



UHI Research Database pdf download summary

Non-breeding areas and timing of migration in relation to weather of Scottish-breeding common sandpipers *Actitis hypoleucos*

Summers, Ron W.; De Raad, A. Louise; Bates, Brian; Etheridge, Brian; Elkins, Norman

Published in:
Journal of Avian Biology

Publication date:
2019

Publisher rights:
© 2018 The Authors. Published by 1999-2020 John Wiley & Sons, Inc. All rights reserved

The re-use license for this item is:
CC BY-NC

The Document Version you have downloaded here is:
Peer reviewed version

The final published version is available direct from the publisher website at:
[10.1111/jav.01877](https://doi.org/10.1111/jav.01877)

[Link to author version on UHI Research Database](#)

Citation for published version (APA):

Summers, R. W., De Raad, A. L., Bates, B., Etheridge, B., & Elkins, N. (2019). Non-breeding areas and timing of migration in relation to weather of Scottish-breeding common sandpipers *Actitis hypoleucos*. *Journal of Avian Biology*, 50(1), 1-11. [e01877]. <https://doi.org/10.1111/jav.01877>

General rights

Copyright and moral rights for the publications made accessible in the UHI Research Database are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights:

- 1) Users may download and print one copy of any publication from the UHI Research Database for the purpose of private study or research.
- 2) You may not further distribute the material or use it for any profit-making activity or commercial gain
- 3) You may freely distribute the URL identifying the publication in the UHI Research Database

Take down policy

If you believe that this document breaches copyright please contact us at RO@uhi.ac.uk providing details; we will remove access to the work immediately and investigate your claim.

1 **Non-breeding areas and timing of migration in relation to weather of Scottish-breeding**
2 **common sandpipers *Actitis hypoleucos***

3

4 **Ron W. Summers¹, A. Louise de Raad², Brian Bates³, Brian Etheridge⁴ and Norman Elkins⁵**

5

6 *R.W. Summers (ron.summers@rspb.org.uk), Lismore, Mill Crescent, North Kessock, Ross-shire, IV1*

7 *3XY, Scotland. A.L. de Raad, Inverness College, University of the Highlands and Islands, 1 Inverness*

8 *Campus, Inverness, IV2 5NA, Scotland. B. Bates, Ballinlaggan, Dunstaffnage Brae, Grantown-on-Spey,*

9 *Morayshire, PH26 3JS, Scotland. B. Etheridge, Beechgrove, Rosehaugh East Drive, Avoch, Ross-shire,*

10 *IV9 8RE, Scotland. N. Elkins, 18 Scotstarvit View, Cupar, Fife, KY15 5DX, Scotland.*

11

12

13 Corresponding author: R.W. Summers *ron.summers@rspb.org.uk*

14

15

16

17 **Keywords:** Common sandpiper, FlightR, geolocator. Guinea-Bissau, mangrove, migration

18 strategy, West Africa.

19

20

21

22 The number of breeding common sandpipers has declined in Britain due to poorer return rates

23 from non-breeding areas. To investigate little known aspects of their annual cycle, breeding

24 common sandpipers were fitted with geolocators to track their migrations and determine their

25 non-breeding areas. Ten tagged birds left Scotland on 9 July (median dates and durations are

26 given throughout the abstract). Short-term staging was carried out by some birds in England
27 and Ireland, then for longer by most birds in Iberia before continuing to West Africa, arriving
28 on 28 July. Six birds spent most of the non-breeding season (October–February) on the coast of
29 Guinea-Bissau, suggesting that this is a key area. Single birds occurred in Sierra Leone, Guinea,
30 the Canary Islands and Western Sahara. The southward migration from Scotland took 17.5 days
31 (range 1.5-24 days), excluding the initial fuelling period. The first northward movement from
32 Africa was on 12 April. Staging occurred in either Morocco, Iberia or France. Arrival in Scotland
33 was on 2 May. The northward migration took 16 days (range 13.5-20.5 days). The main
34 migration strategy involved short- and medium-range flights, using tail-winds in most cases.
35 Variation in strategy was associated with departure date; birds that left later staged for shorter
36 durations. Coastal West Africa provides two major habitats for common sandpipers: mudflats
37 associated with mangroves and rice fields. Although the area of mangrove has been depleted,
38 the scale of loss has probably been insufficient to account for the decline in sandpiper numbers.
39 Rice fields are expanding, providing feeding areas for water-birds. Meteorological data during
40 the migrations suggest that the weather during the southward migration is unlikely to
41 contribute to a population decline but strong cross-winds or head-winds during the northward
42 migration to the breeding grounds may do so.

43

44

45 There is increasing concern about the decline in numbers of Afro-Palaeartic migrant birds that
46 breed in Britain (Balmer et al. 2013). In the 1960s and 1970s, declines were seen mainly in
47 migrants that spend the non-breeding season in the arid Sahelian zone (Winstanley et al. 1974),
48 but since the 1980s, those species that occur in the humid tropics and Guinea forest zone have
49 also declined (Vickery et al. 2014). It is generally accepted that our knowledge about declining
50 species is better for the breeding than the non-breeding parts of the annual cycle, though some
51 studies have obtained more information about the lives of these migrants during the non-
52 breeding season (Jones et al. 1996, Zwarts et al. 2009, Stevens et al. 2010). Part of this involves
53 describing migratory tracks and determining the locations of the non-breeding areas using data-
54 loggers that are now small enough for many medium-sized birds; e.g. European nightjars
55 *Caprimulgus europaeus* (Cresswell and Edwards 2013), common swifts *Apus apus* (Åkesson et al.
56 2012) and great snipes *Gallinago media* (Lindström et al. 2016).

57 The common sandpiper *Actitis hypoleucos* is a Palearctic migrant wader that breeds
58 around lakes and along fast-running rivers from the British Isles in the west to Kamchatka in
59 the east. The non-breeding range includes Africa, India, Southeast Asia and Australia (Cramp
60 and Simmons 1983). The Pan-European population declined by 21% during 1980-2009 (Vickery
61 et al. 2014), a trend which has also been seen in Britain (Ockendon et al. 2012). As with many
62 migrant species, there have been population studies on the breeding grounds (Holland et al.
63 1982, Dougall et al. 2010). An analysis of demographic data indicated that the long-term decline
64 in a small population (mean of 13.6 territories) in northern England was not due to low
65 breeding success but to a low return rate of adults, which was negatively associated with the
66 winter North Atlantic Oscillation (NAO) (Pearce-Higgins et al. 2009). How the NAO influences

67 the survival of common sandpipers is unclear, so Pearce-Higgins et al. (2009) stressed the need
68 to understand more about their migration and non-breeding areas.

69 Despite ringing over 22,000 common sandpipers in the UK to 2015 (Walker et al. 2016),
70 little is known about the migratory route and non-breeding areas once UK birds leave Europe
71 (Wernham et al. 2002). By contrast, recoveries of common sandpipers ringed elsewhere in
72 Europe show that the non-breeding area extends from southern Europe to West Africa
73 (Fransson et al. 2008, Saurola et al. 2013). Ringing recoveries show that UK birds occur in France
74 and Spain during southward and northward migrations and this is reflected in studies of birds
75 caught on migration in Spain (Arcas 1999, Balmori 2005, de Elgea and Arizaga 2016). There are
76 several recoveries of British-ringed birds in Morocco but only two records south of the Sahara.
77 One referred to a bird ringed in September in southeast England, so may have been a migrant
78 from continental Europe (Wernham et al. 2002). The other was a Scottish-breeding common
79 sandpiper on the non-breeding grounds from our initial work using geolocators (Bates et al.
80 2012). This initial study identified Morocco as a staging site on migration and coastal West
81 Africa as its non-breeding area (Bates et al. 2012).

