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Using stable-hydrogen isotopes to reveal immigration in an Arctic-breeding songbird population

Franz Bairlein^{1*}, D. Ryan Norris², Christian C. Voigt³, Erica H. Dunn⁴ and David J. T. Hussell⁵

Abstract

Background: Knowledge of immigration and emigration rates is crucial for understanding of population dynamics, yet little is known about these vital rates, especially for arctic songbirds. We estimated immigration in an Arctic population of northern wheatears on Baffin Island, Canada, by the use of stable hydrogen isotopes in tail feathers ($\delta^2\text{H}_K$). We assumed that $\delta^2\text{H}_K$ values of juvenile (hatch-year) feathers grown at the breeding grounds were representative of the local population, while those of breeding adults were indicative of where they grew their feathers during their post-breeding molt the previous year. The extent to which adult isotope values differ from those of juveniles provides an estimate of the minimum level of immigration into the breeding population.

Results: Mean $\delta^2\text{H}_K$ values did not differ in juvenile birds between years. Breeding adult birds did not differ significantly in mean $\delta^2\text{H}_K$ values compared to juveniles but did differ in their respective standard deviations, reflecting a significantly wider range of isotopic signatures in adults than in juveniles. Thirty-eight percent of the $\delta^2\text{H}_K$ values in adults were greater ± 2 SD of the mean $\delta^2\text{H}_K$ values of juveniles, suggesting that at least 38 % of the breeding adults were of non-local origin, thus immigrants from elsewhere.

Conclusions: Although the use of stable isotopes has limitations, the use of stable-hydrogen isotopic markers has the potential to contribute valuable information towards understanding immigration rates in bird populations. In our study, hydrogen isotope measurements of the feathers of northern wheatears indicated a high rate of immigration into the breeding population, which is consistent with low return rates of banded breeding adults as well as implying high emigration rates of local breeders.

Keywords: Immigration, Dispersal, Stable isotopes, Northern wheatear, *Oenanthe oenanthe*

Background

Dispersal is widely regarded as a key factor driving population dynamics and rate of gene flow [1–6]. Despite its importance, acquiring robust data on immigration and emigration rates has been extremely challenging. Mark-recapture approaches are often used for indirect estimation (e.g., [7–12]), but they require large sample sizes over multiple years and are labor intensive. Directly tracking movements using radio telemetry is also labor intensive and limited by the distribution of receivers across the landscape (e.g., [13]).

Larger-scale marking schemes have recorded some long-distance dispersal events [3] but are still limited in their ability to record shorter distance movements, and detection rates suffer from many biases. Molecular markers have been effectively used to generate quantitative estimates of dispersal [14–16], although this approach relies on the presence of population-specific genetic signatures.

An alternative approach to estimating avian dispersal rates is to make use of stable isotopes [17–23]. Individuals incorporate a local isotopic signature through their diet [24, 25], and that signature is incorporated into growing feathers. Because feathers are metabolically inactive, they retain the isotopic signature from the location where they were grown [26]. Some stable isotopes, such as hydrogen [27], vary geographically and can,

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therefore, be used to estimate the location of feather growth, regardless of where or when the feather is sampled [19, 28–31]. Adult songbirds typically undergo post-breeding molt at or near their breeding sites, such that feathers sampled during the next breeding season carry the signature of the previous year's breeding location. Feathers of juvenile birds have the local isotopic signature, so comparing juvenile and adult signatures can indicate amount of immigration.

We used this approach to estimate immigration rates of adult northern wheatears (*Oenanthe oenanthe*) in a breeding population located in Iqaluit, Nunavut, Canada. The northern wheatear is a small passerine of Old World origin that breeds in hot and cold deserts and open country throughout Europe and Asia and extends its breeding range eastward into western North America in Alaska and the Yukon, and westward from Europe into Iceland, Greenland and the eastern Canadian arctic [32]. All populations winter in sub-Saharan Africa, with western Arctic breeders migrating west to eastern Africa and the eastern Arctic population migrating across the Atlantic Ocean to winter in western Africa [33].

We assumed that the stable-hydrogen isotope values of juvenile feathers grown in July and August were representative of the local population, while those of breeding adults were indicative of where they grew their feathers during their post-breeding molt the previous year. The extent to which adult isotope values differ from those of juveniles provides an estimate of the minimum level of immigration into the breeding population and, by implication, the probable minimum level of emigration of our banded adults out of the population.

Methods

Study site, species and sampling

Our study area comprised about 20 km² adjacent to the north shore of Frobisher Bay, Baffin Island, including the city of Iqaluit, Nunavut, Canada (63.7° N, 68.5° W) and extending about 3.5 km to the NW and 7 km to the SE from the city center. Northern wheatears breed throughout this coastal area, but are not found further inland.

