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1 **Feather stable isotope ($\delta^2\text{H}$) measurements suggest no historical**
2 **variation in latitudinal origin of migrants in two declining songbirds**

3

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15 **Abstract**

16 The geographic origin of migratory birds can be traced using measurements of stable-hydrogen
17 isotopes ($\delta^2\text{H}$) in their feathers. In continental Europe, local amount-weighted mean annual $\delta^2\text{H}$ in
18 precipitation varies with latitude, so that assignments of geographical origin of bird feathers are linked
19 to latitude. Consequently, a potential northward latitudinal shift in the distribution of a species'
20 abundance is expected to translate into a shift in $\delta^2\text{H}$ values for feathers grown on the breeding
21 grounds. We analyzed $\delta^2\text{H}$ in feathers from migrant individuals of Brambling (*Fringilla montifringilla*)
22 and Ortolan Bunting (*Emberiza hortulana*) collected in France from the mid-19th century to recent years
23 (2015), to assess potential temporal trends in feather $\delta^2\text{H}$ that may indicate changes in source
24 populations or a shifting breeding range. These two species have shown long-term population declines
25 in Europe with subsequent range retractions, but we did not find obvious differences in feather $\delta^2\text{H}$
26 values in samples collected over the last 160 years. One potential explanation for this result is that
27 population declines occurred similarly at all latitudes across the breeding ranges without involving a
28 measurable latitudinal shift in abundance that could translate into changes in feather $\delta^2\text{H}$ values.
29 However, this result may also be due to potential temporally shifting terrestrial spatial $\delta^2\text{H}$ gradients
30 (i.e. isoscape) similar to a shift in bird abundances, or to limited northward range shifts that do not
31 translate into detectable trends in feather $\delta^2\text{H}$.

32

33 **Keywords**

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

36 **Introduction**

37 Many common breeding bird species are declining across the northern hemisphere because of global
38 change, including climate change (Stephens et al. 2016, Rosenberg et al. 2019). Climatic change has
39 been linked to northward shifts in bird breeding ranges for some species (Thomas and Lennon 1999,
40 Hitch and Leberg 2007, Gillings et al. 2015). If climate change is responsible for declining population
41 sizes at the southern range limit and increasing population sizes at a northern range limit (Jiguet et al.
42 2010), the average latitudinal origin of migrants should move northwards through time. This trend
43 might be detectable as decreasing mean deuterium values in the feathers grown on the breeding
44 grounds. Land-use change is also affecting bird abundances, especially for habitat specialists in the
45 context of biotic homogenization (Devictor et al. 2008). If land use changes occurred heterogeneously
46 in space, especially along latitudinal gradients, they might also provoke latitudinal shifts in relative
47 abundance that could translate into changing $\delta^2\text{H}_f$ values.

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

62 in the distribution of a species' abundance could translate into a shift in $\delta^2\text{H}_f$ values for feathers grown
63 on the breeding grounds.

64 Terrestrial isotopic landscapes are presumed to be relatively static across recent time scales
65 providing an opportunity to determine temporal trends in migratory connectivity or trophic networks
66 using stable isotopes (e.g. Hobson 2003; Hobson et al. 2010; Guillemain et al. 2019). Isotopic
67 landscapes are reported to have changed in marine environments (Kurle and McWhorther 2017, de la
68 Vega et al. 2019); however, few studies have investigated temporal trends in terrestrial isoscapes.
69 Duliński et al. (2019) found no temporal trend of deuterium in monthly precipitation at Krakow,
70 Poland, over 44 years, though in the same precipitation samples, deuterium concentration decreased
71 with increasing air temperature. Hence, at a continental scale, if a possible shift in the deuterium
72 isoscape could ensue from climate change, such changes have not yet been observed (Reckerth et al.
73 2017). Moreover, if occurring, such shifts should be more obvious in recent decades as the effects of
74 climate change have become more pronounced, but there is currently no evidence for such change for
75 deuterium. As such, we retain here the most plausible hypothesis of a static terrestrial deuterium
76 landscape since the mid-19th century.

