



Migratory connectivity in a declining bird species: using feather isotopes to inform demographic modelling

Thomas S. Reichlin^{1,2*}, Keith A. Hobson³, Leonard I. Wassenaar³, Michael Schaub^{1,2}, Dirk Tolkmitt⁴, Detlef Becker⁵, Lukas Jenni² and Raphaël Arlettaz^{1,2}

¹Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland,

²Swiss Ornithological Institute, CH-6204

Sempach, Switzerland, ³Environment Canada, 11 Innovation Blvd., Saskatoon, SK, Canada,

⁴Menckestrass 34, D-04155 Leipzig,

Germany, ⁵Museum Heineanum, Domplatz 36, D-38820 Halberstadt, Germany

ABSTRACT

Aim Conservation programmes for endangered migratory species or populations require locating and evaluating breeding, stopover and wintering areas. We used multiple stable isotopes in two endangered European populations of wrynecks, *Jynx torquilla* L., to locate wintering regions and assess the degree of migratory connectivity between breeding and wintering populations.

Location Switzerland and Germany.

Methods We analysed stable nitrogen ($\delta^{15}\text{N}$), carbon ($\delta^{13}\text{C}$) and hydrogen (δD) isotopes from wing feathers from two populations of wrynecks to infer their wintering origins and to assess the strength of migratory connectivity. We tested whether variation in feather isotopic values within the Swiss population was affected by bird age and collection year and then considered differences in isotopic values between the two breeding populations. We used isotopic values of summer- and winter-grown feathers to estimate seasonal distributions. Finally, we calculated a species-specific δD discrimination factor between feathers and mean annual δD values to assign winter-grown feathers to origin.

Results Bird age and collection year caused substantial isotopic variation in winter-grown feathers, which may be because of annually variable weather conditions, movements of birds among wintering sites and/or reflect asynchronous moulting or selection pressure. The large isotopic variance in winter-grown feathers nevertheless suggested low migratory connectivity for each breeding population, with partially overlapping wintering regions for the two populations.

Main conclusions Isotopic variance in winter-grown feathers of two breeding populations of wrynecks and their geographical assignment point to defined, albeit overlapping, wintering areas, suggesting both leapfrog migration and low migratory connectivity. On this basis, integrative demographic models can be built looking at seasonal survival patterns with links to local environmental conditions on both breeding and wintering grounds, which may elucidate causes of declines in migratory bird species.

Keywords

Africa, annual climatic variation, isotopic variation (carbon-13, nitrogen-15, deuterium), *Jynx torquilla*, leapfrog migration, long-distance migrant, species conservation.

*Correspondence: Thomas S. Reichlin, Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland. E-mail: thomas.reichlin@iee.unibe.ch

INTRODUCTION

A thorough understanding of population dynamics of migrating animals calls for estimates of seasonal survival (Runge &

Marra, 2005), which requires knowledge of an animal's whereabouts during the different stages of its life cycle (Hobson, 1999). Identifying these areas and understanding the degree to which these are geographically linked (i.e.

migratory connectivity *sensu* Boulet & Norris, 2006) is challenging, but crucial to build integrative population dynamical models that promote sensible conservation actions for endangered species and populations (Webster *et al.*, 2002; Rubenstein & Hobson, 2004; Webster & Marra, 2005).

Naturally occurring geographical variations in stable isotope (e.g. ^{13}C , ^{15}N , ^2H) characteristics of landscapes and their associated biological substrates can be used to interpolate animals to approximate geospatial origins (Hobson & Wassenaar, 2008). Stable isotope values in dietary substrates may exhibit clinal changes across continents or among ecozones forming spatially continuous or discrete 'isoscapes' (Hobson, 2005a; West *et al.*, 2006). Local biomass isotopic values are translated through the food web (DeNiro & Epstein, 1981) and fixed into animal tissues (e.g. feathers). As a result, stable isotope measurements of some tissues can be used as geospatial markers of an organism's origin, which allows inferring wide-scale movements (Chamberlain *et al.*, 1997; Hobson & Wassenaar, 1997, 2008; Hobson, 2005a; Norris *et al.*, 2006).

For birds, stable isotope values remain fixed in feathers following their formation (Hobson & Wassenaar, 2008), thus these intrinsic isotopic markers can provide information about a bird's previous moult location. Moreover, moult origin information can be obtained non-invasively using feathers without the bias and cost associated with conventional mark-recapture methods (e.g. ring recoveries are usually biased towards populated areas, or associated with a huge recapture effort (time and money), especially in remote places; Wassenaar & Hobson, 2001; Hobson, 2008). Finally, provided that the moult timing and pattern of a species is known, simultaneous sampling of several generations of feathers from the same individual offers a unique opportunity to collect, on a single capture event, information on two or even more previous moult locations (the number of potential locations basically depending on the number of feather generations available on one individual).

In avian studies, stable isotope values of hydrogen (δD), nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) have been used to investigate migratory connectivity (e.g. Chamberlain *et al.*, 1997; Evans *et al.*, 2003; Mazerolle *et al.*, 2005; Procházka *et al.*, 2008; Hobson *et al.*, 2009), metapopulation structure (e.g. Chamberlain *et al.*, 2000) and to locate stop-over sites (e.g. Yohannes *et al.*, 2007). With the help of species-specific isotopic basemaps and isotope-specific diet-tissue discrimination factors, feathers can be assigned approximately to geospatial origin (e.g. Greenberg *et al.*, 2007; but see Wunder & Norris, 2008). Isotope discrimination factors account for the difference between environmental and tissue isotopic values because of metabolic stable isotope enrichment or depletion that occur during transfer along the food chain (Hobson & Clark, 1992; Hood-Nowotny & Knols, 2007; reviewed in Caut *et al.*, 2009), although the relationship between geographical location and discrimination factors is likely nonlinear and differ among species or species groups (Wunder, 2009).