In Iqaluit, northern wheatears arrive in early to mid-May and nest in natural rock crevices and under boulders, as well as in similar man-made sites such as rock walls. Most nest sites are inaccessible to humans. Six to ten eggs are laid starting as early as the last few days of May or as late as late June, but a few late or second clutches are started in the first half of July, some by adults that are already starting to molt [34]. The females incubate the eggs and both adults provision the nestlings. Fledging occurs mainly in July and the young are independent in August.

We searched the study area for breeding pairs, nests and fledged broods. Nests are difficult to find during the incubation stage, but relatively easy once the adults start to bring food to the nestlings. The number of person-days of searching effort varied from year-to-year, with greater effort in 2009–2011 when we equipped adults with light-sensitive archival data loggers and searched for their return [33]. During the nestling stage, adults were trapped at or near their nest sites with spring-loaded tent or bow nets baited with meal worms or with a “walk-in” trap placed in the entrance of the nest cavity. Each captured adult was marked with a unique combination of a standard numbered aluminum band and two or three color bands (Avinet Inc., Dryden, New York), which allowed us to recognize those individuals without recapturing them. All banded birds were aged and sexed by plumage where possible [32]. Young-of-the-year (HY for Hatch Year) could not be sexed, and adult females could not be split into age groups and, hence, were all classed as AHY (After Hatch Year). Males were classed as SY (Second Year, i.e. yearlings) or ASY (After Second Year), combined as AHY for certain analyses.

From 2009 to 2013, we sampled the 2nd outermost tail feather of breeding adult birds, and in 2010 and 2011 the same feather of recently fledged fully-grown birds (Nunavut Wildlife Research Permits WL 2009–034, 2010–028, 2011–032, 2012–035, 2013–042 and Canadian Wildlife Service Permits NUN-SCI-09-03, –10-02, –11-03, –12-05, –13-01). Feathers were kept in individual envelopes until analysis.

Stable hydrogen isotope analyses

Stable hydrogen isotope (δD) values of feathers were analysed at the stable isotope laboratory of the Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. A small section of feather tissue was clipped from the tip of the feather ($350 \pm 7 \mu g$) and loaded into silver capsules (IVA Analysetechnik e.K. Meerbusch, Germany). We filled 96 port microtiter trays with silver capsules loaded with feather samples and laboratory keratin standards with known $\delta^2 H$ values for non-exchangeable hydrogen. Trays were allowed to equilibrate with ambient air over more than 7 days. Afterwards, trays were placed in a drying oven over 1 day at 50 °C. Loaded capsules were then transferred to a zero blank autosampler (Costech Analytical Technologies Inc., Cernusco, Italy) above the elemental analyzer (HT elemental analyzer HEKAtech GmbH, Wegberg, Germany). For at least 1 h before combustion, samples were flushed in the autosampler with chemically pure helium (Linde, Leuna, Germany). We used a Delta V Advantage isotope ratio mass spectrometer (ThermoFischer Scientific, Bremen, Germany) that was connected via an interface (Finnigan Conflo III, ThermoFischer Scientific,

Bremen, Germany) with the elemental analyzer. Reference H₂ gases were calibrated against international standards (IAEA NBS 22 and IAEA-CH-7). We used the comparative equilibration method [35] to account for the amount of exchangeable hydrogen in feather keratin. We used three laboratory standards that covered the range of expected δD values in our samples. These standards were also used to determine the δD of non-exchangeable hydrogen [35, 36]. The stable hydrogen isotope ratios of the non-exchangeable hydrogen (mean \pm s.d.) of the standards were: -133.6 ± 1.2 ‰, -109.1 ± 1.2 ‰ and -87.2 ± 1.0 ‰. In the sequential order of one autorun, keratin standards were placed at positions 1–6 (3 standards of 2 replicates) and at the 9th–11th position (3 standards). Hereafter, we refer to δ^2H_K as the stable hydrogen isotope ratios of non-exchangeable hydrogen in feather keratin.

Statistics

All statistics were performed using IBM SPSS Statistics 21. One-way ANOVA with post-hoc Tukey HSD-test was used to test differences between groups and Levene's test to test for homoscedasticity. Prior to analysis, normality was tested using Kolmogorov-Smirnov-test statistics. None of the samples deviated significantly from normality. To estimate immigration rate we took the percentage of δ^2H_K values in adults (AHY) that lie outside the ± 2 SD range of the distribution of δ^2H_K values of the juveniles. The ± 2 SD range is equivalent to 95.4 % of the values around the mean [37].

