

1 Investigating connectivity and seasonal differences in wind
2 assistance in the migration of Common Sandpipers

3 *Running header:* The effect of wind on migration

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9

10 Abstract

11 Many migratory bird species have undergone large recent population declines, but there is
12 considerable variation in trends between species and between populations employing different
13 migratory routes. Understanding species-specific migratory behaviours is therefore of critical
14 importance for their conservation. The Common Sandpiper (*Actitis hypoleucos*) is an Afro-Palearctic
15 migratory bird species whose European populations are in decline. We fitted individuals breeding in
16 England and wintering in Senegal with geolocators to determine their migration routes and breeding
17 or non-breeding locations. We used these geolocator data, and combined them with previously
18 published data from Scottish breeding birds, to determine the distributions and migratory
19 connectivity of breeding (English and Scottish) and wintering (Senegalese) populations of the
20 common sandpiper, and used simulated random migrations to investigate wind assistance during
21 autumn and spring migration. We revealed that the Common Sandpipers tagged in England spent
22 the winter in West Africa, and that at least some birds wintering in Senegal bred in Scandinavia; this
23 provides insights into the links between European breeding populations and their wintering grounds.
24 Furthermore, birds tagged in England, Scotland and Senegal overlapped considerably in their
25 migration routes and wintering locations, meaning that individual breeding populations could be
26 buffered against habitat change, but susceptible to large-scale environmental changes. These
27 findings also suggest that contrasting population trends in England and Scotland are unlikely to be
28 due to population-specific migration routes and wintering regions. Finally, we found that birds used
29 wind to facilitate their migration in autumn, but less so in spring, when the wind costs associated
30 with their migrations were higher than expected at random. This was despite the wind costs of
31 simulated migrations being significantly lower in spring than autumn. Indeed, theory suggests that
32 individuals are under greater time pressures in spring than in autumn because of synchronising
33 reproduction with food availability.

34 Keywords: Climate, migration, simulation, waders, weather

35 Introduction

36 There have been large declines in numbers of migratory bird populations over the last half-century
37 (Vickery *et al.* 2014, Rosenberg *et al.* 2019). This is of major conservation concern, not least because
38 of the ecosystem services that these birds provide (Wilcove & Wikelski 2008). Recent studies have
39 linked migration strategy, distance and stopover site use to population trends (Møller *et al.* 2008,
40 Patchett *et al.* 2018, Lisovski *et al.* 2021). For example, some have found that long-distance migrants
41 are suffering greater population declines than short-distance migrants (Morrison *et al.* 2013),
42 whereas others have shown that the declines in birds wintering in humid bioclimatic zones are more
43 marked than those of birds that winter in arid zones (Ockendon *et al.* 2012). Therefore, identifying
44 the ranges and degree of connectivity between populations, and understanding environmental
45 influences on migration, are important for determining the potential drivers of these declines.
46 Furthermore, these steps are key to the implementation of successful conservation action, especially
47 as the measures needed are unlikely to be the same across the entire flyway (Wilcove & Wikelski
48 2008, Vickery *et al.* 2014, Alves *et al.* 2019).

49 The link between variation in migration patterns and the fate of individuals and populations has
50 received much recent attention. For example, greater declines in the population sizes of long-
51 distance migrants than those of short distance migrants have been linked to the increased
52 probability of encountering degraded habitats (Jones & Cresswell 2010, Morrison *et al.* 2013,
53 Patchett *et al.* 2018). Such environmental conditions can be buffered or enhanced by the degree of
54 overlap in range between populations throughout the lifecycle, known as migratory connectivity
55 (Webster *et al.* 2002, Finch *et al.* 2017, Patchett *et al.* 2018). This is because, for breeding
56 populations that are spread over large areas during the non-breeding season, and vice versa, even
57 large amounts of habitat or climatic change may only affect a relatively small proportion of all
58 individuals (Taylor & Norris 2010, Finch *et al.* 2017). Connectivity during migration is also important,
59 with differences in routes between autumn and spring being linked to the survival of individuals

60 (Hewson *et al.* 2016, Robinson *et al.* 2020). While the spread of single breeding populations over
61 larger areas during winter and migration may promote mixing and thereby buffer whole populations
62 to environmental change, individual survival may be linked to migration routes and the weather
63 conditions experienced therein.

64 A growing number of studies have investigated the effects of environmental conditions during
65 migration on individuals. In particular, several recent studies have sought to understand the effects
66 of wind (Liechti 2006, Shamoun-Baranes *et al.* 2010a, 2017, La Sorte *et al.* 2019). Winds have been
67 suggested as important determinants of migration routes (Erni *et al.* 2005, Klaassen *et al.* 2010,
68 Shamoun-Baranes *et al.* 2017, Norevik *et al.* 2020) and migratory behaviour (Shamoun-Baranes *et al.*
69 2010b). Individuals avoid migrating in adverse wind conditions (Anderson *et al.* 2019, Brust *et al.*
70 2019), which are likely to have a significant effect on mortality rate (Newton 2006, Kranstauber *et al.*
71 2015, Loonstra *et al.* 2019). Conversely, individuals can use favourable wind conditions to reduce the
72 energetic costs of migration (Newton 2010, Kranstauber *et al.* 2015, Shamoun-Baranes *et al.* 2017).
73 Indeed, several studies have found that wind conditions are generally more favourable in spring than
74 autumn (Kemp *et al.* 2010, La Sorte *et al.* 2014). This has been used to explain seasonal differences
75 in the ground speed and total duration of migratory journeys (Nussbaumer *et al.* 2022). It is likely
76 that optimising migration routes and altitudes with respect to wind conditions could significantly
77 reduce the overall physiological costs (Shamoun-Baranes *et al.* 2017), which could be important
78 considering the life-history constraints associated with spring migration. During spring, individuals
79 are thought to be under greater time constraints than in autumn, due to the pressures associated
80 with the breeding season. The timing of arrival to breeding sites is important for obtaining a territory
81 and the need to synchronise reproduction with food availability. Conversely, in autumn, there are
82 fewer pressures associated with reaching the wintering grounds, although the timing of moulting is
83 one exception (McNamara *et al.* 1998, Conklin *et al.* 2013, Nilsson *et al.* 2013). Therefore, tracking
84 work following individuals year-round is needed to understand the influence of winds throughout
85 the lifecycle, especially as they may vary between populations and species.