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

82

83 **Methods**

84 **Study species**

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

87 Siberia. There are no obvious trends reported for the distribution of its breeding range over the last
88 decades. The current winter distribution of this species includes western and southern Europe, from
89 Denmark to Iberia and Turkey. On the wintering grounds, bramblings sometimes form large nocturnal
90 roost sites, where millions of birds gather at night. European breeding populations have declined by
91 48% since 1980 with a consistent decrease in numbers since the early 1990s (PECBMS 2019) attributed
92 to changes in forest structure and management (Lehikoinen et al. 2014) but also to climate change
93 coinciding with a significant 64 km northward shift in average Finnish breeding densities from the
94 1970s into the 2000s (Lehikoinen and Virkkala 2016). Adult Bramblings have a complete summer moult
95 on their breeding grounds, replacing all flight feathers (including rectrices) in July-September. First-
96 winter individuals have at most replaced a few greater coverts (Brown and Mead 2003). Hence, all
97 winter individuals, either adults or first-winter individuals, have feathers grown on the breeding
98 grounds.

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

109 **Sampling Bramblings and Ortolan Buntings**

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

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

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

123 **Hydrogen isotopic measurements**

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

137 **Statistical analyses**

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

145

146 **Results**

147 Figure 1 shows the boxplot of $\delta^2\text{H}_f$ values for Bramblings sampled at different periods (including
148 feathers collected at two dormitories). Average \pm s.d. deuterium concentrations for the different
149 groups were: -95.28 ± 11.00 (1850-1899, $n=17$), -98.36 ± 10.42 (1900-1949, $n=43$), -96.38 ± 16.29
150 ($1950-1999$, $n=19$), -94.95 ± 10.37 (2000-2015, $n=36$), -98.89 ± 13.58 (1969 dormitory), -99.51 ± 12.92
151 (2015 dormitory). We found no significant difference in $\delta^2\text{H}_f$ for the different time periods (Kruskal-
152 Wallis test, $\chi^2=4.38$, $df=5$, $P=0.50$; linear model, $F_{5,449}=1.09$, $P=0.37$), and no difference between
153 sexes (for the subsample of birds of known sex, $F_{1,290}=1.23$, $P=0.27$) and between ages (first-winter vs.
154 older, for the subsample of birds of known age, $F_{1,247}=1.00$, $P=0.32$). We found no significant temporal
155 linear trend in $\delta^2\text{H}_f$ ($t_{453}=-0.71$, $P=0.48$) even when excluding the large samples collected in 1969 and
156 2015 at large roosts ($t_{113}=0.62$, $P=0.54$). No temporal trend was detected in the global dataset even
157 after accounting for sex and age ($t_{244}=0.60$, $P=0.55$).

158 Figure 2 shows the boxplot for Ortolan Buntings sampled at three different periods. Average \pm s.d.
159 deuterium concentrations were -90.18 ± 19.36 (1872-1897, $n=7$), -75.59 ± 15.32 (1951-1969, $n=7$) and
160 -85.28 ± 15.32 (2012-2015, $n=74$). We found no statistical difference in $\delta^2\text{H}_f$ 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 $\delta^2\text{H}_f$ 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 $\delta^2\text{H}_f$ 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