Results

Banding and returns

Over the 8 years, 2007–2014, we determined whether or not the adults were already banded at almost 200 nest cavities, meaning a very high sampling effort. Of 204 banded adults ten returned in a later year (5 males and 5 females), representing 4.9 % of the banded adults from preceding years. Of 75 juveniles one returned (1.3 %), but none of 131 nestlings.

Feather isotopes

Samples were collected from a total of 34 HY birds (2010: 18; 2011: 16) and 174 adults of both sexes (2009: 27; 2010: 46; 2011: 52; 2012: 20, 2013: 29). Of the 174 adults, 10 (2010: 2; 2011: 4; 2012: 3; 2013: 1) had δ^2H_K values of higher than -100 ‰, which was very likely due to replacement of arbitrarily lost tail feathers at a far-distant non-breeding location [33]. Therefore, we excluded these values from any further analysis. For the remaining sample sizes see Additional file 1: Table S1.

There was no significant difference in mean δ^2H_K between the 2 years in HY birds (Fig. 1; ANOVA, $F_{1,36} = 0.138$; $p = 0.71$). We assumed that these values were

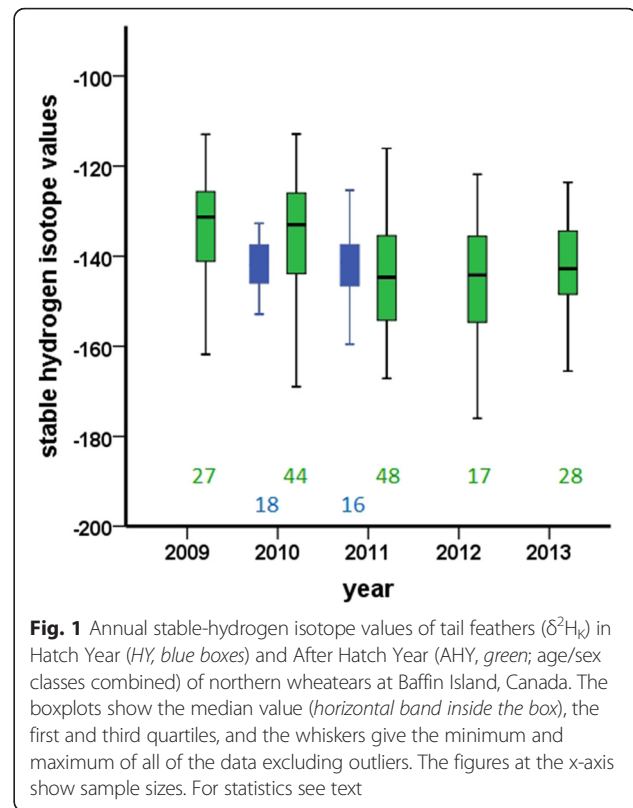
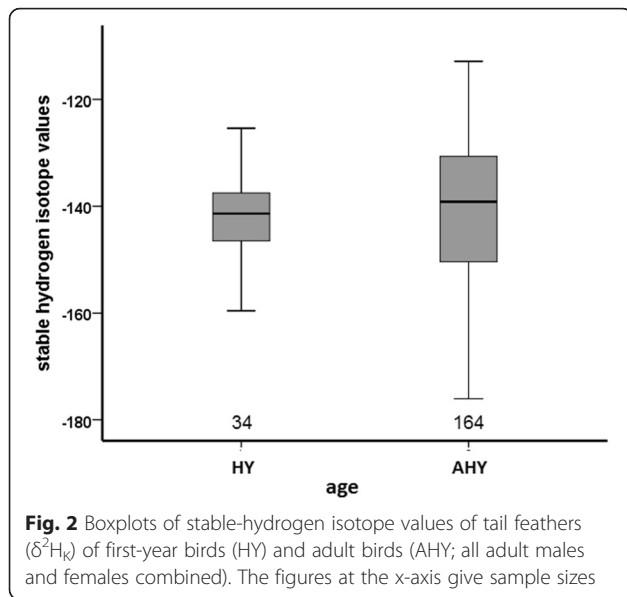


Fig. 1 Annual stable-hydrogen isotope values of tail feathers (δ^2H_K) in Hatch Year (HY; blue boxes) and After Hatch Year (AHY; green; age/sex classes combined) of northern wheatears at Baffin Island, Canada. The boxplots show the median value (horizontal band inside the box), the first and third quartiles, and the whiskers give the minimum and maximum of all of the data excluding outliers. The figures at the x-axis show sample sizes. For statistics see text

representative of δ^2H_K signatures of feathers grown in our study area in Iqaluit and results for the 2 years were combined for further analysis.