86 Here, we use geolocators to investigate migration in the Common Sandpiper (*Actitis hypoleucos*), a
87 wading bird that breeds across Europe and Asia and winters throughout Africa, Southern Asia and
88 Australia (Cramp *et al.* 1983). This species has recently undergone a considerable decline in numbers
89 throughout Britain and Continental Europe (Ockendon *et al.* 2012, Vickery *et al.* 2014). A study of
90 two British populations found that declines in an English population were associated with the
91 correlation between the North Atlantic Oscillation (NAO) and adult survival. Conversely, the Scottish
92 population remained stable over the study period (Pearce-Higgins *et al.* 2009). This suggests that
93 large-scale climatic conditions are unlikely to be the sole driver of declines, prompting calls for a
94 focus on determining their migration routes and wintering grounds (Pearce-Higgins *et al.* 2009).

95 Recent work fitting geolocators to Common Sandpipers in Scotland showed that most birds wintered
96 in West Africa, using the Iberian Peninsula and France as stopover sites in both autumn and spring
97 (Summers *et al.* 2019a). This study found little evidence that population changes were due to long-
98 term shifts in weather on the wintering grounds, but that the spring migration of some individuals
99 may have been slowed by strong headwinds (Summers *et al.* 2019a). The population trends of
100 Common Sandpipers, as with those of many other migratory species, differ between Scotland and
101 England (Baillie *et al.* 2010, Morrison *et al.* 2013, Harris *et al.* 2020). These divergent trends could be
102 the result of populations using different migration routes and wintering sites (Taylor & Norris 2010,
103 Finch *et al.* 2017). However, we do not know the migration routes and wintering locations of bird
104 breeding in England. Furthermore, the common sandpiper has a large breeding and wintering range,
105 and little is known about Europe-wide migration corridors which, for some species, show
106 considerable longitudinal segregation (Cramp *et al.* 1983, van Bemmelen *et al.* 2019). Investigating
107 the breeding distributions of birds wintering in West Africa could help to identify these larger-scale
108 migration corridors and elucidate reasons for European-wide population declines (Vickery *et al.*
109 2014).

110 We were interested in understanding the migration ecology of Common Sandpipers, including the
111 amount of overlap in range among different populations and whether individuals use wind to assist
112 their migratory journeys. Specifically, we used the geolocator data from Common Sandpipers tagged
113 in Scotland by Summers *et al.* (2019a, b) and combined these with data from birds that we tagged in
114 England and Senegal, to investigate: (1) the wintering locations and migration routes of Common
115 Sandpipers breeding in England, (2) the breeding locations and migration routes of birds wintering in
116 Senegal, (3) the amount of overlap in the distribution of different populations during migration and
117 on the wintering grounds, and (4) whether birds use wind to assist their migrations.

118

119 Methodology

120 Capturing and tagging

121 Common Sandpipers were caught and tagged within a 6km radius of Sedbergh, Cumbria, England,
122 UK (54.32°N, 2.53°W), hereafter 'Cumbria', and Djoudj National Bird Sanctuary, Senegal (16.36°N,
123 16.28°W), hereafter 'Senegal'. The breeding population in Cumbria nests along rivers running
124 through a mixture of deciduous woodland and farmland. Here, birds were targeted on their breeding
125 territories and caught using mist nets set across rivers, or walk-in traps placed over nests. Individuals
126 from the wintering population in Senegal were found on isolated saline and freshwater pools
127 created by the rains in June to October and along the River Senegal. Birds were targeted with tape
128 lures using mist nets, walk-in traps and whoosh nets (Holman 1950).

129 All individuals caught for tagging were fitted with a metal British Trust for Ornithology (BTO) ring on
130 their right tarsus and a yellow plastic ring engraved with two black characters on their left tarsus.

131 Two types of geolocator, mounted on a red plastic leg flag on the right tibia, were used in this study.

132 In Cumbria in 2017, twenty-two Lotek MK5040 tags were deployed; these weighed 1.1g including
133 the attachment method. In Senegal in 2018, ten Migrate Technology Intigeo geolocators were

134 deployed, weighing 1g in total. The geolocator and attachment method never exceeded 2.6% of the
135 individual's total body weight in either population (Mondain-Monval *et al.* 2020). Although some of
136 the birds suffered from minor injuries caused by the geolocators, they were unlikely to have affected
137 the migration of recaptured individuals (Mondain-Monval *et al.* 2020). The Common Sandpipers in
138 Scotland were captured and tagged using the methods described in Summers *et al.* (2019a). They
139 tagged birds at two separate breeding populations approximately 140 km apart, one on the River
140 Spey (57.35°N, 3.53°W), and one on two lakes in north Sutherland (58.52°N, 4.33°W). In all analyses
141 we considered these two capture locations as a single site, 'Scotland', by taking the mean of their
142 coordinates, due to their relative proximity and the small sample size from the River Spey. Hereafter,
143 we refer to all individuals by their tagging location.

144 Geolocator data analysis (Cumbria and Senegal)

145 Geolocator data were analysed in R v4.2.1 (Team 2020) using the package 'GeoLight' and following
146 the method outlined in Lisovski *et al.* (2012a). This uses the threshold method for the identification
147 of twilights; a twilight event takes place once light exceeds or goes below a predetermined threshold
148 and provides daily location estimates (Lisovski *et al.* 2019). We used a light intensity threshold value
149 of 3 for the Lotek tags and a light intensity value of 0.5 for the Migrate Technology tags; the rest of
150 the analyses were identical. We ran the geolocator analyses using both the known location and Hill-
151 Ekstrom calibration methods (Lisovski *et al.* 2012b) as Common Sandpipers use both coastal and
152 heavily vegetated habitats. This means that the geolocator is sometimes shaded at dawn and dusk,
153 which can result in imprecise location estimates (Lisovski *et al.* 2012b). We extracted timings of
154 departure and arrival from breeding and wintering sites using the 'Changelight' function (Lisovski *et*
155 *al.* 2012a). We used movement probabilities between 0.97 and 0.98, minimum stopover durations of
156 one to two days, and combined stopover locations that were between two and five hundred
157 kilometres from each other. The calibration method and movement probability values were chosen
158 based on the most accurate breeding locations for birds in Cumbria, or wintering locations for those

159 in Senegal. A distance filter prevented birds moving at more than 75km per hour (Lisovski *et al.*
160 2012b).

161 We removed all position data ten days either side of the autumn and spring equinoxes, because
162 location estimates are inaccurate during this period (Lisovski *et al.* 2012b), and averaged all the
163 location estimates during the non-breeding season in Africa to obtain a single wintering location for
164 use in plots and for the analysis of wind assistance (see below). The dates of the non-breeding
165 season were defined by the first and last location estimate within West Africa as determined by the
166 'ChangeLight' function. These arrival and departure dates to and from West Africa were also used to
167 identify the autumn and spring migration periods. Positional data were twice smoothed for plotting
168 purposes (Carneiro *et al.* 2019), kernel density estimation and the analysis of wind assistance.

