# Exploring the origins of vagrant Yellow-browed Warblers in Western Europe

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#### Abstract

Vagrancy, where individuals occur outside of known population distributions, is a poorly understood ecological phenomenon. It can however be a key driver of site colonisation and range expansion. Evidence is emerging that presumed vagrant Siberian passerines in Western Europe, e.g. Richard's Pipits Anthus ricardii, are colonists, with geolocator-tracked individuals returning to breed in Siberia after wintering in Western Europe. As such, 'vagrancy' patterns in these taxa could provide a model system to understand large-scale range shifts. For example, determining the origins of vagrant individuals and linking these to morphology and arrival date could help to identify the potential drivers of range dynamics. Here, we investigate the origins of vagrant Yellow-browed Warblers Phylloscopus inornatus (a migratory Siberian breeding passerine) in Western Europe by analysing stable hydrogen isotopes, morphology and phenology. We measure the isotopic patterns of feathers grown on the breeding grounds and their relation to those from two sub-species of Common Chiffchaff Phylloscopus collybita. We found that Yellow-browed Warblers have similar hydrogen isotopic signatures ( $\delta 2H$ ) to the Siberian sub-species of Common Chiffchaff Phylloscopus collybita tristis and  $\delta 2H$  values did not overlap with those from the European nominate race of Common Chiffchaff Phylloscopus collybita collybita. There was weak evidence that variation in  $\delta 2H$  values was linked to differences in migratory distances in sampled Yellow-browed Warblers. The variation in  $\delta$ 2H values for Yellow-browed Warblers was similar to Chiffchaffs of the collybita and tristis sub-species. This suggests that Yellow-browed Warblers in Western Europe may originate from a relatively broad-front and not exclusively from an expanding western breeding range margin. It is unclear if vagrant Yellowbrowed Warblers in Western Europe make viable return migrations to Siberia. If they are, the subset of individuals that become colonists could help us understand how vagrancy drives biogeographic processes, such as the establishment of novel migration routes.

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- Yellow-browed Warblers in Western Europe make viable return migrations to Siberia. If they are, the
   subset of individuals that become colonists could help us understand how vagrancy drives
   biogeographic processes, such as the establishment of novel migration routes.
   **Key Words:** Stable Isotope, Common Chiffchaff, Migration, Range shift, Pseudo-vagrant,
- 28

## 30 Introduction

Colonisation

Vagrants represent a rare but frequently detectable subset of individuals who occur outside of a species' known distribution. The definition of vagrancy is unclear but has been cited as individuals occurring outside of the area that comprises 99.99% of individuals in the population (Lees and Gilroy 2021). As such, the scale of vagrancy is context-dependent. For plants with limited dispersal confined to narrow altitudinal bands, a vagrant individual could reside within 100s of metres of nonvagrants. In contrast, vagrants from long-distance migratory bird populations are frequently recorded on different continents from the rest of the population (Dufour et al. 2021).

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39 Vagrancy in birds can be driven by genetically heritable variation in migratory traits, particularly 40 migratory direction and distance (Berthold et al. 1992). Thorup (1998) experimentally demonstrated 41 that vagrant individuals had migratory directions at the extremes of heritable variation. At the 42 positive extremes of migratory distances, individuals will migrate beyond population-level ranges and become vagrants (Veit 2000). The ecological function of vagrancy (if any) is unclear, although 43 genetically programmed intra-clutch variation in migratory traits may represent bet-hedging 44 45 strategies by adults to increase the likelihood that at least some offspring adopt viable migration 46 routes (Reilly and Reilly 2009). The climate, particularly winds, can also contribute to vagrancy, 47 perhaps without individuals exhibiting extremes of migratory direction or distance. Winds can displace individuals over large distances, which juveniles may be particularly prone to (Dufour et al. 48

2022) as wind drift compensation is often learned (Sergio et al. 2022) and juveniles are often vector
rather than true navigators (Thorup et al. 2007). For instance, easterly airflows over Siberian and
Europe in 2016 led to large numbers of Siberian vagrants in Western Europe, including the first
records of Siberian Accentors *Prunella montanella* (Stoddart 2018).