The application of stable isotope measurements to assign an individual to a place of origin using isoscapes has typically

assumed that inter-annual isotopic variation in the base of the food web is fairly small (Hobson, 2005b). For deuterium, in both North America and Europe, feather δD values correlate well with decadal scale weighted average growing season δD values in rainfall from the IAEA Global Network of Isotopes in Precipitation (GNIP; summarized in Hobson, 2008). However, little is still known about intra-annual variation in δD values in most species and especially at low trophic levels. Intra-annual variation in stable isotope values of biota is presumed to be attenuated relative to variation in rainfall because of seasonal averaging that takes place in food webs (Yohannes *et al.*, 2008).

Global variation in $\delta^{13}\text{C}$ isoscapes depends on the predominant photosynthetic pathway and water-use efficiency effects and is therefore primarily dictated by vegetation type and climate (environments with predominantly C3-, C4- or CAM-plants with typical $\delta^{13}\text{C}$ values of $-27 \pm 2\text{‰}$, $-13 \pm 1.2\text{‰}$, -10 to -20‰ , respectively) (O'Leary, 1988; Hood-Nowotny & Knols, 2007; Bowen & West, 2008). Variation in plant $\delta^{15}\text{N}$ values is generally dependent on the type of biome (e.g. ^{15}N enriched in arid regions and depleted in wet regions, Koch *et al.*, 1995 and references therein) and the complexity of N fluxes and the anthropogenic fingerprint in a biome (N-fixation, atmospheric and anthropogenic N; Kendall *et al.*, 2007). In addition to geographical variation, within-site variation in $\delta^{15}\text{N}$ values of biota is highly dependent on the $\delta^{15}\text{N}$ values of the N source and the trophic level of the consumer (reviewed in Kelly, 2000).

So far, only a few studies have used multi-isotope geographical variation to investigate migratory connectivity in European birds (Pain *et al.*, 2004; Yohannes *et al.*, 2008). In this study, we used δD , $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values in feathers collected from two breeding populations of a Palearctic-African long-distance migratory bird, the wryneck *Jynx torquilla* L., to better understand migratory connectivity between its breeding and poorly known wintering grounds. Ring recoveries did not provide strong inferences about the winter grounds of European wrynecks because of low recoveries ($n = 121$) made mostly in Europe, with only a few findings in Africa (Reichlin *et al.*, 2009). However, the data while sparse are suggestive of a migratory divide across Europe: individuals breeding in the western part of the continent migrate to the south-west, while wrynecks from eastern Europe migrate south-eastwards. More precise estimates of wryneck winter locations is essential to better appraise the demographic processes operating during different phases of the annual cycle to inform appropriate conservation action.

Here, we first addressed possible causes of isotopic variation in wryneck feathers, with the following *a priori* hypotheses regarding (1) annual and (2) age-related variation: (1a) variation in weather (mainly amount and pattern of precipitation) could cause δD , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to vary between years, (1b) changes in wintering locations could lead to inter-annual isotopic variation. (2) Isotopic values could vary between age categories because different age classes could migrate to different wintering areas, feed on different prey, and/or moult at different times. We then studied feather C, N

and H isotopic variation between two geographically distinct breeding populations to assess migratory connectivity. Next, we compared the magnitude of isotopic variation between feathers grown on the breeding and wintering grounds to get a relative measure of the extent of the summer and winter range of the two populations (Bearhop *et al.*, 2004). Finally, we calculated a species-specific δD discrimination factor between feathers and mean annual precipitation δD , which we applied to winter-grown feathers to better delineate possible winter locations of the two wryneck populations.

METHODS

Study species and study sites

The wryneck is a small (*c.* 35 g) long-distance migrant, feeding almost exclusively on ground-dwelling ants (Freitag, 1996) and is the only migratory woodpecker of Europe. Wrynecks from the western Palaearctic breed from the boreal to Mediterranean zones and overwinter in the Mediterranean basin as well as south of the Sahara (Cramp, 1985). Yet, wintering locations for specific breeding populations remain largely unknown. In this study, we collected feathers from Swiss and German wryneck breeding populations. The study area (62 km²) in south-western Switzerland (Canton of Valais, 46°14' N, 7°22' E, 450–520 m.a.s.l.) is situated on the plain of the lower Rhône valley, which is characterized by intensive agriculture (predominantly fruit tree plantations and vineyards), and warm and dry summers. The study area (4.5 km²) in north-eastern Germany (Saxony-Anhalt, 52°01' N, 13°04' E, 140–175 m.a.s.l.) is a former military training area, now used as sheep and goat pasture, dominated by dry grassland with a continental climate on the lee side of the Harz mountains (for details see Becker & Tolkmitt, 2007). In both study areas, wrynecks frequently breed in nestboxes.

Feather sampling

In April 2005 and 2006, Swiss wrynecks in the pre-breeding phase or still on passage were mist-netted using tape-luring with their territorial song. Later in May–July, breeding birds (in both Switzerland and Germany) were either directly taken off the brood (but never from the clutch), or caught with mistnets or traps at nestbox entrance. All captured birds were aged according to the moulting pattern as second-year (SY) or older than second-year birds (adults: AD), and feather samples were collected [2005: $n_{\text{Swiss}} = 66$; 2006: $n_{\text{Swiss}} = 73$ (of which nine were recaptures from 2005), $n_{\text{German}} = 21$]. Of 130 Swiss and 21 German birds, 20.8% and 14.3%, respectively, were ringed as nestlings in the study areas, 39.2% and 33.3%, respectively, were ringed as adults in other than the collection year, and 40% and 52%, respectively, were newly ringed in the study areas.