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

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

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

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217

218 **References**

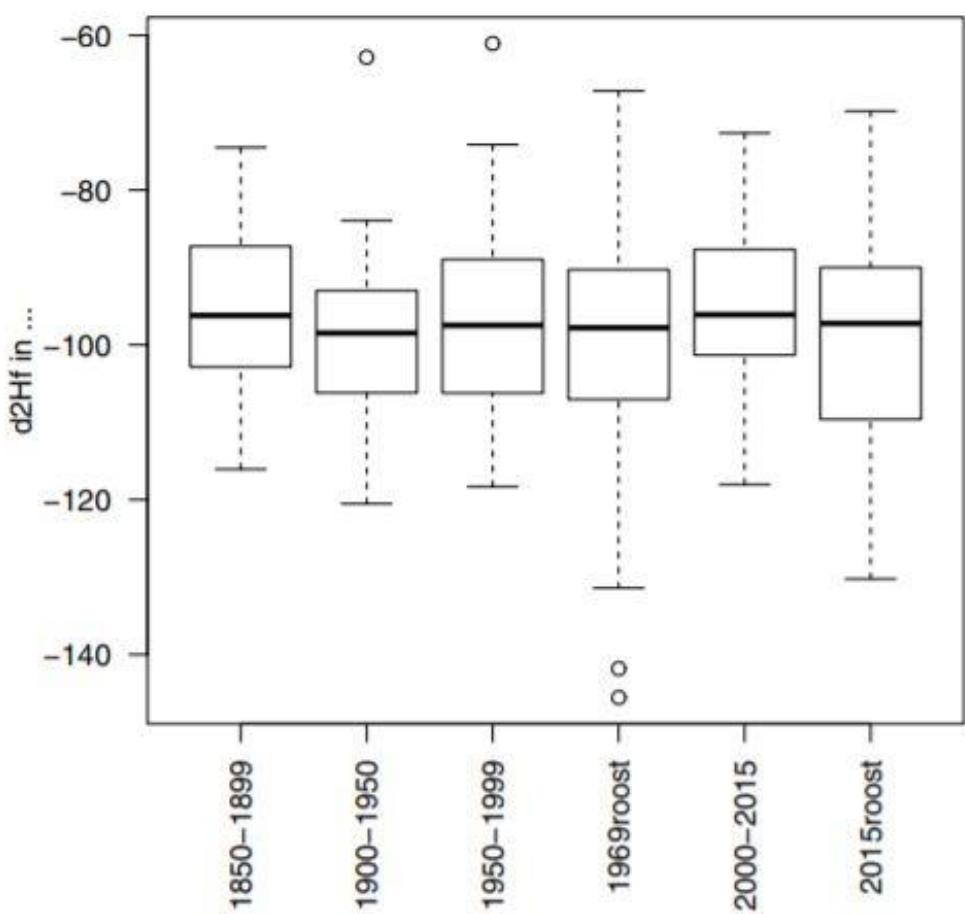
- 219 Bowen GJ, Wassenaar LI, Hobson KA (2005) Global application of stable hydrogen and oxygen
220 isotopes to wildlife forensics. *Oecologia* 143: 337–348
- 221 Browne S, Mead C (2003) Age and sex composition, biometrics, site fidelity and origin of Brambling
222 *Fringilla montifringilla* wintering in Norfolk, England. *Ringing & Migration* 21: 145–153
223 10.1080/03078698.2003.9674283
- 224 de la Vega C, Jeffreys RM, Tuerena R, Ganeshram R, Mahaffey C (2019) Temporal and spatial trends
225 in marine carbon isotopes in the Arctic Ocean and implications for food web studies. *Global
226 Change Biology* 25(12): 4116–4130
- 227 Devictor V, Julliard R, Clavel J, Jiguet F, Lee A & Couvet D (2008) Functional biotic homogenization of
228 bird communities in disturbed landscapes. *Global Ecology and Biogeography* 17(2): 252-261
- 229 Duliński M, Różański K, Pierchała A, Gorczyca Z, Marzec M (2019) Isotopic composition of
230 precipitation in Poland: a 44-year record. *Acta Geophysica* 67, 1637–1648
- 231 Gillings S, Balmer DE, Fuller RJ (2015) Directionality of recent bird distribution shifts and climate
232 change in Great Britain. *Glob Chang Biol* 21: 2155-68
- 233 Gregory RD, Willis SG, Jiguet F, Voříšek P, Pazderová A, van Strien A, Huntley B, Collingham YC,
234 Couvet D, Green RE (2009) An indicator of the impact of climate change on European bird
235 populations. *PloS ONE* 4(3): e4678