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54 Vagrancy is generally a short-lived phenomenon. However, in rare circumstances vagrants find 55 conspecifics to breed with (Boertmann 2008), or successfully return to natal breeding sites (Dufour 56 et al. 2021). This can initiate colonisation of novel breeding and non-breeding sites, thereby 57 expanding the population range. While vagrancy and subsequent colonisations are rare, they can influence the range dynamics of species over evolutionary timescales (Veit 2000). Vagrancy provides 58 59 a mechanism that enables range shifting and allows adaptation to changing isotherms and 60 phenology (Davis and Watson 2018). Understanding the drivers of vagrancy is therefore key to 61 understanding species' responses to anthropogenic climate change. Attempts to deepen our 62 understanding should focus on the mechanisms driving vagrancy at the individual-level and the 63 spatial origins of vagrants and colonising individuals (Dufour et al. 2022).

64

In recent decades the occurrence of passerines that breed in Siberia and overwinter in South Asia as 65 66 vagrants in Western Europe has increased, e.g. Richard's Pipit Anthus richardi, Yellow-browed 67 Warbler Phylloscopus inornatus and Dusky Warbler Phylloscopus fuscatus (Dufour et al. 2021, 2022). 68 In the case of Richard's Pipit, geolocator tracking of individuals in Western Europe during the non-69 breeding season indicates some vagrants are in fact colonists, capable of making viable return 70 migrations to the Siberian breeding grounds (Dufour et al. 2021). This colonisation has been facilitated by a westward expansion of the breeding range and increased suitability of Western 71 72 Europe as a non-breeding site. It is unclear whether other vagrant Siberian passerines in Western 73 Europe also make viable migrations back to Siberia or just occur as vagrants. The Yellow-browed 74 Warbler (YBW, hereafter) is one such Western European vagrant (Figure 1). Dufour et al. (2022)

recently highlighted that YBWs provide an ideal study system to understand the drivers and patterns
of vagrancy, and how a changing climate might facilitate the evolution of long-distance range
expansions.

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79 The YBW is a small (4-9g), abundant (45-46,000 individuals), migrant passerine breeding across 80 Siberia (Figure 2). Autumn migration begins in late August and continues into September. Most 81 individuals migrate in a south-westerly or south-easterly orientation (depending on breeding 82 location) via north-east China to non-breeding grounds in South-East Asia (Thorup 1998, Dufour et 83 al. 2022). Vagrant YBWs in Denmark have been found to orientate along an east-west axis (Thorup 84 1998) and numbers in Western Europe are high when anticyclonic weather produces easterly winds over the breeding grounds (Baker 1977). This implicates variation in innate migratory direction and 85 86 strong easterly winds as drivers of vagrancy in YBW.

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88 Here, we aim to understand the origins of vagrant YBW in the United Kingdom (UK) using stable 89 isotope analysis of tail feathers. Due to rainfall patterns and temperature differences, hydrogen 90 stable isotope ( $\delta^2$ H) values decrease with increasing latitude, higher altitudes and greater distances 91 from the coast (Bowen 2010). Creating a general South-East to North-West gradient in  $\delta^2$ H across 92 Eurasia (Figure 3). This can allow the broad geographical origins of migrants to be determined as the 93  $\delta^2$ H signature within their feathers reflects the location feathers were grown (Inger and Bearhop 94 2008). We compare the mean and variation of  $\delta^2$ H values in tail feathers of YBW to two sub-species 95 of Common Chiffchaff Phylloscopus collybita (P. c. collybita & P. c. tristis) and Chiffchaffs exhibiting 96 intermediate plumage between these two sub-species during autumn migration. The origins of the 97 two Chiffchaff sub-species are better known than YBW and their breeding grounds span from 98 Western Europe to Siberia (Figure 2). We use variation in  $\delta^2$ H values within a species to infer the size 99 of the range that individuals have originated from. Larger variances are indicative of a larger area of 100 migratory origin (Sellick et al. 2009), although given the processes that drive variation in  $\delta^2$ H the two do not increase proportionally. Finally, we examined if individual-level traits associated with
migration distance explained variation in δ<sup>2</sup>H values and capture dates. We expect birds caught later
in the autumn to have travelled further and therefore have longer wings to facilitate longer flights
(Marchetti et al. 1995). Therefore, if individuals are travelling from a range of migratory distances,
then we would expect more negative δ<sup>2</sup>H values (generally further from the capture sites) to be
associated with longer wings and later arrival dates.