The moulting pattern of Eurasian wryneck differs between SY and AD (Glutz von Blotzheim & Bauer, 1980). In the breeding area, SY birds usually carry feathers of three

generations: (1) juvenile feathers, usually the secondary feathers S3 and S4 (counted in ascending order) as well as primary coverts; (2) feathers from the post-juvenile moult of the previous summer (primaries and contour feathers); and (3) winter-grown secondaries S5–S6 and tertials S7–S9. A reliable ageing criterion for SY birds is thus the presence of S3 or S4 from the juvenile plumage, two feathers which are longer and more pointed compared to adjacent secondaries which are moulted in winter. Adults undergo a complete post-breeding moult in the breeding area, whereas in the wintering quarters, they perform a partial moult including body feathers, wing coverts with part of the primary coverts, and usually secondaries. On the breeding grounds, the partially moulted primary coverts are a reliable ageing criterion for AD. In both age categories, we clipped either a piece of the inner vane (2.5–3 cm) or the whole feather tip (2 cm) of S6 (or if S6 was not available S5, $n = 3$) as this feather has an isotopic value representing the winter moulting location in both age classes ($n_{\text{Swiss}} = 139$, $n_{\text{German}} = 21$). In SY Swiss birds, we additionally collected a piece of S3 or S4, which represent isotopic values of the summer natal location ($n = 35$). All feathers were stored in individually labelled paper envelopes until further analysis.

Stable isotope analysis

Feather samples ($n = 195$) were triple washed with 2:1 chloroform/methanol solvent to remove surface oils and air-dried under a fume hood for ≥ 12 h (e.g. Hobson *et al.*, 2009). Approximately 0.35 ± 0.01 mg of feather material was weighed into small silver cups, and the relative abundance of deuterium (D/H) was measured with the comparative equilibrium method (H_2 derived from high-temperature flash-pyrolysis and CF-IRMS; described in detail by Wassenaar & Hobson, 2003), which was referenced with calibrated keratin isotope materials. Three laboratory keratin standards (CFS, CHS, BWB with mean $\delta D \pm SD$ values of $-147.4 \pm 0.79\text{‰}$, $n = 5$, $-187 \pm 0.56\text{‰}$, $n = 5$ and $-108 \pm 0.33\text{‰}$, $n = 5$, respectively) were used to control for the isotopic exchange between samples and ambient water vapour (Wassenaar & Hobson, 2000). All results are expressed in the usual delta (δ) notation, in units of per mil (‰):

$$\delta_{\text{sample}} = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where δ_{sample} is the isotope ratio of the sample relative to a standard, R_{sample} and R_{standard} are the proportions of heavy to light isotopes in the sample and standard, respectively. Deuterium measurements were normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW–SLAP) standard scale (Wassenaar & Hobson, 2003). Measurement error, based on a control keratin reference, yielded a 6-month running SD of 3.3‰ ($n = 76$). While our samples were more positive in δD than the range of keratin standards, a recent study has shown the resulting variance is small because of the exceptional linearity of isotope ratio mass spectrometers (Kelly *et al.*, 2009).

Stable carbon and nitrogen isotope ratios were measured from 0.5 mg of feather material weighed into small tin cups using standard flash combustion elemental analysis and isotope ratio mass spectrometry (Euro EA 3000; EuroVector Instruments, Milan, Italy). The results are presented in delta notation relative to Vienna Pee Dee Belemnite Standard (VPDB) for $\delta^{13}\text{C}$ and relative to atmospheric N_2 (air) for $\delta^{15}\text{N}$. Measurement errors were estimated at $\pm 0.1\text{‰}$ for $\delta^{13}\text{C}$ and $\pm 0.2\text{‰}$ for $\delta^{15}\text{N}$. All feather samples were prepared and analysed at the Environment Canada stable isotope laboratory in Saskatoon (SK, Canada).

Statistical analyses

We used an information-theoretical approach to check whether inter-year differences or bird age contributed more to the observed isotopic variance (Burnham & Anderson, 2002). We applied linear mixed effects models (with individual as random factor) to evaluate the influence of collection year and bird age on each isotope separately and tested all five possible models (including two-way interactions and the null model) resulting from these factors. Based on the Akaike Information Criterion for small sample sizes (AIC_c ; Burnham & Anderson, 2002), we selected the models which best described the variation in stable isotope measurements. Regarding the summer-grown feathers of Swiss wrynecks, we could only test for a year effect, as sufficient data were available only for SY birds. Furthermore, as too little feather material was available, we could only analyse deuterium in some of these feathers. All statistical analyses were performed in R Statistical Computing software (version 2.9; R Development Core Team 2009).

Differences in C, N and H isotopic values of winter-grown feathers between the Swiss ($n = 52$) and the German ($n = 21$) populations were analysed for each stable isotope with a two-sample Student's t -test. We only used data from AD caught in 2006, as the German data set contained no data from 2005 nor for SY birds from 2006.