82 The present study extends our initial study (Bates et al. 2012), to describe the migrations
83 and non-breeding areas of Scottish-breeding common sandpipers. The weather patterns in West
84 Africa are partly determined by variations in the position of the Inter-Tropical Convergence
85 Zone and its influence on the northeast trade winds blowing along the coast of northwest Africa
86 (Lockwood 1974). We examined the weather conditions that the birds experienced during
87 migration and speculate on the cause of the decline in breeding numbers in Britain.

88

89

90 Methods

91

92 Study area

93

94 Study areas included the River Spey, downstream from Grantown-on-Spey (57°21'N, 3°32'W),

95 Loch Loyal (58°24'N, 4°21'W) and a small lake near Tongue (58°31'N, 4°20'W) in north

96 Sutherland, Scotland. The banks and islands of the River Spey are lightly wooded with alder

97 *Alnus glutinosa*, birch *Betula* spp. and Scots pine *Pinus sylvestris*. Small grassy islands and bars of

98 river shingle provide breeding and feeding habitats, respectively, for common sandpipers. By

99 contrast, the Sutherland lakes has stony edges, grading into grassy or heather *Calluna vulgaris*

100 banks with occasional birches.

101

102 Field work

103

104 During 2011 to 2015, breeding common sandpipers were mist-netted or trapped at the nest

105 (Pienkowski 1976). Birds were sexed either on behaviour (males singing) or molecularly from a

106 feather's DNA (Fridolfsson and Ellegren 1999). Mass was recorded to 0.1 g on an electronic

107 balance. Twenty-eight sandpipers were fitted with unique permutations of colour rings and a 1

108 g (Mk 10S) British Antarctic Survey geolocator on leg-loops (5 birds) (Rappole and Tipton 1991,

109 R.E. Green pers. comm.), or a 0.65 g (W65) Migrate Technology Intigeo geolocator on a leg-flag

110 attached to the tibia (23 birds). The leg-loops were made from fixed lengths of soft "Silastic"

111 tubing through which ran elasticated thread, allowing the loops to expand or contract according
112 to any change in the birds' shape during the accumulation and use of migratory fuel. Once a
113 bird returned and was re-trapped, the geolocator was removed and the data were downloaded
114 using BASTrak or IntigeoIF software.

115

116 **Analysis**

117

118 Geolocator data were analysed in R software (R Core Team 2016) using the FlightR package
119 (Rakhimberdiev et al. 2015), following the procedures outlined by Rakhimberdiev et al. (2016).
120 FlightR provides estimates of location (geolocations) at twilight (dusk and dawn), based on a
121 template fit across these twilight periods, rather than on the "threshold method" such the
122 Geolight package (Lisovski & Hahn 2012). Data for individual twilights were excluded if the
123 pattern of change in light levels during transitions between light and dark was erratic two hours
124 either side of the twilights. This could happen due to varying cloud conditions. However, we
125 re-ran the analyses without twilight deletions to check on the timing of key events, such as
126 arrivals and departures. We used the following behavioural masks: birds could not be static
127 more than 50 km from land, and were constrained to between 60°W-50°E and 20°S-70°N.
128 Distances measured between geolocations were along great circles.

129 The geolocation estimates were approximately 12 hours apart. Therefore, it was not
130 possible to determine the actual time of departure and arrival at locations during migration. To
131 account for uncertainty, the start time of a movement was taken as half way between the last
132 record before the movement and first during the movement. Arrival time was taken as between

133 the last record prior to arrival and the first record at a destination. A movement was deemed to
134 have taken place if there was a difference of at least one degree of latitude (c.111 km) between
135 twilights. A change in latitude rather than longitude seemed appropriate given that the
136 migrations were largely north-south.

137 Meteorological data during the migration periods were examined to account for
138 potential influences of weather on the migrations. These included surface and upper air data,
139 synoptic analyses and geostationary satellite imagery, accessed from professional websites:
140 www.ogimet.com/index.phtml.en, www.sat.dundee.ac.uk, www.earth.nullschool.net,
141 www.wetterzentrale.de/topkarten/ and <http://weather.uwyo.edu/upperair/sounding.html>.

142 During the investigation into meteorological conditions, visual interpolation of data (by
143 studying synoptic charts and satellite images) was frequently necessary due to data-sparse
144 areas along the birds' routes (especially prior to 2014 in northwest Africa). Wind speeds and
145 directions are those at the most likely altitudes, given the lack of data regarding the birds' flight
146 levels.

147 Wind directions follow meteorological convention, i.e. the direction from which the
148 wind is blowing. The term 'weather' includes visibility, temperature and precipitation, as well
149 as other severe phenomena described in the text. All may impact upon a migrant's progress to a
150 greater or lesser degree. Synoptic analyses provided overall representations of the conditions
151 during migration. Altitudes are given in metres above sea level.

152 Indices for the NAO from 1948 to 2016 were obtained from
153 (<https://crudata.uea.ac.uk/~timo/datapages/naoi.htm>) and
154 (www.metoffice.gov.uk/research/climate/seasonal-to-decadal/gpc-outlooks/ens-mean/nao-

155 [description](#)). These data were obtained to test whether there had been any long-term trend,
156 which might support the findings by Pearce-Higgins et al. (2009) that declining return rates by
157 common sandpipers were related to the NAO.

158

159

160 **Results**

161

162 **The migrations**

163

164 Ten geolocators were retrieved, two from Speyside and eight from Sutherland. These provided
165 data for ten southward migrations but only eight northward, due to two geolocators failing
166 before northward migration. The mean mass of the 10 birds was 51.3 g (sd = 4.0) at marking,
167 and 50.1 g (sd = 3.6) at recapture. There was no significant difference in the masses between
168 marking and recapture (paired t-test = 1.06, n = 10, P = 0.32).

169

170 *Southward migration*

171 The median last date in Scotland was 9 July (inter-quartile range, IQR 5-24 July, range 2 July-5
172 August). Initial movements by five birds were to staging sites in England or Ireland where they
173 stayed for short periods; median of 6.5 days (range 1.5-14 days) (Fig. 1, Table 1). The other birds
174 departed from Scotland.

175 Eight birds staged in Iberia (Fig. 1, Table 1). The median arrival date was 12 July (IQR

176 10-19 July) and the median length of stay was 10.8 days (range 2-15 days). One bird staged at an

177 additional site in Morocco, but only for 3.5 days. The median number of staging sites used was
178 1.5 (IQR 1-2, range 0-3) and the median for the total number of days staging was 13 days (IQR
179 11.5-15 days, range 0-21.5 days). There was a significant negative correlation between the
180 number of days staging and the last day in Scotland; birds that left earlier staged for longer ($r = -$
181 0.66, $n = 10$, $P < 0.05$).

182 Most then flew without further staging to West Africa, arriving by 28 July (IQR 24 July-7
183 August, range 24 July-13 August) (Fig. 1). The total time to migrate from Scotland to West
184 Africa, including staging periods, but not the initial fuelling period, was 17.5 days (IQR 15-21
185 days, range 1.5-24). There was uncertainty about latitude during the autumn equinox, but after
186 this period, most shifted further south by 480 km (range 380-1300 km). Thereafter, there were no
187 trends in either latitude or longitude from October to February, indicating that the birds were
188 sedentary over this period. Six of the birds spent this period on the coast of Guinea-Bissau, and
189 one each in Guinea, Sierra Leone, the Canary Islands and Western Sahara (Fig. 1, Table 1,
190 Supplementary Material). The median distance between the non-breeding sites during October
191 to February and breeding areas was 5,300 km (range 3,500-5,400 km) (Table 1).