Figure 1. Vagrancy patterns of YBW. Europe/North Africa (panel A) and East Asia (panel B) are
 shown. The predicted density of Yellow-browed Warbler *Phylloscopus inornatus* during the post breeding period (12 Oct - 7 Dec) is derived from eBird (Fink et al. 2022). The breeding and non breeding distribution of YBW are shown (BirdLife International 2022) (panel B). Illustration © Emma
 Wood.



Figure 2. Global distributions for two Common Chiffchaff sub-species (*P. c. collybita & P. c. tristis*)
and Yellow-browed Warbler *P. inornatus*. Distributions cover breeding and non-breeding
distributions (BirdLife International 2022). The breeding range of *P. c. abietinus* is across northern
Scandinavia and into North West Russia (recognised range map not available).



121	Figure 3. Hydrogen isotope composition, $\delta^2 H$ (‰), of average precipitation during the growing
122	season (months with mean temperature > $0^{\circ}$ C). Data derived from the Online Isotopes in
123	Precipitation Calculator v3.2 database (Bowen 2023). The breeding distributions are shown for two
124	Common Chiffchaff sub-species (P. c. collybita & P. c. tristis) and Yellow-browed Warbler P. inornatus
125	(BirdLife International 2022).

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# 127 Methods

### 128 Common Chiffchaff Taxonomy

129Three recognised sub-species of Common Chiffchaff pass through Western Europe. The nominate130sub-species of Common Chiffchaff *P. c. collybita*, 'Scandinavian Chiffchaff' *P. c. abietinus* and

131 'Siberian Chiffchaff' P. c. tristis (Cramp and Brooks 1992). These three sub-species originate from 132 different breeding areas; collybita individuals breeding across Europe and into Western Russia, and tristis individuals breeding across Siberian Russia but not extending into Europe (Figure 2). The 133 134 abietinus sub-species breeds across Northern Scandinavia and North West Russia (partly the overlap 135 zone between the collybita and tristis sub-species) and has plumage intermediate to that of the 136 other two sub-species. Individuals of the collybita and tristis sub-species can be separated on 137 plumage (Sup Table 1.) and this has been confirmed by genetic identification (de Knijff et al. 2012). 138 In Western Europe, however, de Knijff el al. (2012) demonstrated birds identified as abietinus on 139 plumage alone were in fact genetically tristis individuals. We identified birds of intermediate 140 plumage (*n* = 11) between *tristis* and *collybita*, these are unlikely to be *abietinus* based on their rarity 141 in Western Europe (de Knijff et al. 2012) and short wing length (59.9 ± 3.2mm) compared to 142 genetically confirmed abietinus that infrequently had wing lengths >63mm (Hansson et al. 2000, 143 Marova et al. 2017). To avoid assigning intermediate individuals to the incorrect sub-species we 144 analyse them separately and refer to them as intergrades hereafter.

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#### 146 Bird Sampling

147 YBW and all Chiffchaffs were caught in Cornwall, England between 28/08/2017 and 24/11/2017. 148 Mist net trapping took place at Nanjizal Valley (50°03'27.0"N 5°41'03.7"W) and University of Exeter, 149 Penryn Campus (50°10'10.7"N 5°07'14.8"W). All individuals were fitted with unique alphanumeric 150 metal tarsus rings and the age (adult or juvenile) and maximum wing chord (nearest mm) were 151 recorded. Prior to release, a sample (6-10mm) was collected from tail feather three (T3 = the third 152 from outer) from each chiffchaff or T4 from each Yellow-browed warbler for isotopic analysis. Tail 153 feathers were selected since they are grown in the breeding grounds during post-breeding moult for 154 adults or in the nest for juveniles (Demongin et al. 2016) and any retained feathers can be identified by colour and wear. Therefore the isotope ratios in tail feathers reflect those of an individual's 155

breeding site. In the rare occurrence of post-juvenile tail moult the nearest juvenile-type tail feather
was sampled. The following number of tail feathers were available for isotopic analysis; YBW (*n* =
34), *tristis* Chiffchaffs (*n* = 14), *collybita* Chiffchaffs (*n* = 85) and intergrade Chiffchaffs (*n* = 11).