To estimate the relative geographical extent of breeding vs. wintering ranges, we compared (F -Test) the C, N and H isotopic variances between summer- and winter-grown feathers in Swiss SY birds from 2006 (only this sample was large enough for this purpose). We expected the variation in isotopic values within summer breeding areas to be smaller compared to wintering areas, despite the potential diluting effect of natal dispersal into breeding populations. Eight of 35 individuals from which summer-grown feathers were available were born at the study site (based on ring information). The remaining 27 individuals (potential immigrants) had isotopic values comparable to the former eight birds (mean \pm SD of natal Swiss vs. potential immigrants: $\delta\text{D} = -81.1 \pm 8.9\text{‰}$ vs. $-80.1 \pm 9.5\text{‰}$; $\delta^{15}\text{N} = -23.1 \pm 0.2\text{‰}$ vs. $-22.7 \pm 0.5\text{‰}$; $\delta^{13}\text{C} = 9.0 \pm 1.2\text{‰}$ vs. $9.3 \pm 1.0\text{‰}$; statistically non-significant difference for all three isotopes with a α rejection value of 0.05). So, we assumed this diluting effect to be marginal because potential immigrants into the Swiss breeding population were likely to come from

nearby populations, which should cause little variation in isotopic values. In contrast, the variation in isotopic values of feathers grown in winter areas was expected to be much larger merely because of an *a priori* potentially wide geographical extension of the winter range. It must be pointed out, however, that the resolution of the reference isoscapes (i.e. isotopic variance in the environment, or spatial resolution of stable isotope measuring sites) may *per se* affect the outcome. For instance, a currently low resolution of the African isotope for deuterium, compared to the fine-grained isotope available for Europe (Bowen *et al.*, 2005), may bias the interpretations.

Isoscapes

Deuterium (mean annual, as well as mean growing season) in precipitation in Europe shows a gradual change from negative values in the north to more positive values in the south and at lower altitudes (Bowen *et al.*, 2005). There is a continuation of this cline into Africa, although the N–S gradient is less marked across the African continent, and it shows an additional increase in deuterium values from west to east in the north of the continent (see Fig. 6 in Bowen *et al.*, 2005). To calculate a species-specific discrimination factor, which is essential when assigning feathers to a place of origin, we compared known-origin $\delta\text{D}_{\text{feather}}$ values ($n = 8$, δD mean \pm SD = $-81.1 \pm 8.9\text{‰}$) with local mean annual $\delta\text{D}_{\text{precip}}$ values ($\delta\text{D} = -55.8\text{‰}$) retrieved from the Online Isotopes in Precipitation Calculator (OIPC, <http://www.waterisotopes.org>, and Appendix 1). We obtained a δD discrimination factor of -25.3‰ , which is very similar to the frequently applied discrimination factor introduced by Wassenaar & Hobson (2001, -25‰). Wunder & Norris (2008) have pointed to the use of probability surfaces and error propagation approaches to assignment of individuals using stable isotopes (see also Wunder, 2009). This approach has been shown to work well for cases where the relationship between $\delta\text{D}_{\text{feather}}$ and $\delta\text{D}_{\text{precip}}$ has been well established (e.g. Hobson *et al.*, 2009). Here, we lacked an *a priori* data set linking $\delta\text{D}_{\text{feather}}$ and $\delta\text{D}_{\text{precip}}$ for feathers grown in Africa and so instead we used a simpler 'map lookup' approach using an arithmetic conversion of a deuterium precipitation isotope to a deuterium feather isotope for Africa. Because African-grown feathers often were substantially more enriched in δD compared with European and most North American feathers, we decided not to apply variance associated with calibrations between $\delta\text{D}_{\text{feather}}$ and GNIP $\delta\text{D}_{\text{precip}}$ established on those continents.

We could not predict a value for $\delta^{15}\text{N}$ for the Swiss study site as this is difficult because of complex anthropogenic N inputs. The mean $\delta^{15}\text{N}$ value of the Swiss birds might, however, be indicative of the trophic position of the birds (i.e. $\delta^{15}\text{N}$ increases with trophic level by an average of $+2.3\text{‰}$ per consumer, Hood-Nowotny & Knols, 2007). Nor could we predict a value for $\delta^{13}\text{C}$ since this is mostly driven by the different photosynthetic pathways (C3-, C4- and CAM-plants) and hence dictated by type of vegetation and climate.

We matched winter $\delta D_{\text{feather}}$ values (50% and 75% tolerance limits; TL, Walpole & Meyers, 1993) corrected with an isotopic fractionation factor of +25.3‰ from feather to precipitation values of the Swiss and the German population with interpolated δD maps of southern Europe and Africa in an attempt to depict the possible origins of these feathers (Hobson *et al.*, 2007). Maps were generated with ArcGIS based on mean δD_{precip} values for October–February (data available on <http://www.waterisotopes.org>). These particular months were chosen as they reflect the time window of feather renewal.

Table 1 Influence of year, age category and their interaction on isotopic values in (a) deuterium (δD), (b) nitrogen ($\delta^{15}N$) and (c) carbon ($\delta^{13}C$) in winter-grown feathers of Swiss wrynecks ($n = 139$).

Model	Best		2nd Best		3rd Best	
	Estimate	SE	Estimate	SE	Estimate	SE
(a) δD						
Effects						
Intercept	-17.35	3.46	-18.52	3.89	-14.44	3.20
Year	-11.47	3.84	-9.73	4.63	-11.92	3.88
Age	8.285	4.05	11.81	6.68	-	-
Year \times age	-	-	-5.55	8.32	-	-
Selection criteria						
ΔAIC_c	0.00		1.73		2.05	
AIC _c w	0.55		0.23		0.20	
Deviance	971.44		970.98		975.65	
(b) $\delta^{15}N$						
Effects						
Intercept	9.14	0.41	8.74	0.48	8.45	0.24
Year	-0.98	0.49	-0.38	0.58	-	-
Age	-	-	1.56	0.94	-	-
Year \times age	-	-	-2.25	1.13	-	-
Selection criteria						
ΔAIC_c	0.00		0.35		1.70	
AIC _c w	0.36		0.30		0.16	
Deviance	497.89		493.91		501.71	
(c) $\delta^{13}C$						
Effects						
Intercept	-20.83	0.24	-20.89	0.13	-20.99	0.16
Year	-0.22	0.27	-	-	-	-
Age	-1.08	0.49	-	-	0.30	0.29
Year \times age	1.97	0.60	-	-	-	-
Selection criteria						
ΔAIC_c	0.00		6.64		7.69	
AIC _c w	0.92		0.03		0.02	
Deviance	353.76		366.86		365.79	

The three best models (out of five candidate models) are shown for each isotope and ranked according to the Akaike Information Criterion for small sample sizes (ΔAIC_c : difference of AIC_c to best model). AIC_c w indicates the Akaike weight. The intercepts indicate estimates for adult birds (AD) of 2005, whereas the estimates of year and age are differences between these intercepts and the values for 2006 and SY birds (for a definition, see Methods), respectively.

