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Feather stable isotope (δ^2H) measurements suggest no historical variation in latitudinal origin of migrants in two declining songbirds

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Abstract

The geographic origin of migratory birds can be traced using measurements of stable-hydrogen isotopes (δ^2H) in their feathers. In continental Europe, local amount-weighted mean annual δ^2H in precipitation varies with latitude, so that assignments of geographical origin of bird feathers are linked to latitude. Consequently, a potential northward latitudinal shift in the distribution of a species' abundance is expected to translate into a shift in δ^2H values for feathers grown on the breeding grounds. We analyzed δ^2H in feathers from migrant individuals of Brambling (*Fringilla montifringilla*) and Ortolan Bunting (*Emberiza hortulana*) collected in France from the mid-19th century to recent years (2015), to assess potential temporal trends in feather δ^2H that may indicate changes in source populations or a shifting breeding range. These two species have shown long-term population declines in Europe with subsequent range retractions, but we did not find obvious differences in feather δ^2H values in samples collected over the last 160 years. One potential explanation for this result is that population declines occurred similarly at all latitudes across the breeding ranges without involving a measurable latitudinal shift in abundance that could translate into changes in feather δ^2H values. However, this result may also be due to potential temporally shifting terrestrial spatial δ^2H gradients (i.e. isoscape) similar to a shift in bird abundances, or to limited northward range shifts that do not translate into detectable trends in feather δ^2H.

Keywords

Brambling; *Emberiza hortulana*; climate change; deuterium; *Fringilla montifringilla*; northward shift; Ortolan Bunting

Introduction

Many common breeding bird species are declining across the northern hemisphere because of global change, including climate change (Stephens et al. 2016, Rosenberg et al. 2019). Climatic change has been linked to northward shifts in bird breeding ranges for some species (Thomas and Lennon 1999, Hitch and Leberg 2007, Gillings et al. 2015). If climate change is responsible for declining population sizes at the southern range limit and increasing population sizes at a northern range limit (Jiguet et al. 2010), the average latitudinal origin of migrants should move northwards through time. This trend might be detectable as decreasing mean deuterium values in the feathers grown on the breeding grounds. Land-use change is also affecting bird abundances, especially for habitat specialists in the context of biotic homogenization (Devictor et al. 2008). If land use changes occurred heterogeneously in space, especially along latitudinal gradients, they might also provoke latitudinal shifts in relative abundance that could translate into changing δ^2H_f values.

Naturally occurring patterns of stable isotopes in foodwebs across large geographic areas enable the tracking of bird migration (Hobson and Wassennaar 2019). This is based on the principle that stable isotope ratios in tissues (e.g. feathers, blood) can be correlated with values of food and water consumed by birds following well-described processes (Hobson 2003). Protium (^1H) and the heavier isotope, deuterium (^2H), occur naturally in environmental waters, and the ratio of the heavier to lighter isotope ($^2H/^1H$ measured as δ^2H) in precipitation has been shown to change predictably at continental scales forming "isoscapes" (West et al. 2010). Indeed, δ^2H values in precipitation (δ^2H_p) generally have a latitudinal structure across continents (Bowen et al. 2005) and these patterns form the basis of tracing animal movements because such patterns are transferred up food webs and are locked into metabolically inert tissues such as feathers. Feathers grown at a given location generally have δ^2H values (δ^2H_f) proportional to local amount-weighted mean annual or growing-season δ^2H_p (Hobson et al. 2012), so that the geographic origin of migratory birds can be traced by studying stable isotopes in their feathers (Hobson and Wassenaar 2019). In continental Europe, local amount-weighted mean δ^2H_p has a latitudinal structure (Bowen et al. 2005), so that a potential latitudinal shift

in the distribution of a species' abundance could translate into a shift in δ^2H_f values for feathers grown on the breeding grounds.