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#### 160 **Isotope Analysis**

161 For isotopic analysis, 0.2-0.3 mg of feather was weighed precisely into inert, silver capsules. Samples 162 were analysed at the University of New Mexico's Centre for Stable Isotopes (UNM-CSI) for  $\delta^2$ H testing following a similar procedure to Bearhop et al. (2004). Prior to preparation and testing, 163 164 samples were left to equilibrate with the local moisture conditions for a period of 1-2 weeks and 165 subsequently analysed within the same week. Uncontrollable hydrogen exchange occurs between 166 organic samples (e.g. feather) and the local atmosphere (Soto et al. 2017). To correct for this a local 167 standard and kudu horn standard (KHS) were run alongside the feather samples. These standards 168 were calibrated using the old values for international keratin standards (-47.5 ‰), which have since 169 been revised. This does not influence the interpretation of our analysis since the comparisons are 170 relative. Average values of -49 ± 1.9 ‰ for Kudu horn standard across runs compare favourably with the old established international standard (-47.5 %, Soto et al. 2017). The delta notation ( $\delta$ ) is used 171 to express stable isotope data as parts per thousand deviation from the standard. The stable 172 173 hydrogen values ( $\delta^2$ H) were calculated using the following equation (Kelly et al. 2002):

174 
$$\delta^{2}H = \left[ \left( \frac{hydrogen\ isotope\ ratio_{sample}}{hydrogen\ isotope\ ratio_{standard}} \right) - 1 \right] \times 1000$$

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#### 176 Statistical Analysis

177 There was heteroscedascity between groups so to test for differences in  $\delta^2$ H values we used 178 generalised least squares regression in the R package '*nlme*' (Pinheiro et al. 2022), using the 179 *varldent()* function to account for different variances. Taxonomic group (four-level factor) was the 180 sole explanatory variable and  $\delta^2$ H values were the response variable. To formally test for differences 181 in  $\delta^2$ H variance between taxonomic groups we used the Levene's test in the R package '*car*' (Fox and 182 Weisberg 2019). We compared YBW to *collybita*, *tristis* and intergrade Chiffchaffs individually and 183 therefore applied a Bonferroni correction to the Levene's test (corrected alpha = 0.017).

184

To test for relationships between  $\delta^2$ H values and morphology/phenology we also used generalised 185 186 least squares regression. Wing length and arrival date differed between taxonomic groups so a 187 separate model was run for each taxonomic group. In each model the response variable was the  $\delta^2$ H 188 values and we fitted two continuous explanatory variables; 1) wing length and 2) year day of 189 capture. To test for relationships between year day of capture and morphology we used generalised 190 least squares regression for each taxonomic group separately. In each model the response variable 191 was the year day of capture and explanatory variable was wing length. For all models explanatory 192 variables were z-transformed to allow effect sizes to be compared. Likelihood ratio tests on the 193 maximal model were used to test the significance of each explanatory variable. All analysis was 194 carried out in R v4.2.1 (R Core Team 2022).

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## 196 **Results**

197 *Tristis* Chiffchaff (mean= -105.1 ‰ | SD= 12.9) and YBW (-113.0 ‰ | 9.2) had significantly lower  $\delta^2$ H 198 values than *collybita* (-61.8 ‰ | 8.2) and intergrade Chiffchaffs (-68.1 ‰ | 9.2) (p < 0.001, df = 140 199 for all comparisons), see Figure 4. There was no significant difference between collybita and 200 intergrade Chiffchaffs, as well as between tristis Chiffchaffs and YBW. There were no significant 201 differences in the variation of  $\delta^2$ H values between YBW and *tristis, collybita* or intergrade Chiffchaffs. 202 In *collybita* Chiffchaff there was a significant negative correlation between wing length and  $\delta^2 H$  ( $\beta = -$ 203 2.400, p = 0.01, df = 78) but the effect of capture date was insignificant. Therefore longer winged 204 birds had more negative isotope values which tend to be further from the UK. For YBW, there was