169 Geolocator data analysis (Scotland)

170 To understand differences in the migration routes and wintering locations between birds tagged in
171 Cumbria, Senegal and Scotland, we used the data from Summers *et al.* (2019a) downloaded through
172 the Movebank Data Repository (Summers *et al.* 2019b). We reanalysed their data using the methods
173 described above (and a light intensity threshold value of 3) to ensure comparability between
174 populations. To validate our methods, we compared the results of our analyses of the geolocator
175 data from Scottish birds to those of Summers *et al.* (2019a) who analysed their data using the
176 package FLIGHTR (Rakhimberdiev *et al.* 2017). For each Scottish bird, we compared the timing of the
177 departure from the breeding grounds, arrival to the wintering grounds, departure from the
178 wintering grounds and arrival to the breeding grounds. The results from the two analyses were
179 strongly correlated, validating our analyses (Pearson correlations, $r_{\text{breeding departure}} = 0.90$,
180 $P_{\text{breeding departure}} < 0.001$; $r_{\text{winter arrival}} = 0.98$, $P_{\text{winter arrival}} < 0.001$; $r_{\text{winter departure}} = 0.91$, $P_{\text{winter departure}} = 0.002$;
181 $r_{\text{breeding arrival}} = 0.71$, $P_{\text{breeding arrival}} = 0.05$).

182 Breeding locations of Senegal-tagged birds

183 Preliminary analyses of the geolocator data from Common Sandpipers tagged in Senegal showed
184 that they bred in areas with 24-hour daylight. Traditional methods of geolocation using sunrise and
185 sunset times therefore could not be used to obtain location estimates. To determine the breeding
186 locations of these birds, we used the 'PolarGeolocation' package (Lisovski 2018). We followed the
187 workflow outlined in Lisovski (Lisovski 2018) and used the most likely breeding location for plotting
188 purposes and for the analysis of wind assistance (see below).

189 Migratory connectivity (kernel density and overlap)

190 To identify the overlap in the stopover sites and wintering distributions of Common Sandpipers from
191 the different tagging locations, we analysed kernel densities using the package 'adehabitatHR'
192 (Calenge 2019). We were primarily interested in stopover sites throughout Europe, and we therefore
193 assumed that birds had reached the breeding grounds after crossing certain latitudes, depending on
194 their tagging location. For Cumbria, this threshold was 50 degrees north latitude; for the Scottish
195 population it was 52 degrees latitude; and for the Senegalese birds it was 57 degrees latitude. We
196 excluded positions that were above these thresholds for the analyses of overlap during the autumn
197 and spring migration periods.

198 For each season, we obtained the 75% utilisation distribution of the stationary periods of individuals
199 from each tagging location in order to identify overlap in distributions between individuals from
200 different populations in autumn, spring and winter. We determined the amount of overlap during
201 each period by calculating the proportion of the 75% kernel density estimate for each tagging
202 location that was found in the kernels of the other locations (Calenge 2019).

203 *Migratory connectivity during winter*

204 We determined the amount of mixing between breeding populations on the wintering grounds using
205 Mantel correlation tests. These were used to determine whether the distances between individuals
206 on their breeding and wintering grounds are correlated (i.e. whether birds that breed close together

207 also winter close together), using a scale ranging between -1 and 1. Low Mantel coefficients indicate
208 a high degree of mixing, high coefficients indicate low mixing (Ambrosini *et al.* 2009). This was done
209 for individuals from Scotland and Cumbria, but not for the individuals tagged in Senegal because of
210 the small sample size.

211 Analysis of wind assistance

212 To understand whether birds used wind to support their migratory journeys, we compared the wind
213 costs experienced by migrating birds to those of randomly simulated migrations. Costs were
214 determined by the speed and direction of wind, as described below. We used the package 'RNCEP'
215 to obtain daily gridded (2.5-degree resolution) model-derived 'U' and 'V' wind components at 00, 06,
216 12, 18h UTC from the NCEP/NCAR R-1 reanalysis datasets (Kemp *et al.* 2012). We downloaded data
217 for 1000, 925, 850 and 700 millibars which correspond approximately to: 0, 780, 1500 and 3100m
218 a.s.l., respectively. We do not currently know the altitude at which Common Sandpipers migrate,
219 and these altitudes correspond to the range in which most avian migration occurs in radar data
220 (Kemp *et al.* 2013, Kranstauber *et al.* 2015). For the autumn and spring migration periods of each
221 individual in our dataset, we obtained the daily wind conditions across the entire Afro-Palearctic
222 flyway at a 0.5-degree spatial resolution, disaggregated from 2.5 degrees using the 'terra' package
223 (Hijmans 2022). We converted the 'U' and 'V' wind components into wind direction and speed, and
224 calculated the mean wind direction and speed values for each migration at each of the altitudes
225 considered. This produced a gridded map of the average conditions across the entire flyway for the
226 autumn and spring migration periods of each individual tracked with a geolocator, at each of the
227 altitudes described above. We then calculated the transition probabilities between every cell in the
228 flyway, for each altitude separately, with movement into headwinds allowed, but incurring a greater
229 cost penalty than movement with tailwinds (Fernández-López & Schliep 2018). These 'costs' are
230 conductance values between cells, and are determined by the direction and speed of wind
231 conditions rather than referring to the physiological costs associated with bird flight (Fernández-

232 López & Schliep 2018). This provides an index of the costs to movements due to the wind conditions
233 that birds are confronted with during migration.

234 *Observed birds*

235 For each spring and autumn track of an individual, we calculated the cost of moving between
236 sequential positions based on the transition probabilities using the 'costDistance' function from the
237 package 'gdistance' (van Etten 2017). During migration, birds are likely to change their flight altitude
238 to find favourable wind conditions (Kranstauber *et al.* 2015). Therefore, we calculated the cost of
239 moving between sequential positions for each of the altitudes listed above. From these, we selected
240 the altitude at which there was the lowest movement cost, thereby mimicking the ability of birds to
241 change flight altitude in search of favourable wind conditions. The costs of all movements between
242 sequential locations identified by the geolocator analyses in the migratory track were summed and
243 divided by the total number of relocations to obtain a 'cost index'. This equates to the average cost
244 of movement per relocation. This was needed because the number of locations estimated by the
245 geolocators was different for each individual as they travelled different total distances. This made
246 the migration costs calculated for each bird comparable across tagging locations and between the
247 observed and simulated birds.

248 *Simulated birds*

249 We simulated bird migrations to determine the wind costs associated with 'random' migration
250 routes. For each migration of every bird tracked with a geolocator, we generated one hundred
251 'random' tracks (see below). The simulated tracks travelled between the same breeding and
252 wintering location as the observed bird and were subject to the same set of potential wind
253 conditions (i.e. the same transition probabilities). Therefore, a single bird had 100 paired random
254 tracks for each of their migrations (i.e. 200 random tracks for birds which were tracked during both
255 autumn and spring).