Adult birds consisted of SY and ASY males and AHY females (for which age classes are indistinguishable in the field). For all adults combined, mean δ^2H_K differed among years (ANOVA, $F_{4,159} = 5.47$; $p < 0.001$), with 2009 and 2010 showing significantly higher δ^2H_K values than the other years (Fig. 1; post-hoc Tukey-HSD-test, $p = 0.006$ and 0.017 , respectively). However, there were no significant differences in mean δ^2H_K among adult age and sex classes (ANOVA, $F_{4,164} = 0.337$; $p = 0.853$), or in their respective standard deviations (Levene's test; $p = 0.936$). We therefore combined all non-HY sexes into one group (AHY) for comparison with HYs.

HY and AHY birds did not differ significantly in average δ^2H_K values (ANOVA, $F_{1,198} = 0.415$; $p = 0.520$) but did differ in their respective standard deviations (Fig. 2; HY: -141.7 ± 6.7 ‰, $n = 34$; AHY: -140.2 ± 13.2 ‰, $n = 164$; Levene's test; $p < 0.001$), reflecting a significantly wider range of δ^2H_K in adults than in juveniles. In order to address whether the wider range in AHY birds is due to the larger sample size we randomly selected 100 times 34 cases from all the 164 AHY cases. Neither average mean nor average standard deviation of the repeats did differ from the entire data set (-140.4 ± 12.9 ‰ vs -140.2 ± 13.2 ‰). Therefore, we are confident having used the entire data set.



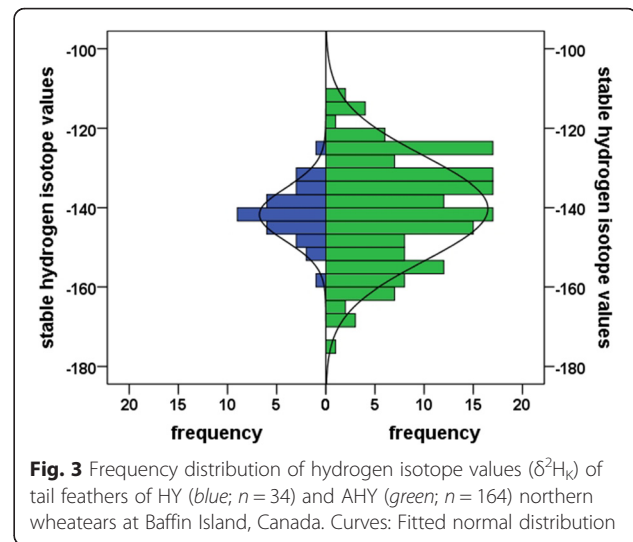
We had repeated measures from six adult birds that returned in the year after first capture. Stable-hydrogen isotope values in feathers averaged -140.5 ± 7.7 ‰ (SD) for returning birds, compared with -130.5 ± 7.6 ‰ in the first year of capture at Iqaluit. Importantly, the mean δ^2H_K value of AHY birds at return was almost identical to the mean value for HY birds that grew their feathers at Iqaluit (-141.7 ± 6.7 ‰), which is consistent with the expectation that δ^2H_K values of AHY and HY feathers are similar if grown at the same place. SD at first capture of these six birds was significantly lower than that for all AHY birds (7.7 vs 13.2 ‰; Levene's test; $p < 0.001$) but similar to HY birds (Levene's test; $p > 0.05$), revealing that returning breeders had a previous history of being more site faithful than is typical.

Immigration rate

Thirty-eight percent of the δ^2H values in adults were greater ± 2 SD of the mean δ^2H values of juveniles (Fig. 3), suggesting that at least 38 % of the breeding adults were of non-local origin, thus immigrants from elsewhere. Having a closer look and comparing within a given year only (HY δ^2H_K values from 2010 vs AHY δ^2H_K from 2011 and HY δ^2H_K values from 2011 vs AHY δ^2H_K values from 2012), we found immigration rates of at least 40 and 28 %, respectively, suggesting that there was some annual variation in immigration rates as well.

Discussion

Knowledge of immigration and emigration rates is crucial for full understanding of population dynamics, yet we know little about those rates in songbirds, especially arctic birds. In a German population of blackcaps *Sylvia atricapilla* in which all breeding adults and all fledged



young were color-banded, 56 % of the breeding birds in the subsequent year were immigrants from other populations [7]. Other studies estimated immigration rates solely of yearling birds. In a Swedish population of colored flycatchers *Ficedula albicollis*, estimated immigration rates of yearling birds in unmanipulated control plots was ca 16 % [11]. In yellow-headed blackbirds *Xanthocephalus xanthocephalus*, Ward [12] recorded a proportion of yearling males of 14 % in Illinois and 24 % in South Dakota, respectively, and he cited several other North American studies of songbirds with annual percentages of yearling males ranging between 16 and 65 %.