also a negative relationship between  $\delta^2$ H and wing length ( $\beta$  = -2.770, p = 0.088, df = 31) but this effect was marginally non-significant. For *tristis* and intergrade Chiffchaffs there were no significant relationships between wing length or capture date and  $\delta^2$ H (Figure 5). For all taxonomic groups there were no significant relationships between capture day and wing length.

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Figure 4. δ<sup>2</sup>H values in tail feathers of two sub-species of Common Chiffchaff (*P. c. collybita & P. c. tristis*), intergrade Chiffchaffs and Yellow-browed Warbler *P. inornatus* collected during autumn 2017
 in Cornwall, England. \*\*\* denotes p < 0.001.</li>



Figure 5. Relationships between wing length and δ<sup>2</sup>H values of tail feathers from two sub-species of
 Common Chiffchaff (*P. c. collybita & P. c. tristis*), intergrade Chiffchaffs and Yellow-browed Warbler
 *P. inornatus* collected during autumn 2017 in Cornwall, England. Each taxonomic group was
 modelled separately but combined to aid visualisation. \* denotes p < 0.05.</li>

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# Discussion

222 Our results are consistent with YBW and *tristis* in the UK coming from more easterly distributions 223 and from a relatively broad range of locations that have little overlap with the ranges of *collybita*. 224 Mean  $\delta^2$ H values differed between YBW and the *collybita* sub-species of Chiffchaff but were similar 225to those observed for the *tristis* sub-species (Figure 2). Intergrade Chiffchaffs that were identified226visually had similar  $\delta^2$ H values to *collybita* Chiffchaffs. For *collybita* Chiffchaffs there was a significant227negative relationship between  $\delta^2$ H values and wing length (Figure 4). No relationships examined in228the other taxonomic groups were significant but there was a marginally insignificant negative229relationship between  $\delta^2$ H values and wing length for YBW that was of the same magnitude as in230*collybita* (Figure 4).

231

232 Given the lack of overlap in  $\delta^2$ H values between YBW/*tristis* Chiffchaffs and *collybita* Chiffchaffs the 233 migratory fronts from which the two groups originate would appear to have little to no overlapping 234 area. Therefore it is unlikely the origins of YBW in the UK are solely an expanding western breeding 235 fringe as this would overlap with the breeding distribution of collybita Chiffchaffs. Intergrade 236 Chiffchaffs had  $\delta^2$ H values largely overlapping with those of *collybita* Chiffchaffs suggesting they 237 share similar origins. However, de Knijff et al. (2012) found that birds identified visually as abietinus 238 Chiffchaffs (akin to the intergrades presented here) were in fact tristis individuals genetically. This is 239 at odds with our isotopic findings. Either our intergrade birds were perhaps hybrids and not in fact 240 tristis Chiffchaffs and/or our intergrades had different origins than those in de Knijff et al. (2012). 241 The variation in  $\delta^2$ H values for YBW and *tristis/collybita* Chiffchaffs were not significantly different. 242 While one interpretation of the  $\delta^2$ H data is that the size of the geographical area from which YBW 243 and *tristis/collybita* Chiffchaffs originate from are of a similar magnitude, we have to be wary of 244 meso-scale heterogeneity in stable hydrogen isotope ratios as a consequence of variation due local 245 hydrology or altitude (e.g. Marshall et al. 2007).

246

For *collybita* Chiffchaffs there was a significant negative relationship between  $\delta^2$ H values and wing length. An effect of the same magnitude but marginally insignificant was found for YBW but no other significant relationships with  $\delta^2$ H values were found. This negative relationship between  $\delta^2$ H and wing length is indicative of individuals arriving from a range of migratory distances, with more

251 negative  $\delta^2$ H values representing more north-easterly origins (Marshall et al. 2007) and therefore 252 those individuals require longer wings to reach suitable non-breeding grounds (Marchetti et al. 253 1995). The lack of significance in the relationship between  $\delta^2$ H and wing length in YBW may just be 254 due to a lower sample size compared to *collybita* and the fact that detecting these trends is difficult 255 due to local heterogeneity in  $\delta^2$ H and individual sex being unknown in our analysis. However we 256 can't rule out that the effect in YBW is spurious.