RESULTS

The model best explaining variation in δD from winter-grown feathers included the factors collection year and age (Table 1). Winter-grown feather δD values were more depleted in 2006 compared to 2005, and SY birds showed more enriched values compared to AD. The variation in $\delta^{15}N$ of these feathers was best explained by year, with lower values in 2006 than in 2005. The second-best model performed almost as well as the best one and included the two factors year and age as well as their interaction term. The best model explaining the variation in $\delta^{13}C$ included year, age and the interaction year \times age. Adults showed higher $\delta^{13}C$ values in 2005 than in 2006, whereas SY birds showed lower values in the year 2005 than in 2006. The best model explaining the variation in summer-grown feather δD values in Swiss wrynecks was the null model. However, the second-best model showed that δD values were lower in 2006 compared to 2005 (Table 2).

There was no significant difference in $\delta^{15}N$ values between Swiss and German winter-grown feathers ($t = -1.31$, d.f. = 71, $P = 0.193$), whereas δD and $\delta^{13}C$ values were higher in feathers from Germany than from Switzerland (δD : $t = -5.71$, d.f. = 71, $P < 0.001$; $\delta^{13}C$ $t = -4.17$, d.f. = 71, $P < 0.001$, respectively; Fig. 1). In the two populations, variances were equal for δD and $\delta^{15}N$ (two-tailed F -test for homogeneity of variances: $F = 0.99$, d.f. = 51, 20, $P = 0.928$; $F = 0.78$, d.f. = 51, 20, $P = 0.463$, respectively), but not for $\delta^{13}C$ ($F = 0.20$, d.f. = 51, 20, $P < 0.001$).

In Table 3, we present summary statistics of each stable isotope, split into feather growth periods and populations. Variances of isotopic values of Swiss SY birds caught in 2006 were generally smaller in summer- than winter-grown feathers for all three isotopes but differed significantly only in $\delta^{15}N$ and $\delta^{13}C$, suggesting a wider winter than summer range (Fig. 2).

Matching the deuterium isoscape in precipitation for Africa with the 50% and 75% tolerance limits (TL) of winter $\delta D_{\text{feather}}$

Table 2 Influence of year on deuterium isotopic values in summer-grown feathers of Swiss wrynecks (only SY birds, $n = 35$).

Model	Best		2nd Best	
	Estimate	SE	Estimate	SE
Effects				
Intercept	-80.31	1.56	-78.36	2.38
Year	-	-	-3.40	3.14
Selection criteria				
ΔAIC_c	0.00		1.34	
AIC _c w	0.66		0.34	
Deviance	253.83		252.61	

The models are ranked according to the Akaike Information Criterion for small sample sizes (ΔAIC_c : difference of AIC_c to best model). AIC_c w indicates the Akaike weight. The intercept indicates an estimate for adult birds (AD) of 2005, whereas the estimate of year is the difference between the intercept and the values for 2006.

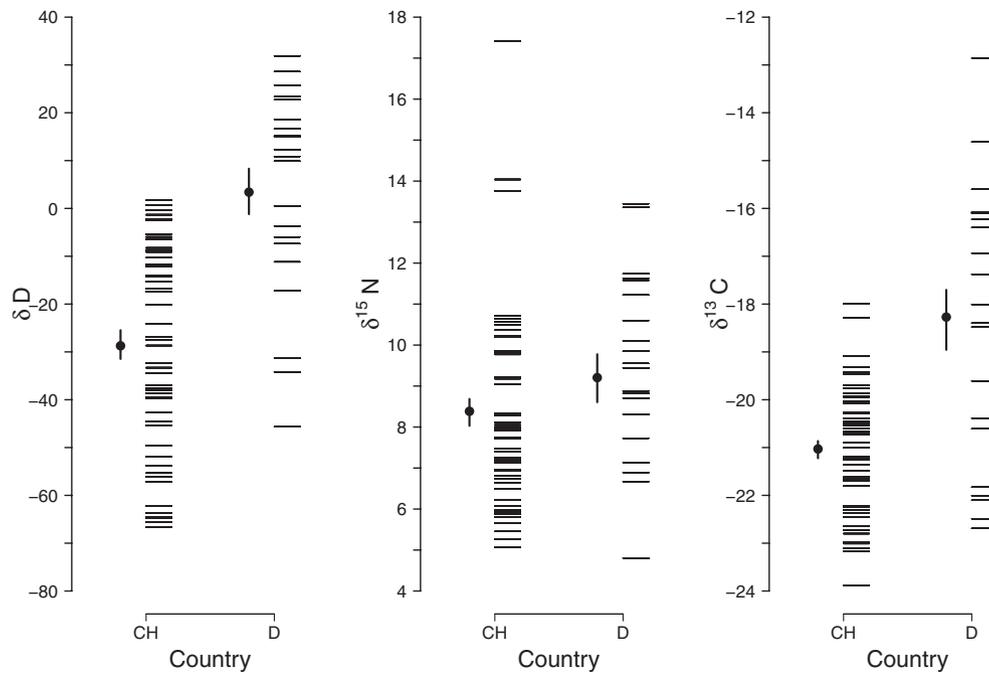


Figure 1 Individual isotopic values of winter-grown feathers (AD birds captured in 2006) from the Swiss (CH, $n = 52$) and the German (D, $n = 21$) populations. Plotted are mean values \pm SE. Horizontal lines indicate the individual isotopic values.

