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## ► To cite this version:

Frédéric Jiguet, Kevin Kardynal, Keith Hobson. Feather stable isotope ( $\delta^2\text{H}$ ) measurements suggest no historical variation in latitudinal origin of migrants in two declining songbirds. *Journal für Ornithologie = Journal of Ornithology*, 2020, 161 (4), pp.1045-1050. <10.1007/s10336-020-01797-2>. <mnhn-03082772>

**HAL Id: mnhn-03082772**

**<https://mnhn.hal.science/mnhn-03082772v1>**

Submitted on 18 Dec 2020

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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-19<sup>th</sup> 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 ( $^1\text{H}$ ) and the  
52 heavier isotope, deuterium ( $^2\text{H}$ ), 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-19<sup>th</sup> 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 19<sup>th</sup> to early 21<sup>st</sup> 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  $\text{H}_2$  gas derived from high-  
129 temperature (1350 °C) flash pyrolysis (Eurovector 3000; Milan, Italy) of  $350 \pm 10$  ug feather subsamples  
130 and keratin standards loaded into silver capsules. Resultant separated  $\text{H}_2$  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:  $-95.28 \pm 11.00$  (1850-1899,  $n=17$ ),  $-98.36 \pm 10.42$  (1900-1949,  $n=43$ ),  $-96.38 \pm 16.29$   
150 (1950-1999,  $n=19$ ),  $-94.95 \pm 10.37$  (2000-2015,  $n=36$ ),  $-98.89 \pm 13.58$  (1969 dormitory),  $-99.51 \pm 12.92$   
151 (2015 dormitory). We found no significant difference in  $\delta^2\text{H}_f$  for the different time periods (Kruskal-  
152 Wallis test,  $\text{chi-sq}=4.38$ ,  $\text{df}=5$ ,  $P=0.50$ ; 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  $-90.18 \pm 19.36$  (1872-1897,  $n=7$ ),  $-75.59 \pm 15.32$  (1951-1969,  $n=7$ ) and  
160  $-85.28 \pm 15.32$  (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  $\delta^2H_f$  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  $\delta^2H_f$  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 Lehtikoinen and Virkkala (2016) observed a significant northward shift in Brambling  
181 abundance in Finland, intensive forestry expanded northward during the 20<sup>th</sup> 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 (Lehtikoinen 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).

211 **Acknowledgements** We are indebted to all ringers who captured, ringed and sampled ortolan buntings and  
212 bramblings, under the license provided by the French national ringing scheme CRBPO. FJ thanks Nicolas Minéry  
213 for organizing the collection of feathers at the 2015 Kirchberg brambling dormitory. Environment and Climate  
214 Change Canada supported the stable isotope analyses through an operating grant to Keith Hobson. We are  
215 indebted to the curators of the bird collections at MNHN, at Museum d’Histoire Naturelle de Bayonne, and  
216 Museum d’Histoire Naturelle de Toulouse.