257

258 There are ecological explanations for only observing a significant effect between wing length and 259  $\delta^2$ H in *collybita* Chiffchaffs. The variation in migration distance within this sub-species may be larger 260 due to overlapping breeding and non-breeding distributions and therefore a mix of short- and long-261 distance migrants (Cramp and Brooks 1992). In YBW and tristis Chiffchaffs, breeding and non-262 breeding grounds are disconnected and all birds make substantial migrations, bypassing the 263 Himalayas and Gobi desert (Cramp and Brooks 1992, Dufour et al. 2022). In addition, for YBW and *tristis* Chiffchaffs we may not observe correlations between  $\delta^2 H$  and wing length if our observed 264 265 variation in  $\delta^2$ H is due to an east-west orientation of migratory origin. In this case individuals would 266 migrate similar distances to reach their regular South Asian non-breeding grounds and therefore any adaptive differences in wing length would not be associated with  $\delta^2 H$  variation (Marchetti et al. 267 268 1995). Many individuals will require stopovers to reach the UK, especially YBW and tristis Chiffchaffs. 269 Therefore any relationships between arrival date and migration distance/wing length could be 270 masked by the location and duration of individual stopovers (Lindström et al. 2019), perhaps 271 contributing to our lack of significant results across all taxonomic groups.

272

This study was conducted during a single migration season (autumn 2017) when vagrant YBWs were relatively abundant in Western Europe compared to the previous 40 years (Dufour et al. 2022). It is unclear if the relatively large migratory front we observed in YBW was associated with these favourable climatic conditions. More favourable easterly winds over the breeding grounds could

feasibly increase migration distances (Vansteelant et al. 2017) enabling the survival of vagrant
individuals into Western Europe from a larger range of origins. Understanding how the success of
vagrants is shaped by wind conditions during migration and climate change at novel sites is key to
predicting whether range shifts will occur and their directionality.

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282 It is unclear whether any sampled YBW were early colonists, and if they were, whether individuals 283 from the full range of isotopic values could have migrated successfully to breeding sites. There is 284 evidence that a small number attempt to return as individuals are observed sporadically during 285 spring migration (Dufour et al. 2022). For Richard's pipit, only individuals from the western edge of 286 the breeding range successfully returned after spending the non-breeding period in Western Europe 287 (Dufour et al. 2021). Understanding the subset of vagrants that could become colonists and the 288 abundance of potential source populations could be helpful when predicting climate change 289 resilience enabled by range shifts. If populations at range boundaries are decreasing, this may 290 impede range expansion due to the low abundance of the most likely colonists. Finally, 291 understanding how vagrancy is influenced by wind conditions, climate amelioration and genetic 292 inheritance of migratory traits could help explain the success and directionality of colonisations 293 under future climate change (Davis and Watson 2018).

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# 295 **References**

- Baker, K. 1977. Westward Vagrancy of Siberian Passerines in Autumn 1975. Bird Study 24: 233–
  242.
- Bearhop, S., Hilton, G. M., Votler, S. C. and Waldron, S. 2004. Stable isotope ratios indicate that body
   condition in migrating passerines is influenced by winter habitat. Proceedings of the Royal Society
   B: Biological Sciences 271: S215–S218.