192

193 *Northward migration*

194 Departure from West Africa overlapped with the spring equinox when estimates for latitude are
195 less reliable for geolocators. The median date on which there was a major northerly movement
196 that exceeded the 95% CLs for previous latitudes took place was 12 April (IQR 8-17 April, range
197 3-20 April). The northward crossing of Africa was followed by staging in Morocco (three birds),
198 Spain (five), France (three) and England (three) (Table 1). The median length of stay in Morocco

199 / Iberia was 7.5 days (range 5-10 days), but only for 3.8 days (range 2.5-16 days) for France /
200 England. The median number of staging sites used was 2 (IQR 1.5-2, range 1-3) and the median
201 for the total number of days staging was 11.5 days (IQR 9.3-13 days, range 6-16.5). This was not
202 significantly different from the total time spent staging during the southward migration (Mann-
203 Whitney U = 51.5, n = 10, 8, P = 0.31).

204 The median arrival date in Scotland was on 2 May (IQR 24 April-4 May, range 19 April-6
205 May). Therefore, the northward migration, excluding the initial fuelling period prior to leaving
206 West Africa, took a median length of 16 days (IQR 13.8-19 days, range 13-20.5 days). This was
207 not significantly different from the southward migration time (Mann-Whitney U = 50, n = 10, 8,
208 P = 0.37).

209 The migration routes for each individual bird are presented in the supplementary
210 material.

211

212

213 **Weather during the migrations**

214

215 *Southward migration*

216 There were no weather-related conditions that might be considered to present difficulties in any
217 of the birds' southward migrations. Most migration began in July with high or weak pressure
218 patterns over or to the west of the British Isles, giving north-easterly tail-winds to the main
219 staging area in southwest Iberia (Fig. 1, Supplementary Material). Six birds departed from the
220 breeding sites almost immediately as adverse wind and weather conditions were clearing, while

221 four did not depart until two to six days after the weather had improved. Onward migration
222 utilised northerly or northeast winds in the trade-wind zone, with one bird stopping briefly in
223 Morocco.

224 Exceptions to this general migration pattern were birds 7 and 9, which departed from
225 Britain later in the season than the other birds. Bird 7 departed from its breeding grounds on 5
226 August 2013, perhaps delayed by a succession of low pressure systems. Bird 9 staged in
227 England in late July and early August (2015), likely being delayed by a similar weather pattern
228 as bird 7, and departed from Britain on 7 August (2015), arriving in Senegal 9 August (2015). It
229 then flew back north in late August to winter in the Canary Islands. Head-winds on this return
230 north may have been avoided if the bird flew above 1,000 m.

231

232 *Northward migration*

233 The first part of the return passage from West Africa for most birds began in fine weather
234 although one experienced low-level head-winds. Thereafter, the fortunes of each bird were
235 dependent on the timing of migration in relation to the passage of weather systems over
236 northwest Africa, Iberia and France (Fig. 1).

237 The weather during the migration of bird 1 has already been described (Bates et al.
238 2012), although our current refinement of the data showed a route some 350 km further west
239 over Iberia than originally indicated. Nevertheless, strong head-winds over the staging area in
240 southern Spain were still likely to have delayed onward migration.

241 In 2014, winds in mid-April were light northerly in West Africa, whence bird 5 departed
242 on 6 April, bird 3 on 15 April and bird 4 on 18 April. None encountered adverse winds or

243 weather during the initial flight over northwest Africa. Bird 6 may have been delayed by a
244 strengthening north-easterly wind of 10-15 m per s, before departing on 20 April. Its eventual
245 northward movement could have been at a higher altitude where the wind became south-
246 westerly. This tail-wind strengthened further north, ahead of a strong upper trough (associated
247 with part of the sub-tropical jet stream) and resulted in marked drift over the Sahara to take the
248 bird into eastern Morocco by 22 April (Fig. 2). An accompanying surface trough brought low
249 level northerly winds gusting to 15-30 m per s. Associated weather included blowing sand,
250 thunderstorms, hail and local tornados, but the poor conditions lasted for only hours at any one
251 place and the bird had moved into eastern Spain by 27 April. By 20 April, bird 5 was in France,
252 followed by bird 3 on 26 April and bird 6 on 1 May. Birds 3 and 6 both encountered
253 unfavourable winds and rain over France but birds 3 and 5 were aided by southeast winds on
254 reaching the UK in late April and early May. Bird 4 made short stopovers in Western Sahara
255 and Morocco, finally leaving its Spanish staging area on 5 May and making rapid progress
256 through the UK on 6 May.

257 In 2015, bird 8 was the earliest to depart and moved through Morocco between 4 and 7
258 April. This coincided with low pressure and troughs, but winds were light. The bird crossed
259 into Spain on 8 April during strong easterly winds (the Levanter) with low level winds of up to
260 25 m per s. For the whole of April 2015, easterly winds blew on a high percentage (70%) of days
261 (Garcia 2016). After staging in Spain for five days, the final return to the UK took place west of
262 France where strong east to southeast winds forced an overseas route, after which rising
263 pressure allowed a steady onward passage to Scotland *via* a short stopover in England.

264 In 2016, bird 9 returned south to Western Sahara from the Canary Islands in late March
265 2016, in fresh north to northeast winds. It staged here until 11 April, whence it departed.
266 Passage north was rapid in southwest winds, and it reached France by 14 April *via* the western
267 Mediterranean, where it staged for 16 days in variable weather conditions. By contrast, bird 10
268 moved only slowly through Morocco, staging there until 23 April. It overtook bird 9 by 26 April
269 but was delayed in northern France and southern England by a succession of weather fronts
270 with changeable winds (Fig. 3). Both birds then returned to northern Scotland in freshening
271 south-westerly winds, with bird 9 arriving one day ahead of bird 10.

272 We examined long-term data (1948-2016) for the NAO indices for April and winter, and
273 did not find significant trends: April $r_s = -0.12$, January $r_s = 0.13$, February $r_s = 0.13$, $n = 70$ for all
274 tests.

275

276

277 **Discussion**

278

279 The above results from the analyses of geolocator data (including weather experienced) plus
280 recoveries of ringed common sandpipers allow us to summarise the migration patterns of
281 Scottish common sandpipers.

282

283 **Southward migration**

284

285 Holland (2009) predicted that common sandpipers with a departure mass of 84 g and lean mass
286 of 45 g would be able to undertake a 4,000 km flight from England. Another estimate based on
287 Pennycuick's (2008) equation predicted a flight range of 5,893 km (Yalden 2012). Similarly long
288 flight ranges were predicted by Iwajomo and Hedenström (2011) for birds with the highest fuel
289 loads in Sweden: 5,902 km for juveniles and 6,102 km for adults. It would therefore seem that
290 common sandpipers have the potential to accomplish their migration from northern Europe to
291 West Africa in a single flight, but our findings from geolocators show that this is not usually the
292 case. Further, ringing recoveries in France and Spain of birds from Britain and elsewhere in
293 northern Europe indicated that many stage in southern Europe, rather than accomplish the
294 migration in a single flight (Arcas 1999, Wernham et al. 2002, Iwajomo and Hedenström 2011). If
295 birds had only average fuel loads, then shorter flights to staging sites in southern Europe were
296 predicted: juveniles 2,182 km; adults 2,324 km (Iwajomo and Hedenström 2011). Our data from
297 birds with geolocators showed that most staged in Iberia for 10 days (range 2-14.5 days).