256 For autumn migration, we created a latitudinal sequence between the breeding and wintering
257 locations in 0.5-degree increments. We then created a sequence between the breeding and
258 wintering longitudes of the same length as the latitudinal sequence. For each latitudinal step in the
259 data, we used the corresponding longitudinal value as the mean in a random number sampler
260 following a normal distribution with a standard deviation of four degrees. This standard deviation
261 was chosen because it generated tracks that covered most of the observed flyway of Common
262 Sandpipers from the three tagging locations (Figure S1). We sampled one random number for each
263 latitudinal step, thereby generating a 'random track'. As individuals approached the end point of
264 their migration (as determined by the breeding and wintering locations of the observed birds), the
265 standard deviation of the normal distribution was reduced. We repeated these steps in the opposite
266 direction for spring migration. The random tracks were twice smoothed.

267 The migration costs were determined in a similar way to those for the observed birds, with costs
268 being calculated between sequential locations. However, the altitude at which each relocation took
269 place was chosen at random from the full set of altitudes listed above, rather than at the altitude
270 which incurred the least cost. This means that the simulated tracks were random in three-
271 dimensional space (i.e. in longitude, latitude and altitude).

272 In order to determine the differences in wind costs experienced during autumn and spring
273 migrations, we fitted models for observed and simulated birds separately. For observed birds, we
274 fitted a linear model with cost index as the response variable and the migration period (autumn or
275 spring) as the only explanatory variable. For simulated birds, we fitted a linear mixed effects model
276 (LME) from the package 'lme4' (Bates *et al.* 2015) using the same variables, but included individual
277 identity as a random intercept to control for repeated simulated tracks for the same observed
278 individual. We then fitted a separate set of LMEs to test whether Common Sandpipers used winds to
279 facilitate their autumn and spring migrations. For each tagging location and each migration
280 separately, we fitted the cost index as the response variable and whether the cost was that of an

281 observed or simulated bird (hereafter 'bird type') as the sole explanatory variable. We also included
282 individual identity as a random intercept, again to control for repeated simulations for the same
283 observed individual. Locations were defined as the tagging locations. We did not test for within-site
284 differences in the cost of migrations between seasons because small sample sizes would have made
285 any results questionable. We validated all models by plotting the distribution of the residuals and
286 the residuals versus fitted values.

287 *Geolocation error*

288 Positional data obtained from geolocators are relatively inaccurate because of shading (e.g. from
289 cloud cover, vegetation or feathers) and their reliance on differing day lengths globally (Lisovski *et al.*
290 2012b). To understand how this error could have affected the results of our wind assistance
291 analyses, we simulated 100 tracks for each migration period of an individual. For each position of an
292 observed individual, we sampled a random, new position from two normal distributions, one for
293 latitude and another for longitude. We used the latitude and longitude values from the track of the
294 corresponding observed bird as the means of the distributions, with standard deviations of 2
295 degrees for latitude and 1 degrees for longitude. These values were chosen because they
296 approximate the errors in geocator position estimates; 250km for latitude and 100km for
297 longitude (Lisovski *et al.* 2012b). We determined the cost indices for each of the one hundred tracks
298 using the wind conditions at the same altitude as the associated observed individual; these tracks
299 differed from the real tracks in their two-dimensional location only (i.e. only in longitude and
300 latitude, not altitude). These were analysed using LMEs. For each tagging location and each
301 migration separately, we fitted the cost index as the response variable and whether the cost was
302 that of an observed bird, a geolocation error bird or a simulated bird as the sole explanatory
303 variable. We also included individual identity as a random intercept to control for repeat sampling of
304 individuals. There were no important differences between the migration costs when accounting for
305 geocator error and those from the raw tracks of individuals (Figure S2, Table S1).

307 Results

308 In Cumbria in 2018, we recovered eleven geolocators after resighting thirteen tagged individuals at
309 the study site (13/22). In Senegal in 2019, we recovered four geolocators, but resighted eight tagged
310 birds in total (8/10). There were no significant differences between the return rate, body condition
311 or reproductive success of birds with geolocators compared with those carrying only rings (Mondain-
312 Monval *et al.* 2020). Additionally, the raw light data of the birds tagged in Senegal showed light
313 patterns indicative of incubation, meaning that they were all breeding individuals. The Scottish study
314 retrieved ten geolocators (10/28, Table 1), but there were no comparisons with a colour ringed
315 control group (Summers *et al.* 2019a). This resulted in twenty-five tracks of autumn migration and
316 twenty-two for spring migration, as three geolocators had failed on the wintering grounds (two from
317 birds in Scotland and one from a bird in Cumbria).

Table 1 The sample sizes, tagging locations and distances between individuals at their tagging locations (tagging max and median dist) and destinations (final max and median dist). All distances are reported in kilometres.

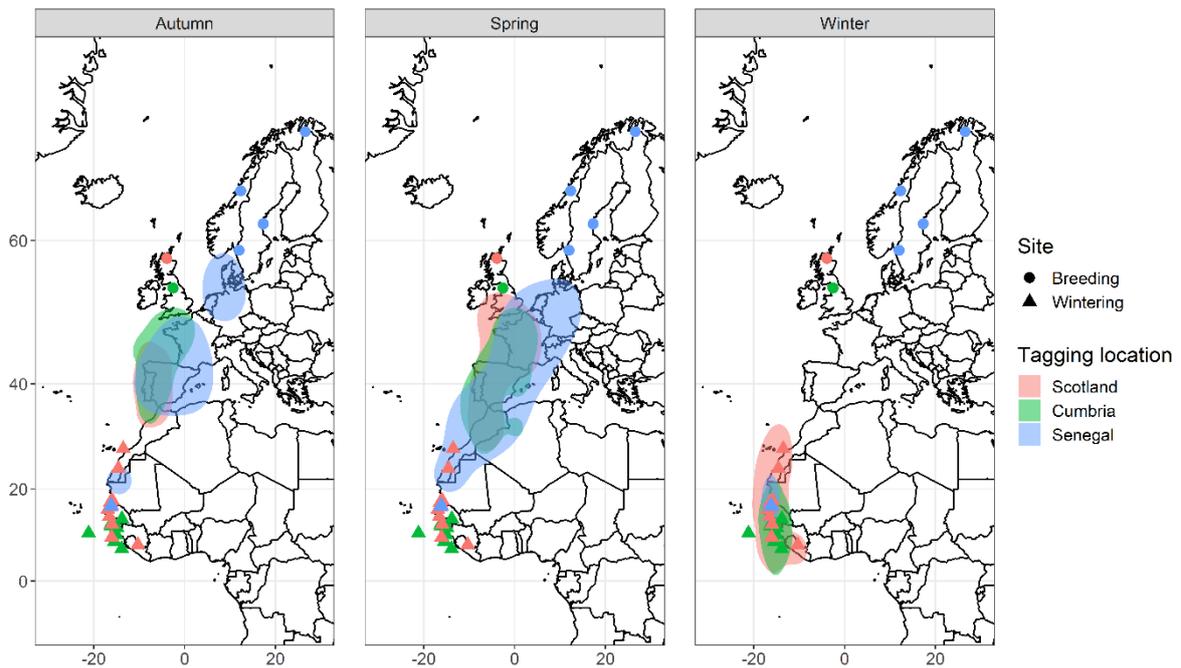
Location	Number tagged	Mean tagging long	Mean tagging lat	Median tagging max dist	Tagging median dist	Final mean long	Final mean lat	Final max dist	Final median dist	Median migration dist
Scotland	10	-4.17	58.26	140	10	-15.28	16.33	2260	800	4760
Cumbria	11	-2.55	54.32	10	3	-15.77	11.09	890	290	4950
Senegal	4	-16.26	16.42	20	12	17.07	63.94	1420	750	5870