- 301 Berthold, P., Helbig, A. J., Mohr, G. and Querner, U. 1992. Rapid microevolution of migratory
- 302 behaviour in a wild bird species. Nature 360: 668–670.
- BirdLife International. 2022. Bird species distribution maps of the world. Version 2022.2. Available at
   http://datazone.birdlife.org/species/requestdis.
- 305 Boertmann, D. 2008. The Lesser Black-Backed Gull, Larus fuscus, in Greenland. Arctic 61: 129–133.
- Bowen, G. J. 2010. Isoscapes: Spatial Pattern in Isotopic Biogeochemistry. Annual Review of Earth
   and Planetary Sciences 38: 161–187.
- 308 Bowen, G. J. 2023. Gridded maps of the isotopic composition of meteoric waters.
- 309 http://www.waterisotopes.org.
- 310 Cramp, S. and Brooks, D. J. 1992. Handbook of the birds of Europe, the Middle East and North Africa.
- 311 In The birds of the western Palearctic, vol. VI. Warblers. Oxford University Press, Oxford.
- 312 Davis, R. A. and Watson, D. M. 2018. Vagrants as vanguards of range shifts in a dynamic world. –
- Biological Conservation 224: 238–241.
- 314 de Knijff, P., van der Spek, V. and Fischer, J. 2012. Genetic identity of grey chiffchaffs trapped in the
  315 Netherlands in autumns of 2009-1. Dutch Birding 34: 386–392.
- 316 Demongin, L., Lelièvre, H. and Candelin, G. 2016. Identification Guide to Birds in the Hand. –
  317 Privately Published.
- Dufour, P., de Franceschi, C., Doniol-Valcroze, P., Jiguet, F., Guéguen, M., Renaud, J., Lavergne, S. and
  Crochet, P.-A. 2021. A new westward migration route in an Asian passerine bird. Current Biology
  31: 5590–5596.
- 321 Dufour, P., Åkesson, S., Hellström, M., Hewson, C., Lagerveld, S., Mitchell, L., Chernetsov, N.,
- 322 Schmaljohann, H. and Crochet, P.-A. 2022. The Yellow-browed Warbler (Phylloscopus inornatus) as a

- 323 model to understand vagrancy and its potential for the evolution of new migration routes. –
  324 Movement Ecology 10: 59.
- 325 Fink, D., Auer, T., Johnston, M., Strimas-Mackey, M. E., Ligocki, S., Robinson, O., Hochachka, H.,

Jaromczyk, L., Rodewald, A., Wood, C., Davies, I. and Spencer, A. 2022. eBird Status and Trends, Data

327 Version: 2021; Released: 2022. – Cornell Lab of Ornithology, Ithaca, New York.

328 https://doi.org/10.2173/ebirdst.2021.

- Fox, J. and Weisberg, S. 2019. An R Companion to Applied Regression, Third Edition. Thousand
  Oaks, CA.
- Hansson, M. C., Bensch, S. and Brännström, O. 2000. Range expansion and the possibility of an
  emerging contact zone between two subspecies of Chiffchaff Phylloscopus collybita ssp. Journal of
  Avian Biology 31: 548–558.
- Inger, R. and Bearhop, S. 2008. Applications of stable isotope analyses to avian ecology. Ibis 150:
  447–461.
- 336 Kelly, J. F., Atudorei, V., Sharp, Z. D. and Finch, D. M. 2002. Insights into Wilson's Warbler migration
- 337from analyses of hydrogen stable-isotope ratios. Oecologia 130: 216–221.
- 338 Lees, A. and Gilroy, J. J. 2021. Vagrancy in Birds. Christopher Helm, London.
- 339 Lindström, Å., Alerstam, T. and Hedenström, A. 2019. Faster fuelling is the key to faster migration. –

340 Nat. Clim. Chang. 9: 288–289.

- 341 Marchetti, K., Price, T. and Richman, A. 1995. Correlates of Wing Morphology with Foraging
- 342 Behaviour and Migration Distance in the Genus Phylloscopus. Journal of Avian Biology 26: 177.
- 343 Marova, I., Shipilina, D., Fedorov, V., Alekseev, V. and Ivanitskii, V. 2017. Interaction between
- 344 Common and Siberian Chiffchaff in a contact zone. Ornis Fennica 94: 66–81.