298 After staging in Iberia (eight birds) and Morocco (one bird), the rest of the migration to
299 West Africa involved a longer flight (c. 3,000 km). One bird was late in departing and migrated
300 without staging, thereby revealing variation in migration strategy. Generally, late departing
301 common sandpipers staged for shorter periods, a pattern that has also been seen in great snipes
302 (Lindström et al. 2016). This variation in strategy is consistent with the observation that a range
303 of fuel loads are stored prior to departure from northern Europe (Iwajomo and Hedenström
304 2011, Bates et al. 2012).

305 All tagged birds departed from the breeding grounds in weather conditions that were
306 suitable for migration, such as high visibility and little cloud cover, and when wind directions
307 were generally favourable (tail-winds).

308

309 **The non-breeding area**

310

311 Ringing recoveries of common sandpipers ringed in Sweden (Fransson et al. 2008) and Finland
312 (Saurola et al. 2013), our initial study with geolocators (Bates *et al.* 2012) and this study showed
313 that coastal West Africa is an important non-breeding area for common sandpipers that breed in
314 northern Europe. The majority of our tagged birds spent most of the non-breeding season
315 (October – February) in the coastal regions of Guinea-Bissau, and thereby were associated with
316 mudflats bordered by mangrove woodland (Feka and Ajonina 2011), presumably in the
317 Archipelago dos Bijagós. Thus, our study pinpoints this area as the most important site for
318 Scottish-breeding common sandpipers. The estimated number of waders wintering on the
319 intertidal flats of Guinea-Bissau is one million, including tens of thousands (mostly whimbrels
320 and common sandpipers) in the mangroves (Zwarts 1988).

321

322 **Northward migration**

323

324 Initial tracks of the northward migration were over the north-western edge of the Sahara.
325 Whereas the northeast trade winds are advantageous in late summer, they act as head-winds in
326 spring (Table 4). In many circumstances, waders make use of tail-winds, but may be forced to

327 migrate in head-winds when tail-winds are rare (Grönroos et al. 2012). Fortunately, the trade
328 winds are weaker in spring and tail-winds are often present at higher altitudes (above 2,000 m),
329 to which migrants may find it expedient to climb (Alerstam 1990, Newton 2008). Flight levels
330 exceeding 2,000 m would be necessary on some inland routes, for example when crossing the
331 Atlas Mountains of Morocco.

332 As in late summer, Iberia was a staging area during northward migration, though some
333 used, or were forced to use Western Sahara and Morocco as the first opportunity to refuel.

334 Weather systems crossing routes between latitudes 30° and 40° N clearly affect returning
335 sub-Saharan migrants because there are instances of mass mortality of small migrants (Smith
336 1968, Elkins 2004). Further, Smith (1968) recorded a fall of 20 common sandpipers in eastern
337 Morocco in April 1963 in northerly gales, showing that migration had been curtailed. Such
338 weather conditions were similar to those described above for bird 6. However, there is no
339 evidence of a trend for an increase in short-term adverse wind and weather events in this
340 region, such as extreme rainfall (Tramblay et al. 2012).

341 Some birds also made short stops in France or England before reaching their breeding
342 grounds. Birds 3, 6 and 10 were possibly delayed in France or England due to adverse winds
343 (Fig. 1). The common theme of strong head-winds and cross-winds in spring was associated
344 with weather systems moving east or southeast across northwest Africa, Iberia and/or France.
345 The degree to which such weather events significantly influence the route or duration of staging
346 periods is not known, although can perhaps cause delays or drift. Any delays must have been of
347 short duration because there was no significant difference between the time spent on the
348 southward and northward migrations.

349 The tracks of the tagged birds were consistent with ringing recoveries of British breeders
350 during northward migration, with birds in Morocco, Spain, Portugal and France during March-
351 April (Wernham et al. 2002), and Scottish-ringed birds recovered in southwest, central and
352 northern England, and Wales (Dougall 1999, 2005).

353 In summary, the data from ringing and geolocators show that most common sandpipers
354 from Scotland migrate to and from West Africa in medium-range flights *via* staging areas,
355 largely in Iberia. The other strategy was to carry out a single flight, but to a closer non-breeding
356 site. Several studies of wader migration using geolocators have involved birds whose strategy
357 has been constrained by the need to make long flights over oceans; *e.g.* Pacific golden-plovers
358 *Pluvialis fulva* and ruddy turnstones *Arenaria interpres* migrating across the Pacific (Johnson et al.
359 2011, Minton et al. 2010), and purple sandpipers *Calidris maritima* crossing the Atlantic
360 (Summers et al. 2014). By contrast, the little ringed plover *Charadrius dubius* (Hederström et al.
361 2013) and Temminck's stint *Calidris temminckii* (Lislevand and Hahn 2015) migrate largely over
362 land, and have shorter flights punctuated by staging. Likewise, the migration of common
363 sandpipers is largely over land where there are opportunities to stop, rest, and refuel, and allow
364 birds to select the wind direction for the next stage of the migration. Migrants crossing oceans
365 can only select winds within different altitude bands once they have departed. Nevertheless, the
366 Sahara is still regarded as an obstacle, requiring at least one long flight for Afro-Palearctic
367 waders; *e.g.* great snipe *Gallinago media* (Lindström et al. 2016).

368

369 **Possible causes of the population decline**

370

371 The decline of a breeding population of common sandpipers in northern England was
372 negatively correlated with the North Atlantic Oscillation (NAO); the return rate to the breeding
373 grounds was lower when the weather was cool and dry in northwest Africa in winter (Pearce-
374 Higgins et al. 2009). The NAO relates to the global wind pattern occurring over the North
375 Atlantic Ocean, mainly during October to March and in mid to high latitudes. Although
376 Barandiaran and Wang (2012) found a correlation between rainfall in West Africa and the NAO,
377 such a link to rainfall where most of the common sandpipers spend the non-breeding season is
378 unclear, especially as common sandpipers are largely associated with intertidal habitats (Zwarts
379 1988). There are no detailed data on long-term changes in winds or rain over the migration
380 routes, so the NAO indices are the only relevant data available. However, we did not detect any
381 long-term (70 years) trends for either the April NAO indices (when the birds are on northward
382 migration) or the winter indices (as used by Pearce-Higgins et al. 2009).

383 It is well known that staging areas are vital to migrants (Alerstam 1990, Newton 2008).
384 In late summer, common sandpipers staging in southwest Iberia and/or Morocco during the
385 southward migration do so during the hottest and driest season. Recent rising temperatures and
386 intensifying droughts in Spain (Meteorological Office 2011) have been implicated in the decline
387 of some migrant species (e.g. Halupka et al. 2017), but there is no current evidence of any
388 significant degradation of the wetland habitats that common sandpipers utilise (E.F.J. Garcia
389 pers. comm.) and it thus seems unlikely that this would cause a population decline. However,
390 birds also staged in Morocco, which has also undergone increasing drought (USAID 2016) and
391 has fewer wetlands than Iberia, so this could have affected common sandpipers.