Table 3 Isotopic values of δD , $\delta^{15}N$ and $\delta^{13}C$ in wrynecks: mean, standard deviation (SD), range and sample size (n) of feathers representing isotopic values of the breeding (summer-grown feathers) and wintering areas (winter-grown feathers) of the populations in Switzerland (CH, 2005 and 2006) and Germany (D, 2006).

		δD (‰)			$\delta^{15}N$ (‰)				$\delta^{13}C$ (‰)				
		Mean	SD	Range	n	Mean	SD	Range	n	Mean	SD	Range	n
CH	Summer	-80.3	9.2	-93.6 to -56.3	35	+9.2	1.1	7.1 to 10.7	20	-22.8	0.5	-23.5 to -21.3	20
	Winter	-22.4	20.6	-66.6 to +17.4	111	+8.5	2.5	4.0 to 17.4	108	-20.9	1.3	-23.9 to -13.1	108
D	Winter	+3.6	21.8	-45.7 to +31.9	21	+9.2	2.7	2.6 to 13.5	21	-18.3	2.9	-22.7 to -12.9	21

values of Swiss ($\delta D_{\text{Switzerland}}$: $TL_{50\%} = -20.4$ to 26.1‰ , $TL_{75\%} = -36.8$ to 42.5‰) and German ($\delta D_{\text{Germany}}$: $TL_{50\%} = 18.2$ – 39.5‰ , $TL_{75\%} = 10.7$ – 47.0‰), wryneck populations suggest that the wintering grounds of the German population are situated probably to the south of the Sahara desert (Sahel zone, higher δD values), while the TLs of $\delta D_{\text{feather}}$ values of the Swiss breeding population also include southern European areas (south-western Spain and Portugal, and southern Italy, lower δD values; Fig. 3).

DISCUSSION

Applicability of the method

Before assigning bird feathers to a place of origin with the help of stable isotopes, we wanted to explore possible causes of variation and bias associated with this technique. We came to the conclusion that stable isotopes are a useful method to

delineate winter grounds and to investigate migratory connectivity of European migratory birds provided that crucial information about moulting patterns and isoscapes is available. Discrepancies between some *ad hoc*-formulated premises and possible biases in reference isoscapes for a specific isotope call for further methodological improvements, especially with regard to the resolution of the species-specific reference maps.

When using stable isotopes to approach questions of migratory connectivity, Hobson (2005) suggested calibrating the method by matching local environmental isotopic values against locally grown feathers of the species in question (Szépl *et al.*, 2009). Perfect matches, however, are rarely obtained, because of uncertainties such as analytical or spatial interpolation errors (discussed in Wunder & Norris, 2008), or because of inter-individual differences in physiology (Powell & Hobson, 2006). Applying our calculated discrimination factor to summer-grown feather δD in Swiss wrynecks of unknown origin nevertheless resulted in a good match with δD_{precip}