217

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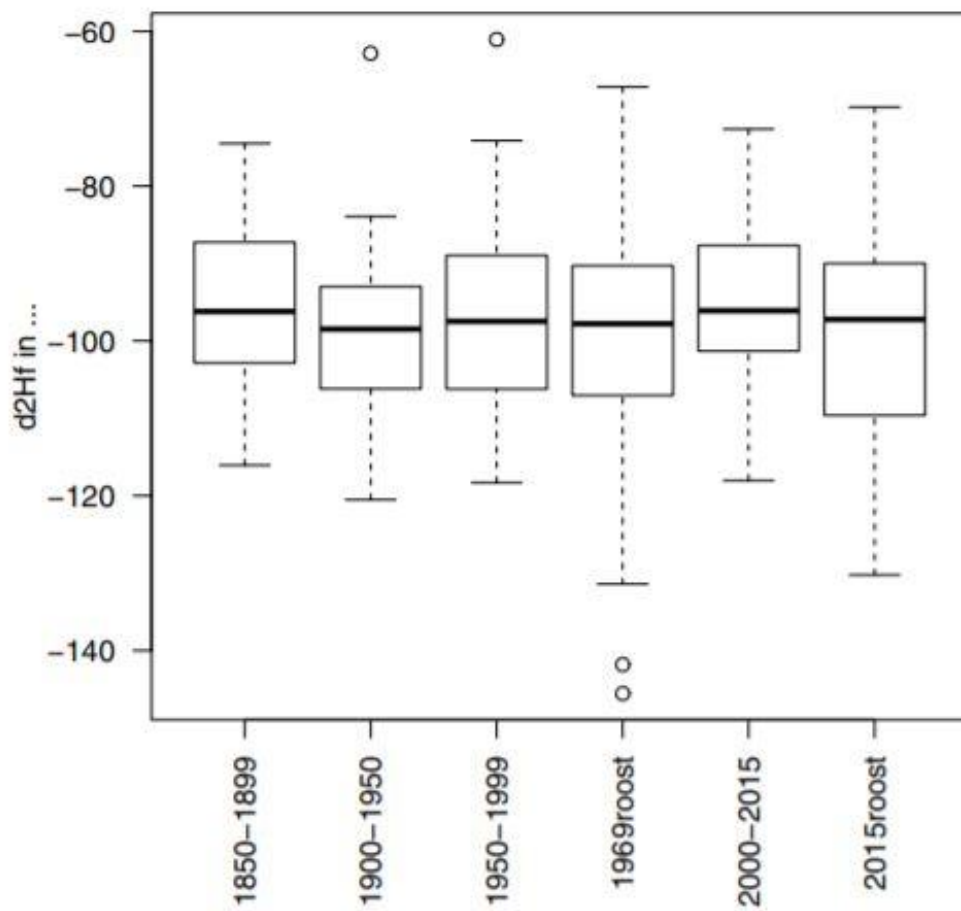
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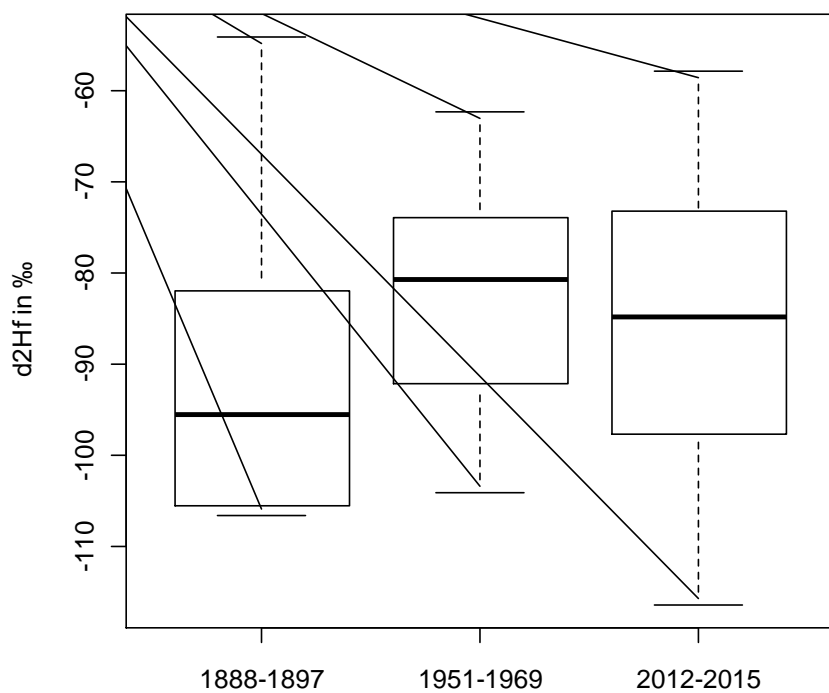
304 Figure 1. Boxplots showing variation in deuterium values in Brambling feathers ( $\delta^2\text{H}_f$  in ‰) for  
305 different time-periods. Each boxplot reports median, 1<sup>st</sup> and 3<sup>rd</sup> quartiles, minimum and maximum  
306 values and dots for outliers. Data from two large dormitories (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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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, 1<sup>st</sup> and 3<sup>rd</sup> 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 1<sup>st</sup> 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.