392 Our study showed that most of the tagged common sandpipers spent the northern
393 winter on coastal mudflats and associated mangrove woodland in Guinea-Bissau. The
394 mangrove woodland in West Africa occurs largely in southern Senegal, The Gambia, Guinea-
395 Bissau, Guinea, Sierra Leone and Nigeria. From 1975 to 2013, the area of mangrove declined by
396 4.8% (984 km²), with the greatest losses in Nigeria (432 km²), whereas Senegal and Guinea-
397 Bissau lost 288 and 220 km², respectively (USAID 2017). The main losses were due to
398 deforestation for wood fuel and conversion to land for agriculture (Feka and Ajoina 2011,
399 USAID 2017). The amount lost (4.8%) is probably insufficient to have had a major effect on the
400 population size of common sandpipers. Some of the loss of mangrove has been due to the
401 creation of rice fields, which will have offset some of the loss of feeding habitat for waders, at
402 least when the fields are wet (Wymenga and Zwarts 2010, Elphick et al. 2010). The area of rice
403 cultivation within the coastal mangrove zone extended over 1,128 km² in 2000-2005 (Bos et al.
404 2006) and the coastal rice fields support 1.17 million wetland birds during the northern winter
405 (Wymenga and Zwarts 2010). Thus, it seems unlikely that loss of habitat in the non-breeding
406 quarters is the reason for the decline in the numbers of common sandpipers in Britain.

407 In terms of explaining the decline in the numbers of common sandpipers, it seems that
408 the northward migration is the only time when they experience unfavourable weather and
409 winds that could possibly lead to higher mortality. Even although some common sandpipers
410 migrate close to the coast (supplementary material), where there are more stop-over
411 opportunities than for trans-Saharan migrants crossing the central Sahara, staging sites may
412 have become increasingly untenable during both spring and autumn migration as drought
413 intensifies in northwest Africa (USAID 2016). Increased mortality among common sandpipers

414 during the northward migration in April would be consistent with results from a study of the
415 Spoonbills *Platalea leucorodia* that breed in The Netherlands and spend the non-breeding season
416 in West Africa. They suffer their highest mortality when crossing the western part of the Sahara
417 during the northward migration (Lok et al. 2015). Although it is plausible that this part of the
418 annual cycle is also a bottleneck for common sandpipers, confirming this would require tags
419 that can track the fate of all birds rather than just for those that return.

420 Our study dealt only with adult birds. It is possible that, rather than a change in adult
421 mortality causing the decline, it is juvenile common sandpipers that are suffering a higher
422 mortality when crossing the Sahara, as found for raptor species during their first autumn
423 migration (Strandberg et al. 2009).

424

425 *Acknowledgements* - Our study is a Highland Ringing Group project for which geolocators were
426 bought from money raised by the group. The *British Birds* Charitable Trust and the Endowment
427 Fund of the Scottish Ornithologists' Club also kindly provided funds to cover some of the costs
428 of the project. Rhys Green provided the design for the leg harness and Clive Minton and Ron
429 Porter advised on flag construction for leg-mounted geolocators. Snæbjörn Pálsson from the
430 University of Iceland carried out the molecular sexing. The Speyside Estate kindly provided
431 permission to trap birds on the River Spey. We thank Teresa Catry, Oliver Fox, Yvonne Verkuil
432 and Leo Zwarts for information about West Africa and Ernest Garcia for information about
433 wetlands in Spain. We are grateful to Tom Dougall, Phil Holland and Åke Lindström who
434 commented on the draft. We plan to deposit our data in Movebank.

435

436 *Declarations* – There were no conflicts of interest. Field work was carried out by BB, BE and RS,
437 and analyses and writing by BB, NE, LdR and RS.

438

439 **References**

440

441 Åkesson, S., Klaassen, R., Holmgren, J., Fox, J.W. and Hedenström, A. 2012. Migration routes
442 and strategies in a highly aerial migrant, the common swift *Apus apus*, revealed by light-level
443 geolocators. - PLoS ONE 7 (7):e41195.doi:10.1371/journal.pone.0041195.

444

445 Alerstam, T. 1990. Bird migration. - Cambridge Univ. Press.

446

447 Arcas, J. 1999. Origin of common sandpipers *Actitis hypoleucos* captured in the Iberian peninsula
448 during their autumn migration. - Wader Study Group Bull. 89: 56-59.

449

450 Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. and Fuller, R.J. 2013. Bird atlas
451 2007-11: the breeding and wintering birds of Britain and Ireland. - BTO Books.

452

453 Balmori, A. 2005. Stopover ecology and diverse migratory strategies use in the common
454 sandpiper (*Actitis hypoleucos*). - Ardeola 52: 319-331.

455

456 Barandiaran, D. and Wang, S-Y. 2012. A teleconnection between geopotential height anomalies
457 over the North Atlantic and precipitation in the Sahel region of Africa. - NOAA Science and
458 Technology Infusion Climate Bulletin.

459

460 Bates, B., Etheridge, B., Elkins, N., Fox, J. and Summers, R.W. 2012. Pre-migratory change in
461 mass and the migration track of a common sandpiper *Actitis hypoleucos* from Scotland. - Wader
462 Study Group Bull. 119: 149-154.

463

464 Bos, D., Grigoras, I. and Ndiaye, A. 2006. Land cover and avian biodiversity in rice fields and
465 mangroves of West Africa. – A and W-report, Altenburg and Wymenga ecological consultants /
466 Wetlands International, Dakar, Senegal / Veenwouden, Netherlands.

467

468 Cramp, S. and Simmons, K.E.L. (eds). 1983. The birds of the western Palearctic, Vol. 3. - Oxford
469 Univ. Press.

470

471 Cresswell, B. and Edwards, D. 2013. Geolocators reveal wintering areas of European nightjar
472 (*Caprimulgus europaeus*). - Bird Study 60: 77-86.

473

474 Dougall, T.W. 1999. Ringing in the Scottish Borders 1996 and 1997. - Borders Bird Report 18: 99-
475 108.

476

- 477 Dougall, T.W. 2005. Ringing in the Scottish Borders 2003 and 2004. - Borders Bird Report 22:
478 139-151.
479
- 480 Dougall, T.W., Holland, P.K. and Yalden, D.W. 2010. The population biology of common
481 sandpipers in Britain. - Brit. Birds 103: 100-114.
482
- 483 de Elgea, A.O. and Arizaga, J. 2016. Fuel load, fuel deposition rate and stopover duration of the
484 common sandpiper *Actitis hypoleucos* during the autumn migration. - Bird Study 63: 262-267.
485
- 486 Elkins, N. 2004. Weather and bird behaviour. 3rd ed. - Poyser.
487
- 488 Elphick, C.S., Baicich, P., Parsons, K.C., Fasola, M. and Mugiga, L. 2010. The future for research
489 on waterbirds in rice fields. - Waterbirds 33 (Special Publication 1): 231-243.
490
- 491 Feka, N.Z. and Ajonina, G.N. 2011. Drivers causing decline of mangrove in West-Central Africa:
492 a review. – Int. J. Biodivers. Sci. Ecosyst. Serv. Manag. 7: 217-230.
493
- 494 Fransson, T., Österblom, H. and Hall-Karlsson, S. 2008. Svensk ringmärkningsatlas, Vol. 2. -
495 Natural History Museum.
496
- 497 Fridolfsson, A.-K. and Ellegren, H. 1999. A simple and universal method for molecular sexing of
498 non-ratite birds. - J. Avian Biol. 30: 116-121.