318

319

320 Common Sandpipers tagged with geolocators in Cumbria used similar migration routes and
321 wintering grounds to the Scottish birds (Summers *et al.* 2019a) (Figure 1, Table S2). In autumn, the
322 birds from Cumbria used southern England, northern France and the western half of the Iberian
323 Peninsula as stopover sites, before wintering in the southern half of West Africa (all south of 18°N).
324 In spring, individuals also stopped in Morocco and, compared with autumn migration, used sites
325 further inland on the Iberian Peninsula and throughout France (Figure 1). The four Common
326 Sandpipers tagged in Senegal all bred in Scandinavia, but in different regions ranging from
327 approximately 59°N in southern Sweden to approximately 70°N in Arctic Norway (Figure 1, Table S2).
328 In autumn, birds from Senegal used northern Europe (Denmark, the Netherlands and northern
329 Germany), western France and the east coast of the Iberian Peninsula as stopover sites. In spring,
330 these birds used sites similar to those used by the birds from Cumbria, although these stopover sites
331 also extended to northern Europe (Figure 1). See Table S2 for a full summary of each individual's
332 migratory schedule as determined by the geolocator analyses; including breeding and wintering
333 locations, and the number of stopover sites and days during each migration.

334



336

337 **Figure 1** The distribution of the wintering sites of individuals from the four tagging locations and
 338 their stopover sites during autumn and spring migrations. The shaded regions represent the 75%
 339 kernel densities of the utilisation distribution of individuals from different tagging locations. Closed
 340 circles are breeding locations, closed triangles are wintering locations.

341

342 Migratory connectivity (kernel density and overlap)

343 The migration routes and wintering locations of birds from the three different tagging locations
 344 overlapped considerably, with the proportion of overlap between the British populations highest.
 345 The proportion of overlap between the Senegal-tagged birds and the British birds was lower in
 346 autumn than spring migration (Table 2). This is because the Senegal-tagged birds flew further East
 347 before crossing the Pyrenees in autumn. In spring there was more overlap between the Senegalese
 348 and British birds than in autumn, as the latter used stopover sites throughout France. In winter,

349 there was considerable overlap in the kernel density distributions between individuals from the
350 different tagging locations, suggesting a low level of migratory connectivity between breeding and
351 wintering areas (Figure 1). However, a Mantel correlation coefficient of 0.26 ($P = 0.001$) suggests
352 some connectivity; i.e. birds that breed close together also winter relatively close together, and vice
353 versa. The median distances between wintering individuals from the Scotland and Cumbria
354 populations were 800km and 290km, respectively (Table 1).

355

Table 2 The proportion of the 75% kernel distribution of individuals from one tagging location (rows) covered by that from other tagging locations (columns) in autumn, spring and winter. The numbers in each cell correspond to the overlap in autumn, spring and winter periods, respectively.

	Scotland	Cumbria	Senegal
Scotland	-	0.83, 0.83, 0.46	0.78, 0.82, 0.15
Cumbria	0.55, 0.83, 0.97	-	0.76, 0.88, 0.23
Senegal	0.26, 0.40, 1	0.37, 0.50, 0.77	-

356

357

358 *Analysis of wind assistance*

359 *Wind costs in autumn and spring*

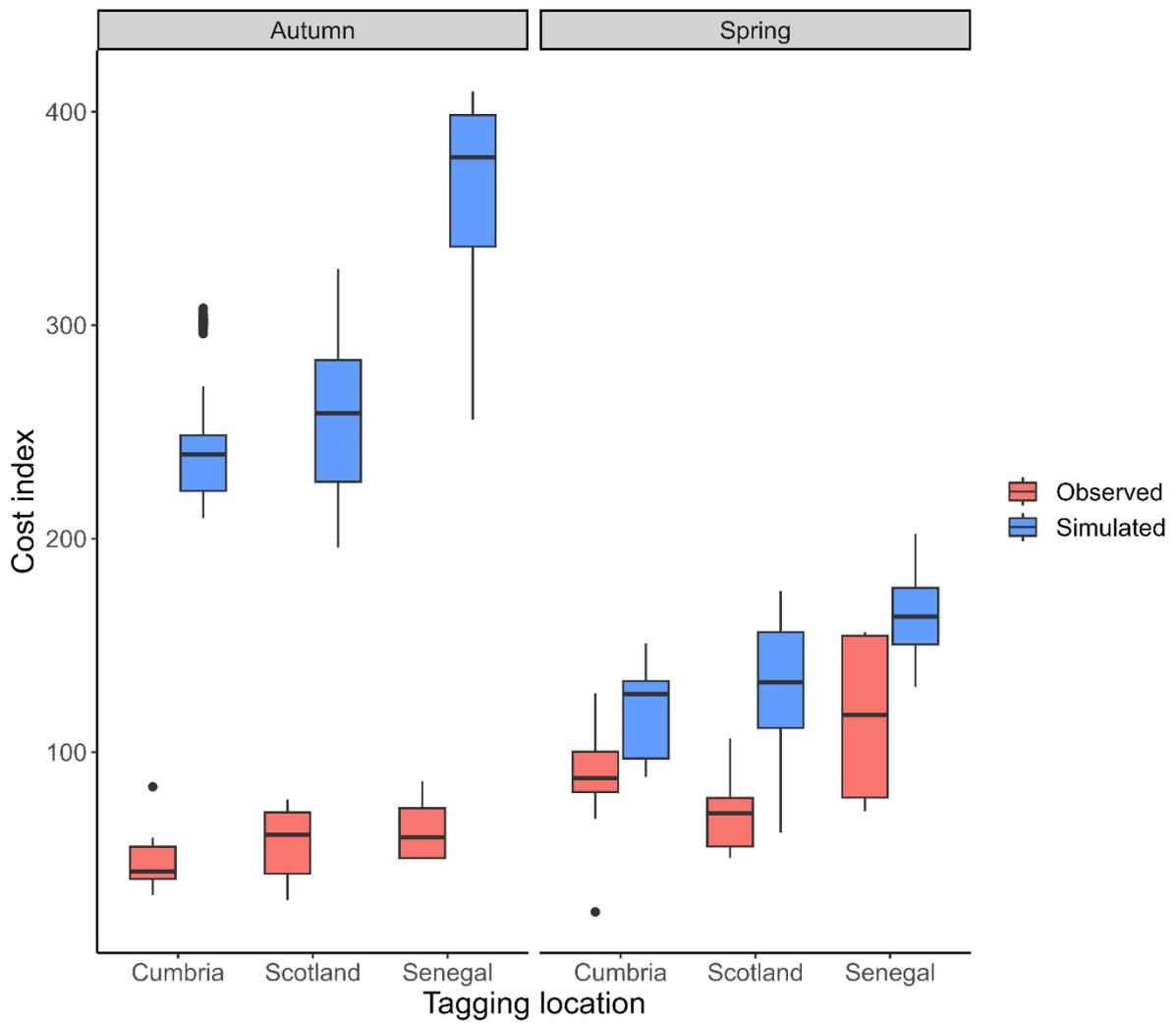
360 For observed birds across all tagging locations, the cost index of autumn migration was significantly
 361 lower than for spring migration. Conversely, for simulated birds, the cost index of autumn migration
 362 was higher than in spring (Figure 2, Table 3).