Terrestrial isotopic landscapes are presumed to be relatively static across recent time scales providing an opportunity to determine temporal trends in migratory connectivity or trophic networks using stable isotopes (e.g. Hobson 2003; Hobson et al. 2010; Guillemain et al. 2019). Isotopic landscapes are reported to have changed in marine environments (Kurle and McWhorther 2017, de la Vega et al. 2019); however, few studies have investigated temporal trends in terrestrial isoscapes. Duliński et al. (2019) found no temporal trend of deuterium in monthly precipitation at Krakow, Poland, over 44 years, though in the same precipitation samples, deuterium concentration decreased with increasing air temperature. Hence, at a continental scale, if a possible shift in the deuterium isoscape could ensure from climate change, such changes have not yet been observed (Reckerth et al. 2017). Moreover, if occurring, such shifts should be more obvious in recent decades as the effects of climate change have become more pronounced, but there is currently no evidence for such change for deuterium. As such, we retain here the most plausible hypothesis of a static terrestrial deuterium landscape since the mid-19th century.

Our objective in this study was to compare δ^2H_f values in samples collected in France over a long time period (from mid 19th to early 21st centuries), by considering two migratory passerine species suffering long-term declines as model subjects: Brambling *Fringilla montifringilla* and Ortolan Bunting *Emberiza hortulana*. We sought to determine whether historical and modern δ^2H_f data have similar distributions, or if putative distributional shifts could mirror spatially structured trends in abundance.

Methods

Study species

The Brambling is a short-distance migrant that breeds in the northern forests and taiga with a breeding distribution in the Palearctic, across Scandinavia (except southern Sweden) and Russia towards eastern

Siberia. There are no obvious trends reported for the distribution of its breeding range over the last decades. The current winter distribution of this species includes western and southern Europe, from Denmark to Iberia and Turkey. On the wintering grounds, bramblings sometimes form large nocturnal roost sites, where millions of birds gather at night. European breeding populations have declined by 48% since 1980 with a consistent decrease in numbers since the early 1990s (PECBMS 2019) attributed to changes in forest structure and management (Lehikoinen et al. 2014) but also to climate change coinciding with a significant 64 km northward shift in average Finnish breeding densities from the 1970s into the 2000s (Lehikoinen and Virkkala 2016). Adult Bramblings have a complete summer moult on their breeding grounds, replacing all flight feathers (including rectrices) in July-September. First-winter individuals have at most replaced a few greater coverts (Brown and Mead 2003). Hence, all winter individuals, either adults or first-winter individuals, have feathers grown on the breeding grounds.

The Ortolan Bunting is a long-distance Palearctic migrant songbird that breeds across Eurasia from Scandinavia to the Middle East and winters south of the Sahara in Africa. European populations have suffered a continuous decline since 1980, with a 90% reduction in population size during the period 1980-2017 (PECBMS 2019). The main drivers have been identified as habitat destruction through agricultural intensification (Menz and Arlettaz 2012), poaching (Jiguet et al. 2019) and potentially climate change (Jiguet et al. 2020). Populations breeding in southern Europe display higher growth rates than those breeding at more northern latitudes (Jiguet et al. 2016). Ortolan Buntings undergo a complete post-breeding moult on the breeding grounds before fall migration, while first-calendar-year individuals maintain feathers grown in the nest. Hence, migrants captured during the autumn have feathers grown on their breeding grounds.

Sampling Bramblings and Ortolan Buntings

Our Brambling sample first benefited from a collection of single tail feathers collected from individuals caught and ringed at a huge nocturnal roost near Pau (Pyrénées-Atlantiques), France, during 22-31

December 1969 (n=192), preserved at the National Museum of Natural History in Paris, France (MNHN, CRBPO ringing scheme). We also organized sampling of feathers by ringers at their garden feeders across the country in winter 2013 -14 and 2014-15 (n=34), including the collection of feathers at a huge roost in January 2015 (up to 4 million bramblings at Kirchberg, Haut-Rhin, France; n=160). We further sampled museum specimens held at MNHN, collected between 1860 and 2009 (n=81). The list of these MNHN specimens is provided in Appendix 1.