- 499
- 500 Garcia, E.F.J. (ed). 2016. Weather summary 2015. - Gibraltar Bird Report 2015:10-11.
- 501
- 502 Grönroos, J., Green, M. and Alerstam, T. 2012. To fly or not to fly depending on winds:
503 shorebird migration in different seasonal wind regimes. – Anim. Behav. 83: 1449-1457.
- 504
- 505 Halupka, L., Wierucka, K., Sztwiertnia, H. and Klimczuk, E. 2017. Conditions at autumn
506 stopover sites affect survival of a migratory passerine. - J. Ornithol. 158: 979-988.
- 507
- 508 Hedenström, A., Klaassen, R.H.G. and Åkesson, S. 2013. Migration of the little ringed plover
509 *Charadrius dubius* breeding in South Sweden tracked by geolocators. - Bird Study 60: 466-474.
- 510
- 511 Holland, P.K. 2009. Relationship between common sandpipers *Actitis hypoleucos* breeding along
512 the River Lune, England, and those fattening for migration near its mouth with a model of their
513 onward migration. - Wader Study Group Bull. 116: 83-85.
- 514
- 515 Holland, P.K., Robson, J.E. and Yalden, D.W. 1982. The breeding biology of the common
516 sandpiper *Actitis hypoleucos* in the Peak District. - Bird Study 29: 99-110.
- 517
- 518 Iwajomo, S.B. and Hedenström, A. 2011. Migration patterns and morphometrics of common
519 sandpipers *Actitis hypoleucos* at Ottenby, southeastern Sweden. - Ring. and Migr. 26: 38-47.
- 520

- 521 Johnson, O.W., Fielding, L., Fox, J.W., Gold, R.S., Goodwill, R.H. and Johnson, P.M. 2011.
522 Tracking the migrations of Pacific golden-plovers (*Pluvialis fulva*) between Hawaii and Alaska:
523 New insight on flight performance, breeding ground destinations, and nesting from birds
524 carrying light level geolocators. - Wader Study Group Bull. 118: 26-31.
525
- 526 Jones, P., Vickery, J., Holt, S. and Cresswell, W. 1996. A preliminary assessment of some factors
527 influencing the density and distribution of palearctic passerine migrants wintering in the Sahel
528 zone of West Africa. - Bird Study 43: 73-84.
529
- 530 Lindström, Å., Alerstam, T., Bahlenberg, P., Ekblom, R., Fox, J.W., Råghall, J. and Klaassen,
531 R.H.G. 2016. The migration of the great snipe *Gallinago media*: intriguing variations on a grand
532 theme. - J. Avian Biol. 47: 321-334.
533
- 534 Lislevand, T. and Hahn, S. 2015. Skipping-type migration in a small Arctic wader, the
535 Temminck's stint *Calidris temminckii*. - J. Avian Biol. 46: 419-424.
536
- 537 Lisovski, S. & Hahn, S. 2012. Geo-light – processing and analysing light-based geolocator data
538 in R. - Methods Ecol. Evol. 3: 1055-1059.
539
- 540 Lockwood, J.G. 1974. World climatology – an environmental approach. - Edward Arnold.
541

542 Lok, T., Overdijk, O. and Piersma, T. 2015. The cost of migration: spoonbills suffer higher
543 mortality during trans-Saharan spring migrations only. – Biol. Lett. 11: 20140944.

544

545 Meteorological Office. 2011. Climate: Observations, projections and impacts.

546 <https://www.metoffice.gov.uk/binaries/content/assets/mohippo/pdf/k/i/spain.pdf>

547

548 Minton, C., Gosbell, K., Johns, P., Christie, M., Fox, J.W. and Afanasyev, V. 2010. Initial results
549 from light level geolocator trials on ruddy turnstone *Arenaria interpres* reveal unexpected
550 migration route. - Wader Study Group Bull. 117: 9-14.

551

552 Newton, I. 2008. The migration ecology of birds. - Academic Press.

553

554 Ockendon, N., Hewson, C.M., Johnston, A. and Atkinson, P.W. 2012. Declines in British-
555 breeding populations of Afro-Palaeartic migrant birds are linked to bioclimatic wintering zone
556 in Africa, possibly via constraints on arrival time advancement. - Bird Study 59: 111-125.

557

558 Pearce-Higgins, J.W., Yalden, D.W., Dougall, T.W. and Beale, C.M. 2009. Does climate change
559 explain the decline of a trans-Saharan Afro-Palaeartic migrant? - Oecologia 159: 649-659.

560

561 Pennycuik, C.J. 2008. Bird flight performance. A practical calculation manual. - Oxford
562 University Press.

563

- 564 Pienkowski, M. 1976. Methods of catching and studying breeding waders – continued again. -
565 Wader Study Group Bull. 18: 14-15.
566
- 567 R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for
568 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
569
- 570 Rakhimberdiev, E., Winkler, D.W., Bridge, E., Seavy, N.E., Sheldon, D., Piersma, T. and
571 Saveliev, A. 2015. A hidden Markov model for reconstructing animal paths from solar
572 geolocation loggers using templates for light intensity. - *Movement Ecology* 3: (25).
573 DOI:10.1186/s40462-015-0062-5.
574
- 575 Rakhimberdiev, E., Senner, N.R., Verhoeven, M.A., Winkler, D.W., Bouten, W. and Piersma, T.
576 2016. Comparing inferences of solar geolocation data against high-precision GPS data: annual
577 movements of a double-tagged black-tailed godwit. - *J. Avian Biol.* 47: 589-596.
578
- 579 Rappole, J.H. and Tipton, A.R. 1991. New harness design for attachment of radio transmitters to
580 small passerines. - *J. Field Ornithol.* 62: 335-337.
581
- 582 Saurola, P., Valkama, J. and Velmala, W. 2013. Finnish bird ringing atlas, Vol. 1: - Suomen
583 Rengastusatlas 1 Helsinki Luomus. Finnish Museum of Natural History and Ministry of
584 Environment.
585

- 586 Smith, K. D. 1968. Spring migration through southeast Morocco. - *Ibis* 110: 452-492
587
- 588 Stevens, M., Sheehan, D., Wilson, J., Buchanan, G. and Cresswell, W. 2010. Changes in Sahelian
589 bird biodiversity and tree density over a five-year period in northern Nigeria. - *Bird Study* 57:
590 156-174.
591
- 592 Strandberg, R., Klaassen, R.H.G., Hake, M. and Alerstam, T. 2009. How hazardous is the Sahara
593 Desert crossing for migratory birds? Indications from satellite tracking of raptors. - *Biology*
594 *Letters* doi: 10.1098/rsbl.2009.0785.
595
- 596 Summers, R.W., Boland, H., Colhoun, K., Elkins, N., Etheridge, B., Foster, S., Fox, J.W., Mackie,
597 K., Quinn, L.R. and Swann, R.L. 2014. Contrasting trans-Atlantic migratory routes of Nearctic
598 purple sandpipers *Calidris maritima* associated with low pressure systems in spring and winter. -
599 *Ardea* 102: 139-152.
600
- 601 Trambly, Y., Badi, W., Driouech, F., El Adlouni, S., Neppel, L. and Servat, E. 2012. Climate
602 change impacts on extreme precipitation in Morocco. - *Global Planet. Change* 82-83: 104–114.
603
- 604 USAID 2016. Climate Change Risk in Morocco. - Country fact sheet. United States Agency for
605 International Development.
606