363 *Wind assistance during migration*

364 In both autumn and spring, the cost indices of observed birds were significantly lower than those of
 365 the simulated birds, suggesting that they use more favourable wind conditions than would be
 366 expected at random (Figure 2, Table 4). However, in spring, the cost indices of the observed birds
 367 were slightly higher than in the autumn, despite the costs of the simulated birds being considerably
 368 lower. This means that even though the background wind conditions were more favourable in spring
 369 than in autumn, the observed birds were more affected by them. This suggests that there may be a
 370 smaller influence of wind on migration route in spring than in autumn (Figure 2, Table 4).

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373

374 **Figure 2** The cost index of migration of observed and simulated Common Sandpipers from the three
375 tagging locations. Boxplots show the median, interquartile range and 1.5 times the interquartile
376 range (vertical lines); outliers are any points that fall beyond this.

377

Table 3 Results of a linear model (GLM, for observed birds) and a linear mixed effects model (LMM, for simulated birds) of the difference in the cost of the autumn and spring migrations. The P value for the LMM was determined using a likelihood ratio test comparing the full model against the null model. The marginal R² value is not shown for the model of the observed birds because this did not have mixed effects.

Bird type	Model	Autumn cost index (intercept)	Spring cost index (estimate)	Test statistic	P value	Marginal R ²	Adjusted / Conditional R ²
Observed	GLM	54.85	86.72	T = 20.63	<0.001	NA	0.29
Simulated	LMM	266.59	130.04	$\chi^2 = 4974$	<0.001	0.70	0.91

380

Table 4 Results of the linear mixed effects models comparing the cost indices of observed and simulated birds from Cumbria, Senegal and Scotland in autumn and spring. The P values were determined using a likelihood ratio test comparing the full models against the respective null models.

Location	Migration	Observed birds	Simulated birds	Standard error (estimate)	χ^2	P value	Marginal R ²	Conditional R ²
		cost index (intercept)	cost index (estimate)					
Cumbria	Autumn	49.29	241.65	7.51	3920.59	<0.001	0.37	0.99
Senegal	Autumn	64.10	355.87	32.42	1269.83	<0.001	0.16	0.99
Scotland	Autumn	57.26	258.30	11.78	3553.22	<0.001	0.22	0.99
Cumbria	Spring	87.39	119.38	6.35	908.93	<0.001	0.02	0.98
Senegal	Spring	115.88	164.10	13.42	190.12	<0.001	0.03	0.95
Scotland	Spring	57.29	128.13	11.41	1695.66	<0.001	0.03	0.99

381

382

383 Discussion

384 Our simulations suggest that the migration of Common Sandpipers is facilitated by wind, with the
385 evidence indicating that this effect is stronger in the autumn than the spring. In spring, the wind
386 costs associated with their migratory journeys were higher than the costs in spring, but still lower
387 than expected at random. The wind costs of simulated migrations were actually significantly lower in
388 spring than autumn on average, suggesting a decrease in wind speed or more tailwinds, perhaps due
389 to changes in prevailing wind direction leading to generally more favourable conditions (Kemp *et al.*
390 2010, Nussbaumer *et al.* 2022). Therefore, it appears that the migrations of Common Sandpipers are
391 less affected by prevailing wind conditions in autumn than in spring. These findings could suggest
392 that the timing of autumn migration is under lower selection pressure than spring migration. In
393 spring, early arrival to the breeding grounds is important for reproductive success (Morrison *et al.*
394 2019) and therefore, individuals may migrate more quickly or take the most direct route,
395 irrespective of wind conditions (McNamara *et al.* 1998, Nilsson *et al.* 2013, Gutierrez Illan *et al.*
396 2017). In autumn, individuals could be under reduced pressure, allowing them to select the most
397 optimal migratory routes that involve more tailwinds or fewer cross and headwinds (Nilsson *et al.*
398 2013, Duijns *et al.* 2017). It is also possible that individuals are in poorer body condition in autumn
399 following reproduction, meaning they are less able to fly during adverse wind conditions. In our
400 study, the time window available for migration was the same for the observed and simulated tracks,
401 meaning that any differences in wind costs between the two were due to differences in route and
402 flight speed only. In reality, individuals can also change the total duration of migration by waiting at
403 stopover sites for adverse wind conditions to pass (Watts *et al.* 2021). Our results show that
404 Common Sandpipers face higher wind costs during spring migration, as suggested by Summers *et al.*
405 (2019a), and as shown for other species (Lok *et al.* 2015, Loonstra *et al.* 2019).