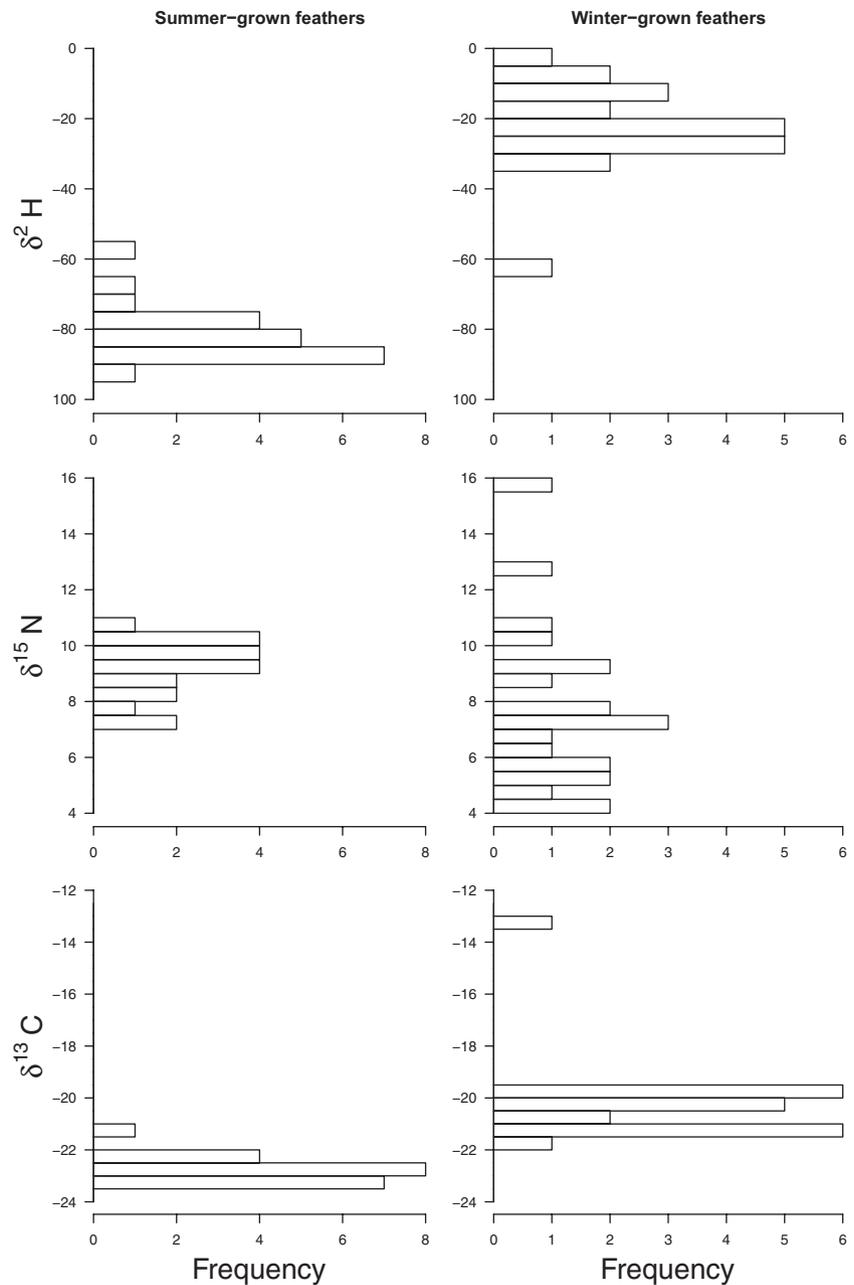


Figure 2 Frequency distribution of isotopic values in deuterium ($\delta^2\text{H}$), stable nitrogen ($\delta^{15}\text{N}$) and stable carbon ($\delta^{13}\text{C}$), respectively, for summer- and winter-grown feathers in Swiss SY (for definition see Methods) wrynecks in 2006 ($n = 41$). There are significant differences in variances between summer- and winter-grown feathers in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (two-tailed F -tests for homogeneity of variances: δD : $F = 0.47$, d.f. = 19, 20, P -value = 0.11; $\delta^{15}\text{N}$: $F = 0.13$, d.f. = 19, 20, P -value = <0.001 ; $\delta^{13}\text{C}$: $F = 0.07$, d.f. = 19, 20, P -value = <0.001).

mean annual values (expected δD value: -81.1‰ vs. obtained $\delta\text{D}_{\text{feather}} -80.1 \pm 9.5\text{‰}$, $n = 27$). This illustrates that potential immigrants to the Swiss wryneck population showed similar isotopic values as those known-origin Swiss SY birds (see Methods). Despite the fact that we have indication of moderate immigration to this population (Reichlin *et al.* submitted), these birds appear largely local and we cannot shed additional light on their origins using the isotope measurements.

We used a simple ‘map lookup’ approach to describe potential moult origins of birds in Africa, although this can be problematic as Wunder & Norris (2008) have recently pointed out. Future studies should pursue the derivation of probability surfaces, ideally using an established $\delta\text{D}_{\text{feather}}$ and $\delta\text{D}_{\text{precip}}$ calibration for feathers of known moult origin in sub-Saharan

Africa. Until such probability surfaces are established, our predictions of origins of wrynecks using $\delta\text{D}_{\text{feather}}$ values and assumed $\delta\text{D}_{\text{precip}}$ values along with the application of a species-specific precipitation to feather discrimination factor should be considered with some caution. Nevertheless, we consider our comparison of the multiple isotopes from two breeding populations and isotopic variance as a reasonable proxy for the broadness of geographical wintering origins to be informative (Møller & Hobson, 2004).

Variation of isotopic values within populations

We showed that bird age and collection year both influenced isotopic values of winter-grown feathers within the Swiss



Figure 3 Overlap of δD values of winter-grown feathers of wrynecks from the (a) Swiss and (b) German breeding populations with the δD_{precip} isoscape (discrimination factor: +25.3‰ from feather to precipitation). Dark grey areas represent a match between the δD isoscape (modelled mean δD_{precip} values for months October–February, <http://www.waterisotopes.org>) and the 50% tolerance limits (TL 50%) of winter-grown feathers; light grey areas represent a match between the δD isoscape and the 75% tolerance limits (TL 75%) of winter-grown feathers. Tolerance limits represent the limits within which a specified proportion of the population (50% and 75%, respectively) will fall at an expressed level of confidence (95%) (Walpole & Meyers, 1993). The maps are projected in the Aitoff projection, with isolines for areas with the same underlying δD_{precip} values.

breeding population, although this effect was marginal for $\delta^{15}\text{N}$ measurements regarding bird age (Table 1). Our model selection approach did not enable us to disentangle these two effects; a larger sample size would be needed to directly test for this (Reichlin *et al.* in prep.). Regarding summer-grown feathers, collection year had no effect on δD . These results are in line with the expectation that deuterium isotopic values are predictable and repeatable between years at a given location (small inter-year variation in $\delta\text{D}_{\text{precip}}$ in Europe; Hobson, 2005b). Regarding winter-grown feathers, we found a collection year effect in all three isotopes. Inter-annual variation in the wintering area, combined with asynchronous moulting could, at least partly, account for the variation in isotopic values. In addition, more mesic environments would lead to lower $\delta^{15}\text{N}$ values (this study: feathers of 2006). Actually, precipitation in Sahelian Africa was higher in 2005 compared to 2004 (NOAA/National Weather Service, Climate Prediction Center: <http://www.cpc.ncep.noaa.gov/products/fews/africa/>), which provides a potential mechanism for the observed inter-year isotopic differences in feathers. Moreover, asynchronous moulting within an age category or differences in moult periods between SY and AD on the wintering grounds may also affect the δD isotopic feather values (Kelly *et al.*, 2008). As a result, higher deuterium values in feathers (Table 1) could be associated with a comparatively late moult in SY birds corresponding to the annual variation of $\delta\text{D}_{\text{precip}}$ (e.g. see $\delta\text{D}_{\text{precip}}$ of January and February on <http://www.waterisotopes.org>).