For the Ortolan Bunting, we first collected a few body feathers from individuals captured during autumn migration in France in 2012, 2013, 2014 and 2015 (n=74; Jiguet et al. 2019). We also collected body feathers from museum specimens collected in France during autumn migration (n=7 for the period 1872-1897; n=7 for 1951-1969). The list of these specimens in provided in Appendix 1. We stored feathers in individual envelopes at ambient temperature until isotopic analysis.

Hydrogen isotopic measurements

Feathers were cleaned in 2:1 chloroform:methanol solvent rinse and prepared for δ^2H analysis at the Stable Isotope Laboratory of Environment Canada, Saskatoon, Canada. The δ^2H of the non-exchangeable hydrogen of feathers was determined using the method described by Wassenaar and Hobson (2003) based on two calibrated keratin hydrogen-isotope reference materials (CBS: -197 ‰, KHS: -54.1 ‰). We performed hydrogen isotopic measurements on H_2 gas derived from high-temperature (1350 °C) flash pyrolysis (Eurovector 3000; Milan, Italy) of 350 ± 10 ug feather subsamples and keratin standards loaded into silver capsules. Resultant separated H_2 was analysed on an interfaced Isoprime (Crewe, UK) continuous-flow isotope-ratio mass spectrometer. Measurement of the two keratin laboratory reference materials corrected for linear instrumental drift were both accurate and precise with typical within-run measurement error < 2 ‰. All results are reported for non-exchangeable H expressed in the typical delta notation, in units of per mil (‰), and normalized on the Vienna Standard Mean Ocean Water–Standard Light Antarctic Precipitation (VSMOW-SLAP) standard scale.

Statistical analyses

To detect potential temporal trends in δ^2H_f values within species, we performed both Kruskal-Wallis rank sum tests (as some subsamples are of small size), but also generalized linear models, as the specific global datasets did not depart from a normal distribution (Shapiro-Wilk normality tests: bramblings W=0.99, P=0.19; buntings, W=0.97, P=0.054). Potential temporal differences were tested by comparing periods (Kruskal-Wallis tests and linear models) or as a linear temporal trend (linear models). When applicable (for Bramblings only), we also tested for potential differences in δ^2H_f between age classes and/or sexes in linear models.

Results

Figure 1 shows the boxplot of δ^2H_f values for Bramblings sampled at different periods (including feathers collected at two dormitories). Average ± s.d. deuterium concentrations for the different groups were: -95.28 ± 11.00 (1850-1899, n=17), -98.36 ± 10.42 (1900-1949, n=43), -96.38 ± 16.29 (1950-1999, n=19), -94.95 ± 10.37 (2000-2015, n=36), -98.89 ± 13.58 (1969 dormitory), -99.51 ± 12.92 (2015 dormitory).We found no significant difference in δ^2H_f for the different time periods (Kruskal-Wallis test, chi-sq=4.38 , df=5, P=0.50; linear model, $F_{5,449}$=1.09, P=0.37), and no difference between sexes (for the subsample of birds of known sex, $F_{1,290}$=1.23, P=0.27) and between ages (first-winter vs. older, for the subsample of birds of known age, $F_{1,247}$=1.00, P=0.32). We found no significant temporal linear trend in δ^2H_f (t_{453}=-0.71, P=0.48) even when excluding the large samples collected in 1969 and 2015 at large roosts (t_{113}=0.62, P=0.54). No temporal trend was detected in the global dataset even after accounting for sex and age (t_{244}=0.60, P=0.55).

Figure 2 shows the boxplot for Ortolan Buntings sampled at three different periods. Average ± s.d. deuterium concentrations were -90.18 ± 19.36 (1872-1897, n=7), -75.59 ± 15.32 (1951-1969, n=7) and -85.28 ± 15.32 (2012-2015, n=74). We found no statistical difference in δ^2H_f measured from specimens

161 collected during these three periods (Kruskal-Wallis, chi-sq= 1.28, df=2, P=0.53; linear model,
162 $F_{2,85}$=0.43, P=0.65).