406 The physiological cost of migration is likely to be high for many species, especially when making large
407 desert or ocean crossings (Alerstam *et al.* 2003, Klaassen *et al.* 2014, Lok *et al.* 2015). For many,

408 mortality is particularly high during spring migration (Lok *et al.* 2015, Loonstra *et al.* 2019, Robinson
409 *et al.* 2020). This could be because in spring, individuals migrate regardless of weather conditions or
410 take more direct routes (Loonstra *et al.* 2019, Robinson *et al.* 2020). For example, unfavourable wind
411 conditions may have caused eastward drifts across the Sahara for some of the tracked Common
412 Sandpipers (Summers *et al.* 2019a); such drifts have also been observed in Wood Sandpipers *Tringa*
413 *glareola* (Summers *et al.* 2021). If the wind costs associated with spring migrations increase due to
414 climate change (Cohen *et al.* 2014, Taylor *et al.* 2017), this could reduce the survival of migrating
415 birds and could impact population trends (Newton 2006, Robinson *et al.* 2020). Particularly extreme
416 adverse weather conditions are likely to cause high levels of mortality (Loonstra *et al.* 2019). We
417 were unable to investigate this because geolocators need to be recovered to download data and so
418 we can only estimate the wind costs of returning birds. This likely biases our results; the wind costs
419 faced by birds which died during migration may have been significantly higher than those of
420 individuals carrying out successful migrations. It could be, for example, that only those individuals
421 which are able to use winds can complete their migrations successfully. Further research into how
422 wind conditions shape migratory behaviours, mortality during migration and population trends is
423 important given the influence climate change will have on global wind patterns.

424 We are the first to report the migration routes and wintering distributions of Common Sandpipers
425 breeding in England. While our Mantel test revealed some connectivity between tagging and
426 wintering locations, the birds tagged in England, Scotland and Senegal had overlapping and
427 widespread distributions on migration and during winter as determined by the kernel density
428 analysis. This could be because of the biases associated with Mantel correlations when analysing
429 small samples and from few discrete sites (Vickers *et al.* 2021). However, if the overlap of individuals
430 determined by our kernel density analyses reflects connectivity more broadly, it could potentially
431 buffer distinct breeding populations from habitat change in non-breeding areas (Taylor & Norris
432 2010, Finch *et al.* 2017, Summers *et al.* 2019a). The overlap also means that birds from different
433 breeding regions are likely to experience similar wintering conditions; major habitat or climatic

434 changes affecting the whole of the West African coast would therefore likely have large-scale
435 impacts across Europe. In West Africa, there has been significant agricultural intensification and a
436 small reduction in the amount of mangrove forest (Vickery *et al.* 2014, Summers *et al.* 2019a). In
437 West Africa there has been a large expansion of the rice industry (Elphick 2000, Wymenga & Zwarts
438 2010). While rice fields do provide habitat for foraging waders, these are unlikely to be equivalent to
439 natural wetlands (Waterbird use of Rice Fields in Australia 2010, Wymenga & Zwarts 2010); but see
440 (Elphick 2000). Therefore, it is possible that individuals using rice fields could suffer from poor body
441 condition, affecting their ability to perform their spring migration (Duijns *et al.* 2017) or cope with
442 adverse conditions on the breeding grounds (Morrison *et al.* 2013). Patchett *et al.* (2018) found that
443 in the Afro-Palearctic flyway, species which are spread over large non-breeding areas are more likely
444 to be affected by habitat change in Africa, as they are more likely to encounter poor quality habitats.
445 More work is needed on the wintering grounds to investigate links between changes in habitat and
446 the population trends of migratory species.

447 Our findings suggest that steeper population declines in England than Scotland are unlikely to be
448 caused by large-scale differences in migration routes and wintering sites. However, even with
449 considerable overlap during the non-breeding season, greater population declines in England than in
450 Scotland could be driven by fine-scale differences in habitat selection that are not discernible using
451 geolocator data (Baillie *et al.* 2010, Harris *et al.* 2020). For example, the amount of anthropogenic
452 disturbance, which has important implications for wintering migrants, varies across West Africa and
453 could lead to localised variation in the suitability of sites (Vickery *et al.* 2014, Ruiz-Sánchez *et al.*
454 2017, Patchett *et al.* 2018, Willemoes *et al.* 2018). It is also possible that declines are primarily linked
455 to the influence of conditions on breeding success, rather than those during the non-breeding
456 season as seen in other species (Allen *et al.* 2021).

457 Finally, our study is the first to track Common Sandpipers wintering in West Africa. Our small sample
458 of wintering birds were tagged within 20km of one another in Senegal but were spread across the

459 entire length of Scandinavia during the breeding season. Several ringing expeditions in West Africa
460 have also caught Common Sandpipers originally ringed in Fennoscandia (Fransson & Pettersson
461 2001, Saurola *et al.* 2013), confirming the importance of West Africa for Fennoscandian breeders.
462 The breeding locations of these birds are surprising, as theory and previous research suggest
463 longitudinal segregation in migration routes and wintering grounds for many species (Cramp *et al.*
464 1983, van Bemmelen *et al.* 2019, Briedis *et al.* 2020), whereas our findings reveal an east-west
465 migration corridor. This could reflect the small number of major coastal wetlands in West Africa,
466 meaning that birds are concentrated in a few key sites, such as the Banc d'Arguin and Archipelago
467 dos Bijagós (Summers *et al.* 2019a). The birds from all tagging locations wintered along the West
468 African coast, but it is not known where birds from the eastern parts of the Sahel, and those
469 wintering along the Central African coast, breed. More work documenting the migration routes of
470 Common Sandpipers breeding and wintering further east is needed, especially as many studies of
471 other migratory waders have revealed major differences in migration routes and destinations
472 between populations (van Bemmelen *et al.* 2019).

473 Declarations

474 Ethics approval and approval to participate

475 All catching and ringing was done under BTO licencing, including special permits for the use and
476 attachment of geolocators.

477 Consent for publication

478 Not applicable.

479 Availability of data and materials

480 All data will be deposited in the Movebank Data Repository on publication of the manuscript. All
481 code to run the analyses is available at: “**GitHub link hidden for review**”.