<ul> <li>346 composition of plants. In Michener, R. &amp; Lajtha, K. (eds) Stable Isotopes in Ecology and</li> <li>347 Environmental Sciences. – Oxford: Blackwell Publishing.</li> <li>348 Pinheiro, J., Bates, D. and R Core Team. 2022. nlme: Linear and Nonlinear Mixed Effects Model</li> <li>349 package version 3.1-157.</li> <li>350 R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for</li> <li>351 Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>352 Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>	345	Marshall, J. D., Brookes, J. R. and Lajtha, K. 2007. Sources of variation in the stable isotopic
<ul> <li>Environmental Sciences. – Oxford: Blackwell Publishing.</li> <li>Pinheiro, J., Bates, D. and R Core Team. 2022. nlme: Linear and Nonlinear Mixed Effects Model</li> <li>package version 3.1-157.</li> <li>R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for</li> <li>Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>	346	composition of plants. In Michener, R. & Lajtha, K. (eds) Stable Isotopes in Ecology and
348Pinheiro, J., Bates, D. and R Core Team. 2022. nlme: Linear and Nonlinear Mixed Effects Model349package version 3.1-157.350R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for 351351Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.352Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall	347	Environmental Sciences. – Oxford: Blackwell Publishing.
<ul> <li>pinneiro, J., Bates, D. and R Core Team. 2022. nime: Linear and Nonlinear Mixed Effects Mode</li> <li>package version 3.1-157.</li> <li>R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for</li> <li>Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>	240	Disksing L. Dates, D. and D. Caro Taam, 2022, sloper Linger and Marlinger Mixed Effects Medels, F
<ul> <li>349 package version 3.1-157.</li> <li>350 R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for 351 Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>352 Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>	348	Pinneiro, J., Bates, D. and R Core Team. 2022. nime: Linear and Nonlinear Mixed Effects Models. R
<ul> <li>R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for</li> <li>Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>	349	package version 3.1-157.
<ul> <li>R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for</li> <li>Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>		
<ul> <li>Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.</li> <li>Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall</li> </ul>	350	R Core Team. 2022. R: A language and environment for statistical computing. R Foundation for
Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall	351	Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.
Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall		
	352	Reilly, J. R. and Reilly, R. J. 2009. Bet-hedging and the orientation of juvenile passerines in fall
353 migration. – Journal of Animal Ecology 78: 990–1001.	353	migration. – Journal of Animal Ecology 78: 990–1001.

- Sellick, M. J., Kyser, T. K., Wunder, M. B., Chipley, D. and Norris, D. R. 2009. Geographic Variation of
   Strontium and Hydrogen Isotopes in Avian Tissue: Implications for Tracking Migration and Dispersal.
   PLOS ONE 4: e4735.
- Sergio, F., Barbosa, J. M., Tanferna, A., Silva, R., Blas, J. and Hiraldo, F. 2022. Compensation for wind
   drift during raptor migration improves with age through mortality selection. Nature Ecology and
   Evolution 1–12.
- 360 Soto, D. X., Koehler, G., Wassenaar, L. I. and Hobson, K. A. 2017. Re-evaluation of the hydrogen
- 361 stable isotopic composition of keratin calibration standards for wildlife and forensic science
- 362 applications. Rapid Communications in Mass Spectrometry 31: 1193–1203.

# 363 Stoddart, A. 2018. Siberian Accentors in Europe in autumn 2016 and the first British records. – British 364 Birds.

365	Thorup, K. 1998. Vagrancy of Yellow-browed Warbler Phylloscopus inornatus and Pallas's Warbler
366	Ph. proregulus in north-west Europe: Misorientation on great circles? – Ringing and Migration 19: 7–
367	12.

368 Thorup, K., Bisson, I.-A., Bowlin, M. S., Holland, R. A., Wingfield, J. C., Ramenofsky, M. and Wikelski,

- 369 M. 2007. Evidence for a navigational map stretching across the continental U.S. in a migratory
- 370 songbird. Proceedings of the National Academy of Sciences 104: 18115–18119.
- 371 Vansteelant, W. M. G., Kekkonen, J. and Byholm, P. 2017. Wind conditions and geography shape the
- 372 first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa.
- 373 Proceedings of the Royal Society B: Biological Sciences 284: 20170387.
- Veit, R. R. 2000. Vagrants as the Expanding Fringe of a Growing Population. Auk 117: 242–246.