163

164 **Discussion**

165 We failed to find any temporal structure in the δ^2H_f values for two species that have declined
166 precipitously over the last century, Brambling and Ortolan Bunting. If climate change was responsible
167 for a substantial northward shift in abundance for these species, we might have detected a decrease
168 in δ^2H_f values either throughout the studied period, or in more recent periods when temperature
169 increases were more obvious (Gregory et al. 2009). Our failure to detect such a structure might be due
170 to several factors. The first explanation is technical, not biological, as small sample sizes reduce the
171 statistical power to detect any existing trends. Although if this holds for the Ortolan Buntings here, as
172 we had only 7 samples for each of the two old periods, we had large samples of Bramblings. A biological
173 explanation is that population declines occurred similarly at all latitudes across the breeding range, so
174 without provoking an obvious latitudinal shift in abundance. Such a pattern could occur either because
175 the effects of climate change were balanced across latitudes, or because the effects of land-use
176 changes counter-balanced directional effects of climate change. As there is strong support for
177 latitudinal trends structuring long-term population growth rates facing climate change for common
178 songbirds in Europe (Jiguet et al. 2010), this would suggest an antagonistic strong latitudinal trend in
179 land-use change, affecting farmland (Ortolan Bunting) as well as woodland (Brambling) habitats. As an
180 example, while Lehikoinen and Virkkala (2016) observed a significant northward shift in Brambling
181 abundance in Finland, intensive forestry expanded northward during the 20th century in the same
182 country (Kotilainen and Rytteri 2011). Furthermore, the Brambling is a forest-habitat generalist, and
183 therefore its trends are not likely to be explained by habitat alterations caused by forestry (Virkkala
184 1991), while its range is bounded northwards by the Barents Sea, making any northwards expansion
185 impossible - although an average northwards shift has been found (Lehikoinen and Virkkala 2016). We

sampled from only one area in France and migratory connectivity between breeding and non-breeding areas for this sampling region may not represent shifts in breeding ranges across the entire populations of both study species. Therefore, similar studies in other parts of the non-breeding range would be useful but are currently unattainable due to a lack of historic samples.

A plausible alternative is that latitudinal shifts occurred but not to the extent of translating into a detectable shift in feather hydrogen isotope values. For example, the northward shift in density of Brambling in Finland since the 1970s is statistically significant but only 64 km, while it is non-significant at 9 km for Ortolan Bunting (Lehikoinen and Virkkala 2016). These short and recent shifts in ranges are unlikely to result in a significant shift in δ^2H_f values because δ^2H_p gradients occur at larger scales on the order of hundreds of kilometres. Finally, our inferences are based on the assumption that the δ^2H_p isoscape for Europe has not changed significantly over this period of feather sampling. Unfortunately, the International Atomic Energy Agency (IAEA) Global Network of Isotopes in Precipitation (GNIP) is only ~60 years old. Nonetheless, there appears to be little evidence for a systematic change in the GNIP data for western Europe during that time period based on surface waters (Reckerth et al. 2017) and the long-term GNIP precipitation isoscape for Europe provides excellent calibration between feather and mean annual δ^2H_p (Prochazka et al. 2013).

Although there is published evidence for some shifts in marine isoscapes (Kurle & McWhorther 2017, de la Vega et al. 2019), there is no such evidence for terrestrial environments, while this is also not the general rule in marine environments (MacKenzie et al. 2014). Indeed, broad geographic variations in stable carbon and nitrogen isotope distributions across the North Sea are consistent with previously published variations seen in archaeological fish bones from the ninth to seventeenth centuries, despite dramatic changes in land use in the past 1,000 years (MacKenzie et al. 2014). Therefore, stable isotope-based studies of movements in animals can consequently be referenced to available modern isoscape models, unless a contradictory evidence is produced. Nevertheless, more retrospective studies are needed for terrestrial ecosystems to definitely validate this assumption (Hobson et al. 2010).