482 Competing interests

483 The authors have no competing interests to declare.

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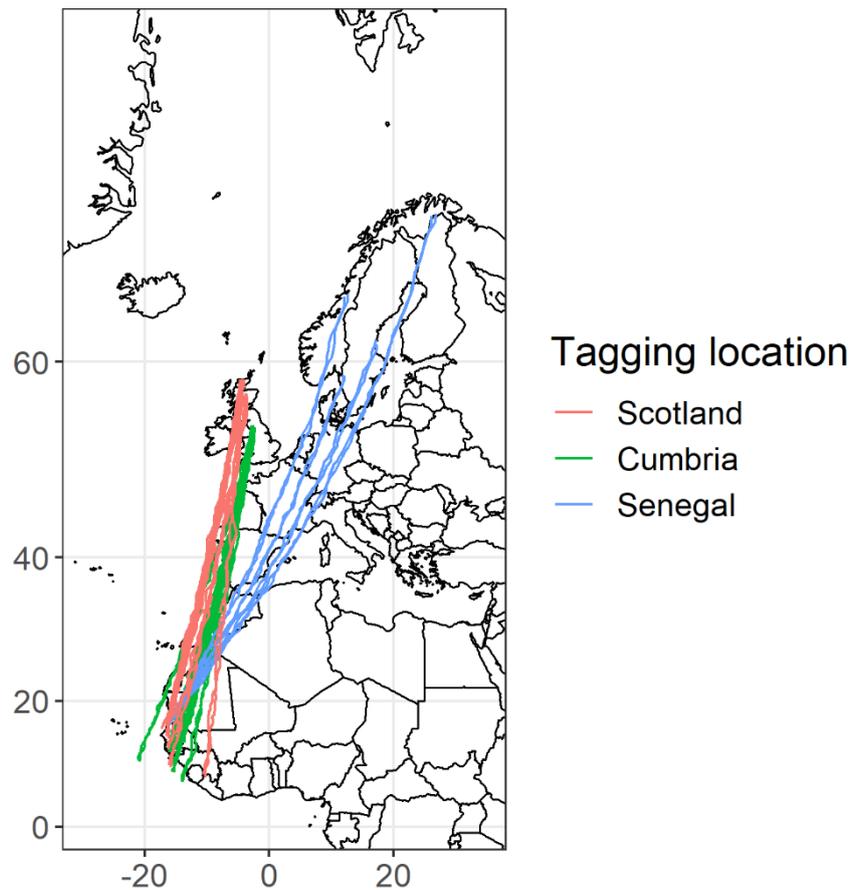
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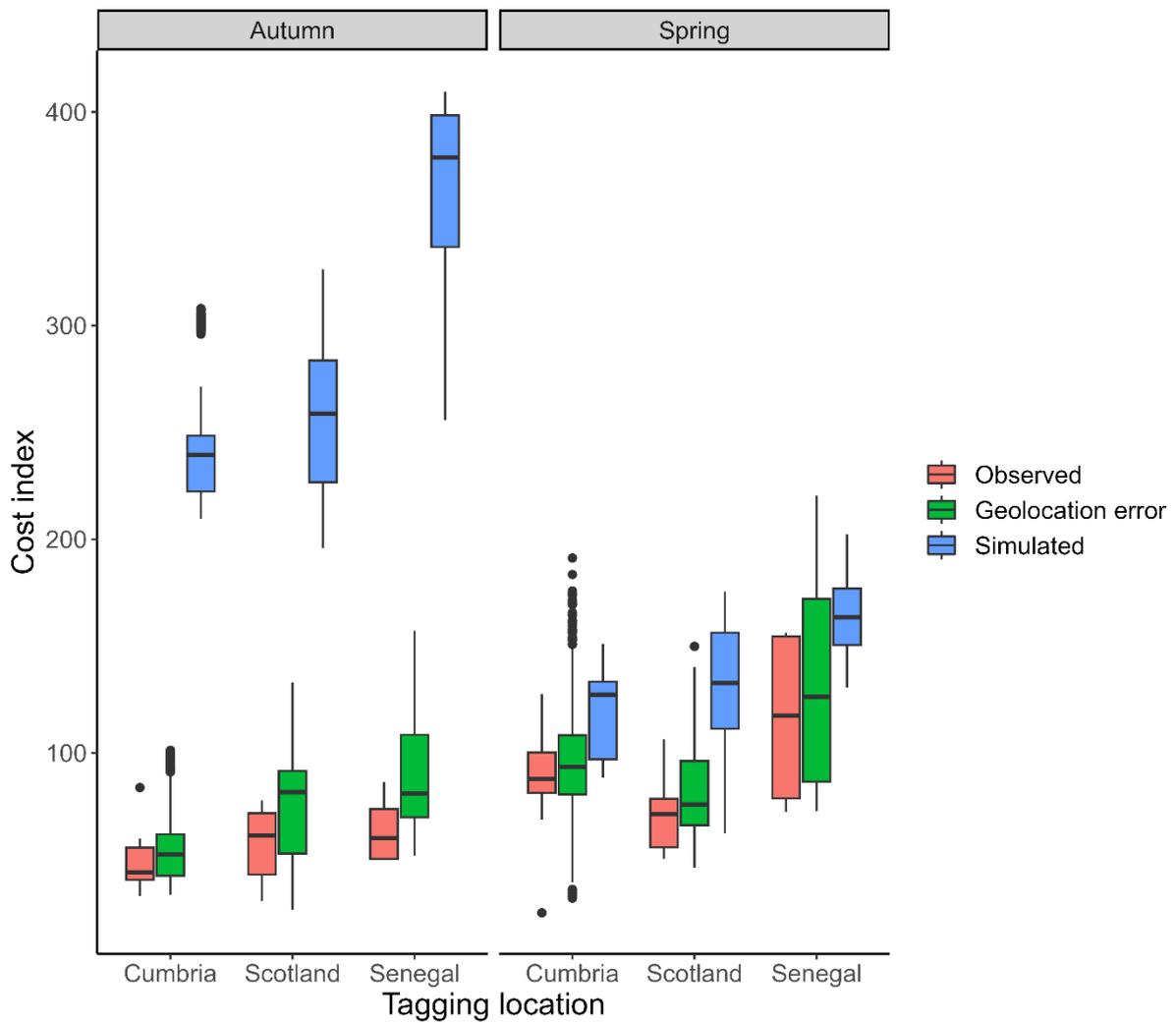
676 [Supplementary material](#)



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678 **Figure S1** The average of 100 simulated tracks for each observed individual in autumn and spring.

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681 **Figure S2** The cost index of migration of observed bird tracks, tracks accounting for geolocation error
682 and simulated Common Sandpipers from the three tagging locations. Boxplots show the median,
683 interquartile range and 1.5 times the interquartile range; outliers are any points that fall beyond this.

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Table S1 Results of the linear mixed effects models comparing the cost indices of observed birds, observed tracks accounting for geolocation error and simulated birds from Cumbria, Senegal and Scotland in autumn and spring.

Location	Migration	Observed birds (intercept)	Geolocation error estimate	Simulated estimate	Standard error (estimate)	T value	RE variance	RE stdev	Marginal R ²	Conditional R ²
Cumbria	Autumn	49.29	54.96	241.65	4.96	10.06	268.75	16.39	0.95	0.98
Senegal	Autumn	64.10	90.74	355.87	20.78	3.01	1721.13	41.49	0.88	0.97
Scotland	Autumn	57.26	74.91	258.30	9.18	9.02	841.48	29.01	0.89	0.98
Cumbria	Spring	87.39	95.08	119.38	5.48	10.06	328.87	18.13	0.22	0.70
Senegal	Spring	115.88	131.17	164.10	7.69	3.16	224.88	15.00	0.16	0.30
Scotland	Spring	57.32	68.07	128.13	10.24	9.02	1045.31	32.33	0.41	0.89

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