- 607 USAID 2017. Land Use and Land Cover Dynamics. Mangrove changes. West Africa. - Country
608 fact sheet. United States Agency for International Development.
609
- 610 Vickery, J.A., Ewing, S.R., Smith, K.W., Pain, D.J., Bairlein, F., Škorpilova, J. and Gregory, R.D.
611 2014. The decline of Afro-Palaeartic migrants and an assessment of potential causes. - *Ibis* 156:
612 1-22.
613
- 614 Walker, R.H., Robinson, R.A., Leech, D.I., Moss, D., Barimore, C.J., Blackburn, J.R., Barber, L.J.,
615 Clewley, G.D., de Palacio, D.X., Grantham, M.J., Griffin, B.M., Kew, A.J. Schaefer, S. and Clark,
616 J.A. 2016. Bird ringing and nest recording in Britain and Ireland in 2015. – *Ring. and Migr.* 31:
617 115-159.
618
- 619 Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. and Baillie, S.R.
620 (eds). 2002. *The Migration Atlas: movements of the birds of Britain and Ireland.* - T. and A.D.
621 Poyser.
622
- 623 Winstanley, D., Spencer, R. and Williamson, K. 1974. Where have all the whitethroats gone? -
624 *Bird Study* 21: 1-14.
625
- 626 Wymenga, E. and Zwarts, L. 2010. Use of rice fields by birds in West Africa. - *Waterbirds* 33
627 (Special Publication 1): 97-104.
628

- 629 Yalden, D.W. 2012. Wing area, wing growth and wing loading of common sandpipers *Actitis*
630 *hypoleucos*. - Wader Study Group Bull. 119: 84-88.
- 631
- 632 Zwarts, L. 1988. Numbers and distribution of coastal waders in Guinea-Bissau. - *Ardea* 76: 42-
633 55.
- 634
- 635 Zwarts, L., Bijlsma, R.G., van der Kamp, J. and Wymenga, E. 2009. Living on the edge: wetlands
636 and birds in a changing Sahel. - KNNV Publishing.
- 637
- 638

639 Table 1. The timing of key events during the southward (autumn) and northward (spring)
 640 migrations of common sandpipers marked with geolocators in Highland Scotland as breeding
 641 adults. Sex (M = male, F = female) is given beside the bird code. The first two refer to birds
 642 breeding in Strathspey, whilst the rest were from Sutherland. The migration duration does not
 643 include the initial period of fuelling and only to the July-August locations. The great circle
 644 distances are from breeding grounds to October-February locations.

645 Southward migration

Bird code (sex)	Last day in Scotland	Staging details	First day in West Africa	Migration duration (days)	Location (Jul-Aug)	Location (Oct-Feb)	Distance (km)
1. (M)	8 July	England (8-20 July) Spain (22-23 July) Morocco (24-27 July)	29 July	21	Senegal	Guinea-Bissau	5,200
2. (M)	2 July	England (3-10 July) Portugal (12-25 July)	27 July	24	Mauritania	Sierra Leone	5,400
3. (F)	5 July	Portugal (8-19 July)	24 July	18	Senegal	Guinea-Bissau	5,300
4. (F)	4 July	Spain (8-22 July)	26 July	21.5	Senegal	Guinea-Bissau	5,300
5. (M)	9 July	Spain (11-20 July)	24 July	14	Senegal	Guinea-Bissau	5,300
6. (M)	12 July	Ireland (13-14 July) Portugal (16-25 July)	28 July	15	Senegal	Guinea-Bissau	5,300
7. (M)	5 August	None	7 August	1.5	Morocco	Western Sahara	3,600
8. (M)	6 July	France (8-10 July) Spain (11-20 July)	24 July	17	Liberia	Guinea	5,400
9. (F)	24 July	England (24 July-7 August)	9 Aug	16	Senegal	Canary Islands	3,500
10. (M)	25 July	England (26-27 July) Portugal (30 July-11 August)	13 August	18.5	Mauritania	Guinea-Bissau	5,300

646	Median	9 July	28 Jul	18	5,300
-----	--------	--------	--------	----	-------

647 Northward migration

Bird code (sex)	Last day in West Africa	Staging details	First day in Scotland	Migration duration (days)
1. (M)	10 April	Spain (12-18 April) England (19-23 April)	24 April	13.5
3. (F)	15 April	Spain (20-25 April)	1 May	15.5
4. (F)	18 April	Western Sahara (23-26 April) Morocco (27-29 April) Spain (30 April-5 May)	6 May	18
5. (M)	6 April	Morocco (8-17 April) France (20-22 April)	23 April	16.5
6. (M)	20 April	Spain (23-30 April) France (1-4 May)	4 May	14
8. (M)	3 April	Spain (8-13 April) England (14-16 April)	19 April	15
9. (F)	11 April	France (14-30 April)	2 May	20
10. (M)	12 April	Morocco (14-23 April) England (28 April-2 May)	3 May	20.5
Median	12 April		2 May	16

648

649

651

652

653 Legends for figures

654 Figure 1. (a) Southward migration and (b) northward migration of common sandpipers with
655 marking locations (stars), southward and northward staging areas (southward and northward
656 facing triangles), locations during July-August (squares) (Figure 1a) and locations during
657 October to February (circles). Symbols for two birds overlap with others in Guinea-Bissau,
658 making six birds in total. Wind roses for Britain, France, Spain/Iberia and West-Africa (from top
659 to bottom) show the number of birds experiencing low/moderate wind speeds (<5 m per s)
660 (grey) and high wind speeds (>5 m per s) (black) during their migration, whereby each ring
661 represents one bird (e.g. in Figure 1a, during southward migration in Spain/Iberia [third wind
662 rose from the top], one bird experienced low/moderate north-westerly winds, two birds
663 experienced low/moderate northerly winds and one bird experienced high northerly winds,
664 and two birds experienced low/moderate north-easterly winds and two birds experienced high
665 north-easterly winds).