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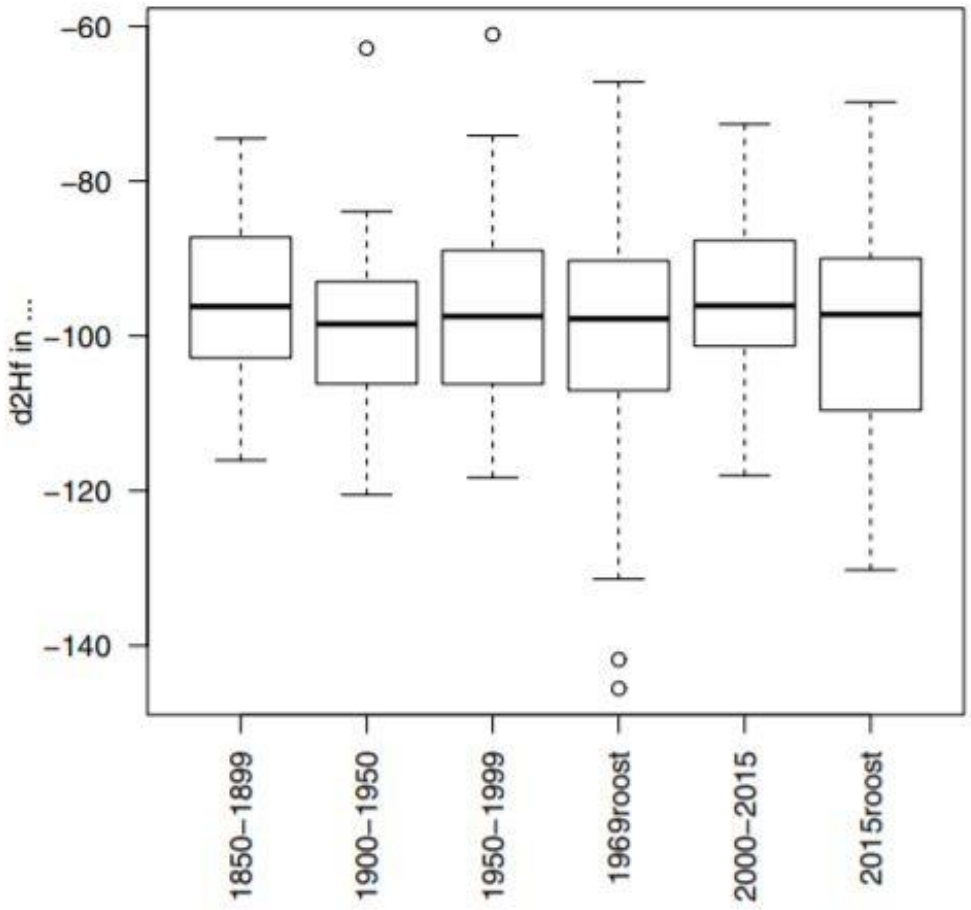
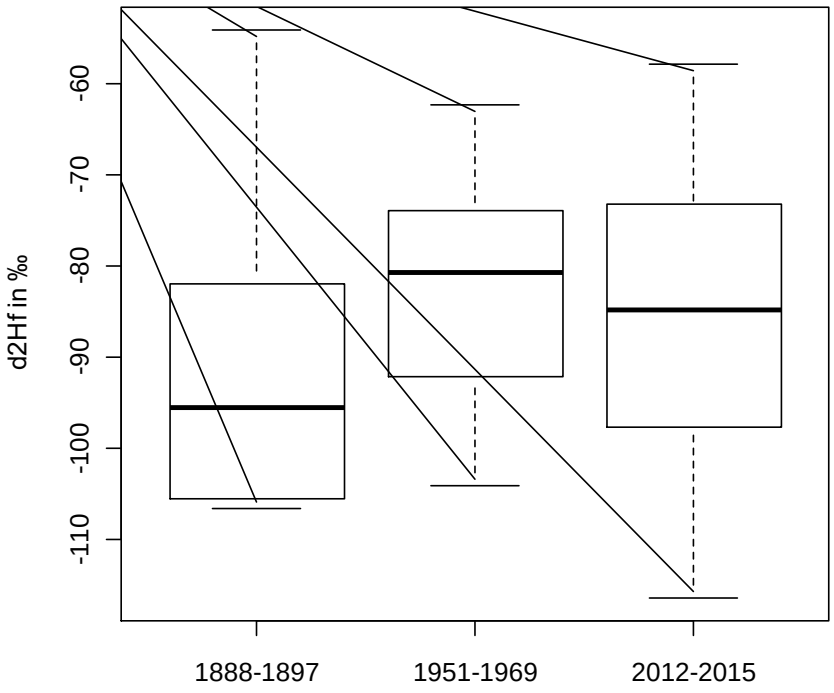
Figure 1. Boxplots showing variation in deuterium values in Brambling feathers (δ^2H_f in ‰) for different time-periods. Each boxplot reports median, 1st and 3rd quartiles, minimum and maximum values and dots for outliers. Data from two large dormitories (in December 1969 and January 2015) have been separated. Sample sizes are as follows: 1860-1899 (n=17), 1900-1950 (n=43), 1950-1999 (n=19), 1969 roost (n=192), 2000-2015 (n=24), 2015 roost (n=160).