- 236 Guillemain, M., L. Bacon, K. J. Kardynal, A. Olivier; M. Podhrazsky, P. Musil and K. A. Hobson. 2019.
- 237 Combining stable isotopes ($\delta^2\text{H}$) with rings and neck collars: geographic origin of Greylag Geese
- 238 (*Anser anser*) wintering in Camargue, southern France. European Journal of Wildlife Research,
- 239 <https://doi.org/10.1007/s10344-019-1304-4>
- 240 Hitch AT, Leberg PL (2007) Breeding distributions of North American bird species moving North as a
- 241 result of climate change. *Cons. Biol.* 21: 534–539
- 242 Hobson, K.A. 2003. Making Migratory Connections with Stable Isotopes. In *Avian Migration* (P.
- 243 Berthold, E. Gwinner & E. Sonnenschein, eds). Springer-Verlag, Berlin Heidelberg New York
- 244 Hobson KA, Van Wilgenburg SL, Wassenaar LI, Larson K (2012) Linking Hydrogen ($\delta^2\text{H}$) Isotopes in
- 245 feathers and precipitation: sources of variance and consequences for assignment to isoscapes,
- 246 *PLoS One* 7(4): e35137
- 247 Hobson KA, Wassenaar LI (2019) Tracking Animal Migration using Stable Isotopes. *Handbook of*
- 248 *Terrestrial Ecology Series*, Academic Press / Elsevier, Amsterdam, ISBN: 9780128147238
- 249 Hobson KA, Greenberg R, Van Wilgenburg S, Mettke-Hofmann C (2010) Migratory connectivity in the
- 250 Rusty Blackbird (*Euphagus carolinus*) in North America: Isotopic evidence from feathers of
- 251 historical and contemporary specimens. *Condor* 112: 778–788
- 252 Jiguet F, Devictor V, Ottvall R, Van Turnhout C, Van der Jeugd H, Lindström Å (2010) Bird population
- 253 trends are linearly affected by climate change along species thermal ranges. *Proceedings of the*
- 254 *Royal Society B-Biological Sciences* 277: 3601–3618
- 255 Jiguet F, Arlettaz R, Bauer HG, Belik V, Copete JL, Couzi L, Czajkowski MA, Dale S, Dombrovski V, Elts J,
- 256 Ferrand Y, Hargues R, Kirwan GM, Minkevicius S, Piha M, Selstam G, Skierczyński M, Siblet J-P,
- 257 Sokolov A (2016) An update of European breeding population sizes and trends of the Ortolan
- 258 Bunting (*Emberiza hortulana*). *Ornis Fennica* 93: 186–196
- 259 Jiguet F, Robert A, Lorrillière R, Hobson KA, Kardynal KJ, Arlettaz R, Bairlein F, Belik V, Bernardy P,
- 260 Copete JL, Czajkowski MA, Dale S, Dombrovski V, Ducros D, Efrat R, Elts J, Ferrand Y, Marja R,
- 261 Minkevicius S, Olsson P, Pérez M, Piha M, Raković M, Schmaljohann H, Seimola T, Selstam G, Siblet

- 262 J-P, Skierczyński M, Sokolov A, Sondell J, Moussy C (2019) Unravelling migration connectivity
263 reveals unsustainable hunting of the declining ortolan bunting. *Science Advances* 5: eaau2642
- 264 Jiguet F, Burgess M, Thorup K, Conway G, Arroyo Matos JL, Barber L, Black J, Burton N, Castelló J,
265 Clewley G, Copete JL, Czajkowski MA, Dale S, Davis T, Dombrovski V, Drew M, Elts J, Gilson V,
266 Grzegorczyk E, Henderson I, Holdsworth M, Husbands R, Lorriilliere R, Marja R, Minkevicius S,
267 Moussy C, Olsson P, Onrubia A, Pérez M, Piacentini J, Piha M, Pons J-M, Procházka P, Raković M,
268 Robins H, Seimola T, Selstam G, Skierczyński M, Sondell J, Thibault J-C, Tøttrup AP, Walker J,
269 Hewson J (2020) Desert crossing strategies of migrant songbirds vary between and within species.
270 *Scientific Reports* 10.1038/s41598-019-56677-4
- 271 Kotilainen J, Rytteri T (2011) Transformation of forest policy regimes in Finland since the 19th
272 century. *Journal of Historical Geography* 37: 429–439
- 273 Kurle CM, McWhorther JK (2017) Spatial and temporal variability within marine isoscapes:
274 implications for interpreting stable isotope data from marine systems. *Marine Ecology Progress Series*
275 Series 568: 31-45
- 276 Lehikoinen A, Green M, Husby M, Kålås JA, Lindström Å (2014) Common montane birds are declining
277 in northern Europe. *Journal of Avian Biology* 45: 3–14
- 278 Lehikoinen A, Virkkala R (2016) North by north-west: climate change and directions of density shifts
279 in birds. *Global Change Biology* 22: 1121–1129. doi.org/10.1111/gcb.13150
- 280 MacKenzie KM, Longmore C, Preece C, Lucas CH, Trueman CN (2014) Testing the long-term stability
281 of marine isoscapes in shelf seas using jellyfish tissues. *Biogeochemistry* 121, 441–454
- 282 Menz MHM, Arlettaz R (2012) The precipitous decline of the ortolan bunting *Emberiza hortulana*:
283 time to build on scientific evidence to inform conservation management. *Oryx* 46: 122–129