666

667

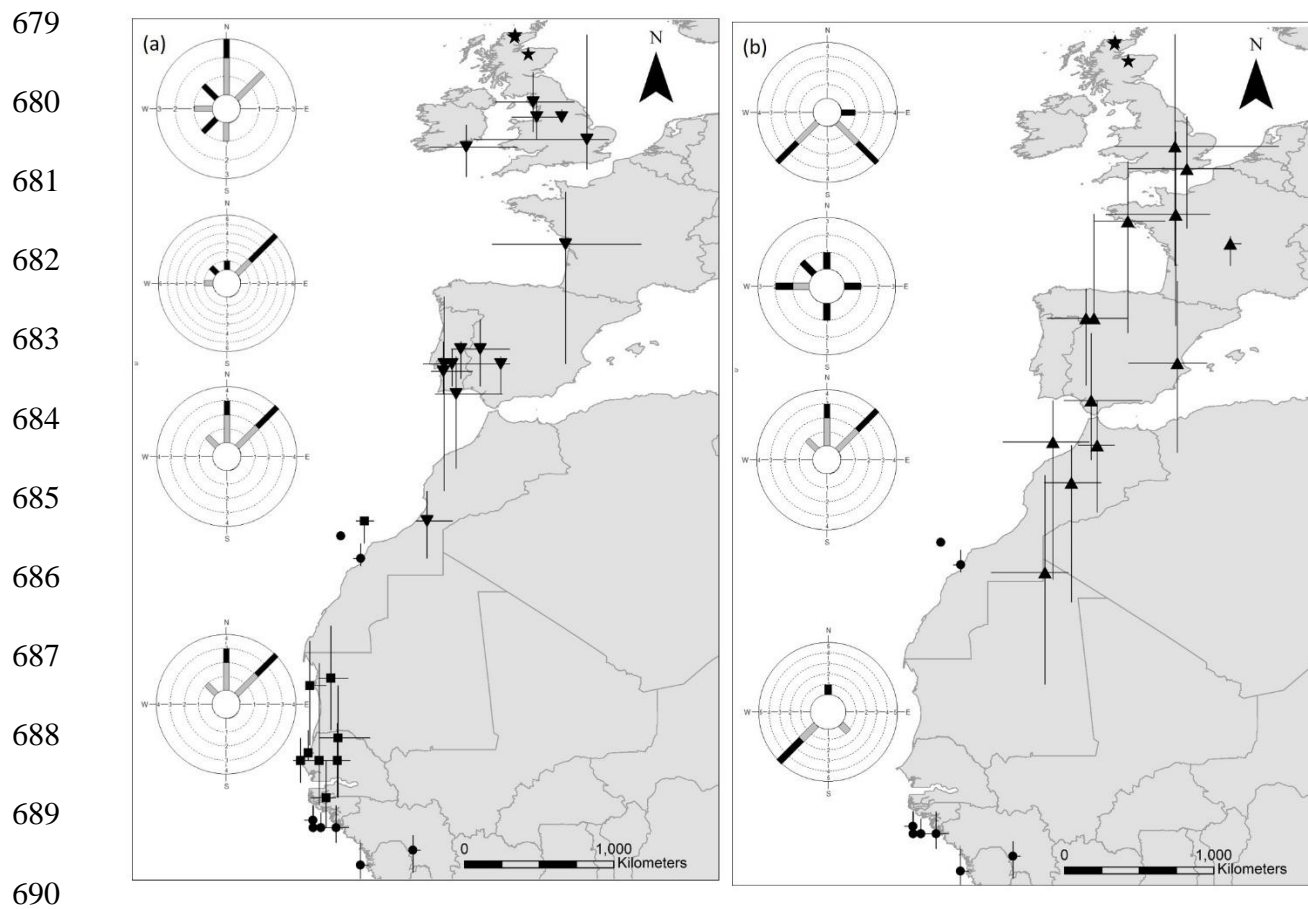
668

669 Figure 2. Synoptic chart for 00hrs, 22 April 2014. The troughs of low pressure over Algeria and
670 Morocco brought surface wind gusts up to 30 m per s with local thunderstorms and tornados,
671 affecting the track of bird 6. Its location is shown as a cross (see also Fig. 3).

672 (<http://www.wetterzentrale.de/reanalysis.php?uur=0000&var=45&nmaps=24&map=1&model=ns&jaar=2014&maand=04&dag=22>)

674

675 Figure 3. Synoptic chart for 00hr, 29 April 2016. Bird 10 (its location shown as a cross) was
676 possibly delayed by the passage of fronts in northern France and southeast Britain, before
677 reaching northern Scotland on 3 May in clearing weather. Reproduced by permission of the
678 Meteorological Office.



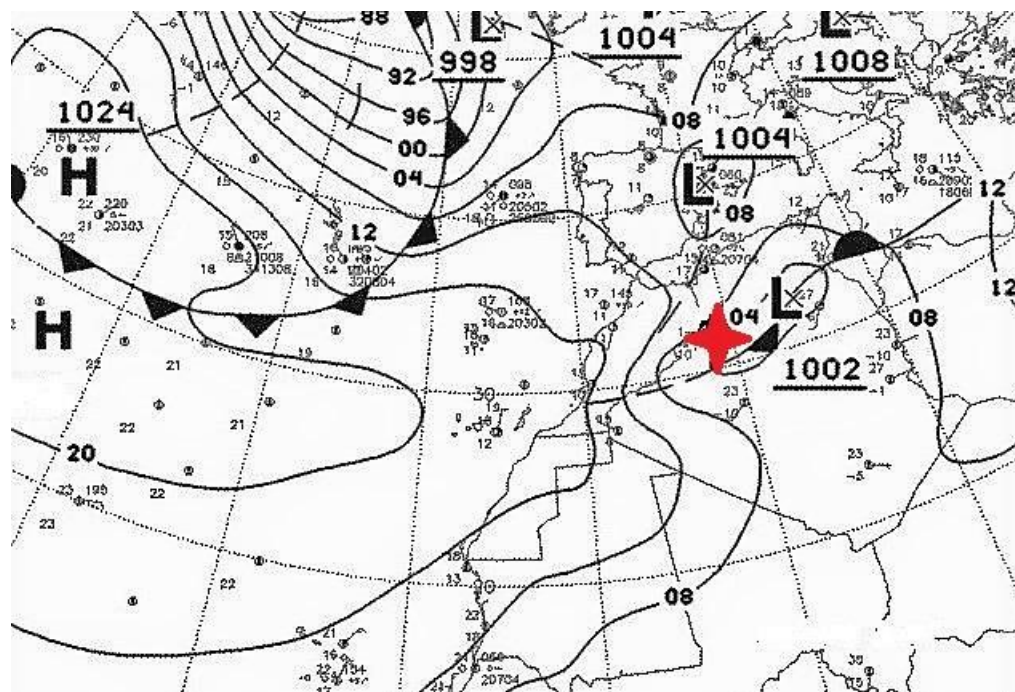
691

692 Fig. 1

693

694

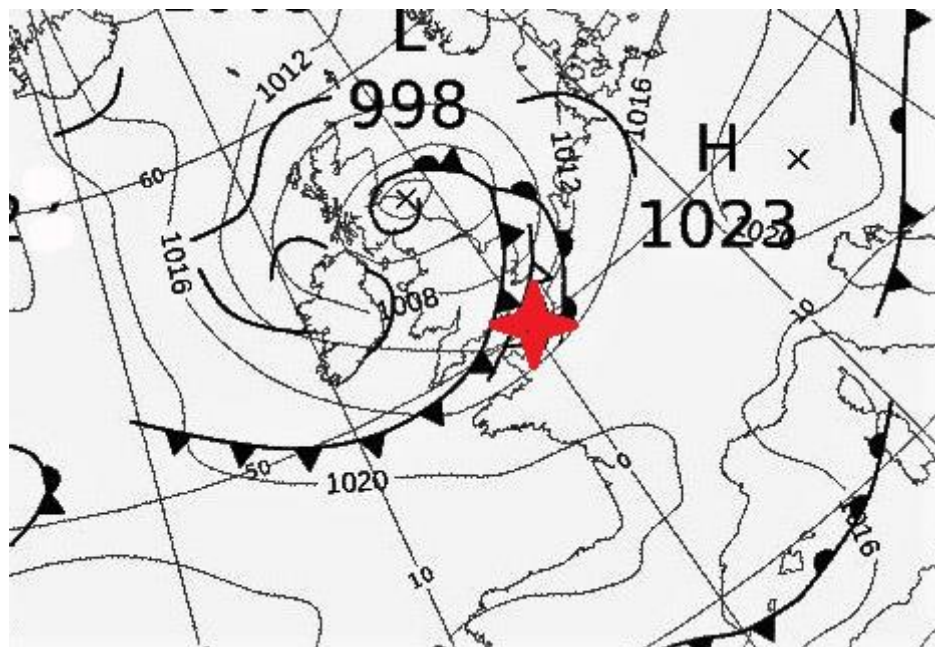
695
696
697
698
699



700
701
702 Fig.2

703

704



705

706

707 Fig. 3

708

709

710

711