is legally permitted.

In addition, we emphasize that knowledge about woodcock population trends and dynamics is generally poor, and more investment in the development of reliable monitoring techniques is urgently needed (Heward et al., 2024; Mollet, 2015; O'Neill et al., 2026). Without robust data to understand the population dynamics and the effects of hunting mortality, the consequences of existing or potential alternative hunting regulations cannot be

quantified. A better understanding of sustainable harvest levels would be useful to coordinate hunting bags and regulations along the flyway (Lormée et al., 2020), because migratory species like the woodcock can rarely be effectively protected by regulations in any single country.

AUTHOR CONTRIBUTIONS

Pierre Mollet, Gilberto Pasinelli, Martin U. Gruebler and Lukas Jenni conceived the study. Steffen Oppel, Pierre Mollet, Thierry Bohnenstengel, Vincent Rocheteau, Christian C. Voigt and David X. Soto developed the methodology. Pierre Mollet, Thierry Bohnenstengel, Vincent Rocheteau, Benjamin Homberger, Adele Powell, Andrew N. Hoodless and Elizabeth Yohannes collected and curated the data. Steffen Oppel, Jaume A. Badia-Boher and David X. Soto analysed the data. Steffen Oppel prepared the visualizations and, together with Lukas Jenni, wrote the first draft of the manuscript. Pierre Mollet, Gilberto Pasinelli and Martin U. Gruebler supervised the project and coordinated project administration. Martin U. Gruebler and Lukas Jenni secured funding. All authors contributed to reviewing and editing the manuscript and approved the final version for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code to replicate the analyses are available at the Vogelwarte Zenodo Open Repository (Oppel et al., 2026): <https://doi.org/10.5281/zenodo.20734330>.

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SUPPORTING INFORMATION

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

Table S1. Numbers of individual woodcocks that were ringed, equipped with a tracking device, found dead, shot and never re-recorded between 2005 and 2018 in Switzerland split by the time when they were captured and marked (note that not all birds marked during the migration season were necessarily migratory individuals).

Table S2. Numbers of individual woodcocks that were ringed per year of the study period in Switzerland.

Figure S1. Proportion of individually marked woodcocks that were last observed in a given week of the year in the study area in Switzerland shown for either confirmed local breeders (marked between April and August, blue) or all birds (which may have included migratory individuals, orange). Woodcocks were marked with rings or with transmitters and the last recorded observation of an individual depends on the effort and probability of detection and is therefore the earliest possible time when migration may have occurred. Dashed lines indicate median date of last observation for each group.

Figure S2. Frequency distribution of hydrogen isotope values ($\delta^2\text{H}$ in ‰) of woodcock secondary feathers sampled in Switzerland between 2013 and 2018, based on their origin: orange bars reflect birds of unknown origin collected by hunters throughout Switzerland ($n=842$), blue bars represent birds sampled during the breeding season with feathers of known origin in north-western Switzerland ($n=72$).

Figure S3. Map of sampling location of 207 woodcock feathers obtained at known breeding areas of woodcocks across Europe (red points) and used to calibrate the relationship between mean annual precipitation and feather hydrogen isotope values. Underlying colour gradient shows the distribution of average annual rainfall hydrogen isotope values in potential origin areas of woodcocks for the year 2017 (note that areas without forest and above 2200m are white, as are countries that are not the focus of this study).

Figure S4. Parts of the woodcock's European distribution where hydrogen isotope values of annual precipitation may encompass the rainfall hydrogen isotope values at the locations where woodcocks were shot in Switzerland (red dots). The colour scale indicates the probability that the local rainfall hydrogen isotope value is equal to or higher than the rainfall hydrogen isotope value at sampled sites in Switzerland (red dots), and if this probability is very high (dark colour) then feather isotope values of woodcocks may be indistinguishable from local birds. Birds originating from areas approaching a probability of 1 may therefore erroneously be considered of 'local' origin in our assessment (JU=Jura, NE=Neuchatel; BE=Bern, VS=Valais, FR=Fribourg, TI=Ticino, VD=Vaud).

Figure S5. Temporal distribution of the harvest date of 842 woodcocks in Switzerland between 2013 and 2018 (grey bars), overlaid with the general abundance phenology (blue line) derived from citizen-science data and the probability of local birds to have

departed on migration (orange line) derived from our data and model (Figure 1). Note that most woodcocks are shot at a time when around 40%–60% of local birds have departed, thus leading to maximum ambiguity in the assignment of origin based on migration timing.

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