- 284 Procházka P, van Wilgenburg S, Neto J, Yosef R, Hobson KA (2013) Using stable hydrogen isotopes
285 ($\delta^2\text{H}$) and ring recoveries to trace natal origins in a Eurasian passerine with a migratory divide.
286 *Journal of Avian Biology* 44:1-10.
- 287 PECBMS (2019) <https://pecbms.info/trends-and-indicators/species-trends/>. Consulted 20 December
288 2019
- 289 Reckerth A, StichlerW, Schmidt A, Stumpp C (2017) Long-term data set analysis of isotopes in German
290 rivers. *Journal of Hydrology* 552:718–731
- 291 Rosenberg et al. (2019) Decline of the North American avifauna. *Science*. eaaw1313.
292 doi:10.1126/science.aaw1313
- 293 Thomas C, Lennon J (1999) Birds extend their ranges northwards. *Nature* 399: 213.
294 doi:10.1038/20335
- 295 Virkkala R (1991) Population trends of forest birds in a Finnish Lapland landscape of large habitat
296 blocks: Consequences of stochastic environmental variation or regional habitat alteration? *Biol.*
297 *Conserv.* 56: 223–240
- 298 Wassenaar LI, Hobson KA (2003) Comparative equilibration and online technique for determination
299 of non-exchangeable hydrogen of keratins for use in animal migration studies, *Isotopes Environ.*
300 *Health Stud.* 39: 211–217
- 301 West JB, Bowen GJ, Dawson TE, Tu KP (Eds) (2010) Isoscapes: understanding movement, pattern, and
302 process on Earth through isotope mapping, Springer, Dordrecht, The Netherlands, ISBN:
303 9789048133536

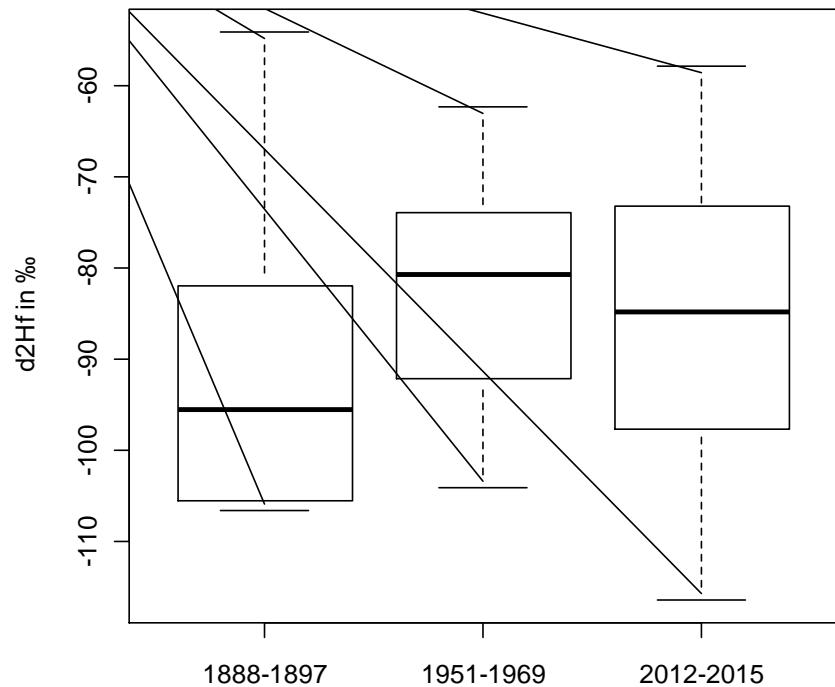
304 Figure 1. Boxplots showing variation in deuterium values in Brambling feathers ($\delta^2\text{H}_f$ in ‰) for
305 different time-periods. Each boxplot reports median, 1st and 3rd quartiles, minimum and maximum
306 values and dots for outliers. Data from two large dormitories (in December 1969 and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



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310

311 Figure 2. Boxplot of deuterium concentration values in Ortolan Bunting feathers ($\delta^2\text{H}_f$ 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).



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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.