For northern wheatears, our minimum estimate for all immigrants was at least 38 %, so at least 40 of the 104 adult males we captured were immigrants. Hatch-year birds made up 56.7 % of captured males, so 23 (about 22 %) of immigrant males were yearlings. These estimates fall within the range of values for temperate songbirds.

There is limited and often anecdotal data on breeding site fidelity of arctic songbirds. In a 6-year study of Lapland longspurs (*Calcarius lapponicus*) at Barrow, Alaska cumulative return of banded birds for all years yield 11.6 % for males and 23.5 % for females [38]. At Sarcpa Lake, Nunavut, 47 of 86 (55 %) adult Lapland longspurs were detected as returnees in a subsequent year and 31 adults from an unknown number banded at McConnell River, Nunavut, returned the next year [39]. In a 3-year study of Eastern yellow wagtails (*Motacilla tschutschensis*) at Cape Romanzof, Yukon Delta National Wildlife Refuge, Alaska, at least 12 of 23 (52 %) banded males returned in the following year but none of 23 banded females returned, for an overall adult return rate of 26 % [40]. Fragmentary data on snow buntings (*Plectrophenax nivalis*) appear to indicate considerably lower breeding site fidelity: at Sarcpa Lake, Nunavut, 2 of 9 banded

males and zero of 10 banded females returned the next year; on Devon Island, Nunavut, of 32 adults banded over a 3-year period, one male and two females returned the following year [41]; and at Iqaluit, Nunavut, only two (1 male and 1 female) of 22 adults fitted with geolocators in 2013 were found in 2014 (DJTH, pers. obs.). These figures suggest about 10 % return rate for adult snow buntings; still twice the rate of 5 % we found for northern wheatears by banding.

Although the use of stable isotopes provides a promising approach for estimating immigration and emigration in a population [17, 18, 20–23], there are several potential limitations to this approach. First, in most landscapes, stable isotopes do not provide the level of spatial accuracy to detect short distance ($\sim <100$ km) movements, even when multiple isotopes are combined [23]. Thus, in our case, stable isotopes could underestimate the true number of immigrants. Second, our approach relies on population-specific values from known-origin tissues of a relatively large sample. Acquiring known-origin tissue can involve intensive fieldwork, as it typically requires locating and monitoring nests or catching juveniles soon after they leave the nest. A less intensive approach would be to characterize local $\delta^2\text{H}$ distribution based on interpolated precipitation values [27] and then offset this distribution with a diet-tissue discrimination factor [29, 30]. We chose not to take this approach because we did not have an estimated diet-tissue discrimination factor for Arctic-breeding populations of this species or an ecologically similar species. However, obtaining such an estimate would, in theory, also allow us to assign the geographic origin of immigrants with a certain degree of confidence. Third, different diets of juveniles versus adult birds could have influence on the isotopic signatures of feathers. However, there is no evidence that adults and juvenile wheatears differ in their diets at the breeding grounds (e.g. [42–44]). Metabolism is certainly different in growing birds as compared to adults. But Storm-Suke et al. [45] provide experimental evidence in quail that metabolic rate does not influence diet-tissue discrimination in hydrogen isotope values. Moreover, the consistency in average similarity in the isotopic signatures between juvenile and adult wheatear tail feathers hints on no substantial effects of age.

Immigration and emigration are crucial factors driving demography and dynamics of bird populations but not much is known about their magnitude or their annual variation. The use of stable isotopes may help fill this gap. In our study, isotope measurements of the feathers of northern wheatears indicated a high rate of immigration into the breeding population, which is consistent with low return rates of banded breeding adults as well as implying high emigration rates of local breeders. If emigration of adults is high throughout their breeding

lives, calculations of apparent survival may be inaccurate or impossible, and may not closely reflect true survival. However, in songbirds with high site-faithfulness once they become breeders [1], apparent survival of adult birds as revealed by return rates may not be far off of true survival.

Additional file

Additional file 1: Table S1. Sample sizes. Abbreviations: HY = hatch-year, SY = second year, AHY = after hatch-year, ASY = after second year. (XLSX 11 kb)

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

FB, DH and RN designed the study, FB, ED, DH and RN performed the study, CV performed the isotope analysis on the feathers, FB performed the statistical analysis and all authors contributed to the text. All authors read and approved the final manuscript.

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