Year and age variation in stable isotope values may be related to non-fidelity to wintering sites or because of diffuse migratory connectivity between breeding and wintering grounds. Selection regarding survival could cause differences in stable isotope profiles between age classes. Our data, however, did not allow us to reliably test for dissimilarities in isotope values between survivors and non-survivors, as only approximately 11% of sampled Swiss birds were recaptured in a later year. Also, age-specific feeding strategies could theoretically result in variation in isotopic values (e.g. Meehan *et al.*, 2003; Bearhop *et al.*, 2006). Wrynecks are exclusive ant predators (Glutz von Blotzheim & Bauer, 1980; Freitag, 1996), but the range of isotopic variation within this diverse prey group on the wintering grounds is unknown.

Variation of isotopic values between populations

We showed that the Swiss and German wryneck populations have distinctive isotopic values in winter-grown feathers for two (deuterium and carbon) of three analysed isotopes (Fig. 1). By comparing only one age class in 1 year, we could rule out confounding effects of year and age. This comparison suggested that the wintering ground overlapped little between the two populations (see frequency distributions in Fig. 1), with wintering grounds of the German population probably situated in the Sahel zone (more positive δD , Fig. 3b), probably in western Africa (Reichlin *et al.*, 2009), while mean

δD values of the Swiss breeding population also include the south-western part of the Iberian peninsula and North Africa (i.e. more negative δD , Fig. 3a). Using only the δD isoscape for Swiss birds does not lead to a more precise localization of their wintering areas. Yet another indication of different wintering grounds between populations is the $\delta^{13}\text{C}$ values: German birds appeared to moult in a more xeric landscape (C4- or CAM-plants), while feather values of Swiss birds may have originated from (more mesic) regions with larger proportions of C3-plants (10–15° N upwards, Still *et al.*, 2003), which is compatible with a scenario of overwintering in southern Iberia and northern Africa. The use of different wintering areas points to a low degree of migratory connectivity between these breeding populations. Furthermore, these findings hint at a possible leapfrog migration system with northern breeding populations wintering further south than more meridional breeding populations. Similar conclusions were drawn from δD values in Wilson warblers (*Wilsonia pusilla*, Kelly *et al.*, 2002).

Separate wintering grounds could have consequences for the population dynamics of these two breeding populations. Changing conditions, e.g. droughts perturbing some regions of the Sahel (e.g. Newton, 2004), could affect demographic parameters differently within two breeding populations (Kanyambwa *et al.*, 1990; Schaub *et al.*, 2005). German wrynecks could be more susceptible to such climatic perturbation in the Sahel, as they primarily winter in these regions and might not be genetically apt to switch to other wintering areas (i.e. Mediterranean basin). There is, however, no evidence for distinct demographic trajectories in breeding European wryneck populations so far, although the information remains scarce (BirdLife International, 2010; personal unpublished data). Integrative demographic models accounting for variation in seasonal mortality could incorporate environmental fluctuations in wintering areas to disentangle factors operating on breeding vs. wintering grounds.

Isotopic variation in breeding vs. wintering range

Isotopic variances for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were significantly smaller in summer- than winter-grown feathers of Swiss wrynecks. This corroborates our assumption that the variance of isotopic values in a confined breeding area (here our study site in Switzerland plus the adjacent areas probably yielding immigrants) is comparatively smaller than the variance observed in an (unknown) winter range. A wider range of geographical areas including many different foraging grounds (with site-specific isotopic values) in winter is the most plausible explanation here (Møller & Hobson, 2004), although Bearhop *et al.* (2004) have proposed that a large variance in isotopic values of winter-grown feathers could result from a more plastic trophic niche in wintering birds. However, the very specific diet of wrynecks, which is exclusively based on ants, and the fact that physiology of ants are not expected to differ among species lend less support to this hypothesis.

Perspectives

This study suggests the existence of ‘diffuse migratory connectivity’ *sensu* Webster *et al.* (2002), because of the fact that breeding individuals stemming from the two European populations winter in geographically distinct, and in the case of Swiss birds, rather broad areas. Furthermore, we found some evidence for leapfrog-like migration in the wryneck. This may have consequences when assessing population dynamics of different breeding populations because local demographic trajectories may be impacted by factors operating at different places, i.e. affecting different components of seasonal mortality (Marra *et al.*, 1998; Runge & Marra, 2005; Webster & Marra, 2005). Future demographic analyses should take the encountered environmental conditions during different phases of the annual cycle into account to better understand the mechanisms of population changes. Thus, stable isotopes facilitate refined integrated demographic analyses for migratory species, paving the way for spatially and seasonally explicit population dynamical models and improvements of conservation action of declining populations (Esler, 2000; Webster & Marra, 2005).

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BIOSKETCHES

This work is part of **Thomas S. Reichlin's** PhD thesis under the supervision of **Raphael Arlettaz**, **Michael Schaub** and **Lukas Jenni**. In his PhD work, T.S.R. studied the population dynamics of wrynecks and hoopoes in a long-term study in south-western Switzerland. He has broad interests in the field of conservation biology and bird ecology and shows particular interests in the application of stable isotopes in ecological studies. His mentors in stable isotope analysis in bird migration studies were **Keith A. Hobson** and **Leonard I. Wassenaar**.

Author contributions: T.S.R., M.S., L.J. and R.A. conceived the ideas; T.S.R., M.S., D.T. and D.B. collected the data; T.S.R. did the isotopic analysis under the supervision of K.A.H. and L.I.W.; T.S.R. and M.S. performed the statistical analyses; and T.S.R., K.A.H., M.S. and R.A. led the writing.

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APPENDIX 1

Monthly precipitation δD values (in ‰, V-SMOW; <http://www.waterisotopes.org>, accessed 10 February 2010) for the study site in Switzerland (Canton Valais, Sion, δ^2H estimates for latitude 46.228°, longitude 7.349°, altitude 500 m a.s.l.)

	January	February	March	April	May	June	July	August	September	October	November	December
δD	-72	-70	-63	-62	-49	-45	-35	-35	-45	-53	-66	-75