311 Figure 2. Boxplot of deuterium concentration values in Ortolan Bunting feathers (δ^2H_f in ‰) for three

312 different time periods. Each boxplot reports median, 1st and 3rd quartiles, min and max values.

313 Sample sizes as follows: 1888-1897 (n=7), 1951-1969 (n=7), 2012-2015 (n=74).



314

315

316 Appendix 1. List of referenced museum specimens considered in this study.

317 Ortolan Buntings. Muséum National d'Histoire Naturelle de Paris (MNHN): CG1888-2141, CG1888-
318 2140 (both collected 31 August 1888, in Gironde), CG1997-518 (21 September 1956, Gironde),
319 CG1997-519 (16 August 1951, Gironde), CG1997-520 (17 August 1952, Gironde), CG1997-521 (9
320 September 1954, Gironde), CG1972-1548 (25 August 1952, Gironde), CG1972-1547 (22 August 1952,
321 Gironde), CG1969-1106 (20 August 1969, Savoie), CG1995-22 (19 August 1993, Hautes Alpes), and
322 two specimens from the collection labeled E. Anfrie (both 6 September 1888, Hautes-Pyrénées).
323 Muséum d'Histoire Naturelle de Bayonne: one collected at Gaillac 29 August 1897, one collected at
324 Arros-Nay 1st September 1889. Muséum d'Histoire Naturelle de Toulouse: MHNT EMB 1999 8
325 (collected 15 August 1880 at Vieille Toulouse).

326 Bramblings. Muséum National d'Histoire Naturelle de Paris (MNHN): CG1937-1279, CG1948-31,
327 CG1948-28, CG1968-1722, CG1968-1723, CG1968-1724, CG1948-29, CG1948-30, CG1960-78,
328 CG1960-2567, CG1960-2568, CG1965-2810, CG1970-1065,CG1970-1066, CG1970-1067,CG1972-
329 1472, CG1972-1468,CG1965-2811, CG1965-2812, CG1965-2813, CG1965-2816, CG1913-554,
330 CG1911-204, CG1911-203, CG1908-280,CG1908-279, CG1907-899, CG1907-539, CG1997-482,
331 CG1997-1452, CG2006-304, CG2001-1213, CG2001-1206, CG2000-1646, CG1991-200, CG1978-249,
332 CG1978-248, CG1978-247, CG1976-66, CG1975-302, CG1978-250, CG1978-251, CG1990-445,
333 CG1978-254, CG1978-252, CG1997-1453, CG2005-1935, CG2005-1936, CG1997-484, CG1997-483,
334 CG1997-486, CG1913-553, CG1937-1280, CG1960-2569, CG1960-2570, CG1960-2571, CG1960-2572,
335 CG1962-3375, CG1965-2817, CG1965-2815, CG1970-1068, CG1970-1069, CG1978-253, CG1978-255,
336 CG1986-136, CG1989-178, CG1904-1232, CG1888-1924, CG1888-1925, CG1888-1927, CG1888-1928,
337 CG1888-1923, CG1888-1921, CG1888-1920, CG1888-1929; and three specimens labelled "collection
338 of E. Anfrie" without CG references.