

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

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

**Keywords:** climate, migration, simulation, waders, weather.

There have been large declines in the numbers of many migratory bird populations over the last half-century (Vickery *et al.* 2014, Rosenberg *et al.* 2019). This is of major conservation concern, not least because of the ecosystem services that

these birds provide (Wilcove & Wikelski 2008). Recent studies have linked migration strategy, distance and stopover site use to population trends (Møller *et al.* 2008, Patchett *et al.* 2018, Lisovski *et al.* 2021). For example, studies have found greater population declines among long-distance than short-distance migrants (Morrison *et al.* 2013), and have reported that declines in species wintering in humid bioclimatic zones of Africa are more

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marked than in birds that winter in arid zones (Ockendon *et al.* 2012). Therefore, identifying the ranges and degree of connectivity between populations, and understanding environmental influences on migration, are important for determining the potential drivers of these declines. Furthermore, these steps are key to the implementation of successful conservation action, especially as the measures needed are unlikely to be the same across the entire flyway (Wilcove & Wikelski 2008, Vickery *et al.* 2014, Alves *et al.* 2019).

The link between variation in migration patterns and the fate of individuals and populations has received much recent attention. For example, greater declines in the population sizes of long-distance migrants than in those of short-distance migrants have been linked to the increased probability of encountering degraded habitats (Jones & Cresswell 2010, Morrison *et al.* 2013, Patchett *et al.* 2018). Such environmental conditions can be buffered or enhanced by the degree of overlap in range between populations throughout the life cycle, known as migratory connectivity (Webster *et al.* 2002, Finch *et al.* 2017, Patchett *et al.* 2018). This is because, for breeding populations that are spread over large areas during the non-breeding season, and vice versa, even large amounts of habitat or climatic change may only affect a relatively small proportion of individuals (Taylor & Norris 2010, Finch *et al.* 2017). Connectivity during migration is also important, with differences in routes between autumn and spring being linked to the survival of individuals (Hewson *et al.* 2016, Robinson *et al.* 2020). While the spread of single breeding populations over larger areas during winter and migration may promote mixing and thereby buffer whole populations to environmental change, individual survival may be linked to migration routes and the weather conditions experienced therein.

A growing number of studies have investigated the effects of environmental conditions during migration on individuals. In particular, several recent studies have sought to understand the effects of wind (Liechti 2006, Shamoun-Baranes *et al.* 2010a, 2017, La Sorte *et al.* 2019). Winds have been suggested as important determinants of migration routes (Erni *et al.* 2005, Klaassen *et al.* 2010, Shamoun-Baranes *et al.* 2017, Norevik *et al.* 2020) and migratory behaviour (Shamoun-Baranes *et al.* 2010b). Individuals avoid migrating in adverse wind conditions (Anderson *et al.* 2019,

Brust *et al.* 2019), which are likely to have a significant effect on mortality risk (Newton 2006, Kranstauber *et al.* 2015, Loonstra *et al.* 2019). Conversely, individuals can use favourable wind conditions to reduce the energetic costs of migration (Newton 2010, Kranstauber *et al.* 2015, Shamoun-Baranes *et al.* 2017). Indeed, several studies have found that wind conditions are generally more favourable in spring than in autumn (Kemp *et al.* 2010, La Sorte *et al.* 2014; but see Alves *et al.* 2016). This has been used to explain seasonal differences in the ground speed and total duration of migratory journeys (Nussbaumer *et al.* 2022). It is likely that optimizing migration routes and altitudes with respect to wind conditions could significantly reduce the overall physiological costs (Shamoun-Baranes *et al.* 2017), which could be important considering the life-history constraints associated with spring migration. During spring, individuals are thought to be under greater time constraints than in autumn, because of the pressures associated with the breeding season. The timing of arrival at breeding sites may be important for obtaining a territory and the need to synchronize reproduction with food availability. Conversely, in autumn, there may be fewer pressures associated with reaching the wintering grounds, although the timing of moulting is one exception to this (McNamara *et al.* 1998, Conklin *et al.* 2013, Nilsson *et al.* 2013, Carneiro *et al.* 2022). Therefore, tracking work following individuals year-round is needed to understand the influence of winds throughout the life cycle, especially as they may vary between populations and species.

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

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

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

## METHODS

### Capturing and tagging

Common Sandpipers were caught and tagged within a 6-km radius of Sedbergh, Cumbria, England, UK (54.32°N, 2.53°W), hereafter 'Cumbria', and

Djoudj National Bird Sanctuary, Senegal (16.36°N, 16.28°W), hereafter 'Senegal'. The breeding population in Cumbria nests along rivers running through a mixture of deciduous woodland and farmland. Here, birds were targeted on their breeding territories and caught using mist-nets set across rivers, or walk-in traps placed over nests. Individuals from the wintering population in Senegal were found on isolated saline and freshwater pools created by the rains in June to October and along the River Senegal. Birds were targeted with tape lures using mist-nets, walk-in traps and whoosh nets (Holman 1950).

All individuals caught for tagging were fitted with a metal British Trust for Ornithology ring on their right tarsus and a yellow plastic ring engraved with two black characters on their left tarsus. Two types of geocator, mounted on a red plastic leg flag on the right tibia, were used in this study. In Cumbria in 2017, 22 Lotek MK5040 tags were deployed; these weighed 1.1 g including the attachment method. In Senegal in 2018, ten Migrate Technology Intigeo geolocators were deployed, weighing 1 g in total. The geocator and attachment method never exceeded 2.6% of the individual's total body-weight in either population (Mondain-Monval *et al.* 2020). Although some of the birds experienced minor injuries caused by the geolocators, these were unlikely to have affected the migration of recaptured individuals (Mondain-Monval *et al.* 2020). Common Sandpipers in Scotland were captured and tagged over 5 years, from 2011 to 2015, using the methods described in Summers *et al.* (2019a). They fitted five birds with 1-g British Antarctic Survey geolocators on leg-loops and 23 birds with Migrate Technology Intigeo geolocators glued to a leg flag on the tibia (Summers *et al.* 2019a). These birds were from two separate breeding populations approximately 140 km apart, one on the River Spey (57.35°N, 3.53°W), and one on two lakes in north Sutherland (58.52°N, 4.33°W). In all analyses we considered these two capture locations as a single site, 'Scotland', by taking the mean of their coordinates, due to their relative proximity and the small sample size from the River Spey. Hereafter, we refer to all individuals by their tagging location.

### Geocator data analysis (Cumbria and Senegal)

Geocator data were analysed in R v4.2.1 (R Core Team 2020) using the package 'GeoLight' and

associated methodology (Lisovski *et al.* 2012a). This uses the threshold method for the identification of twilights; a twilight event takes place once light exceeds or goes below a predetermined threshold and provides daily location estimates (Lisovski *et al.* 2019). We used a light intensity threshold value of 3 for the Lotek tags and a light intensity value of 0.5 for the Migrate Technology tags; the rest of the analyses were identical. We ran the geolocator analyses using both the known location and Hill–Ekstrom calibration methods (Lisovski *et al.* 2012b) as Common Sandpipers use both coastal and heavily vegetated habitats. This means that the geolocator is sometimes shaded at dawn and dusk, which can result in imprecise location estimates (Lisovski *et al.* 2012b). We extracted timings of departure and arrival from breeding and wintering sites using the ‘ChangeLight’ function (Lisovski *et al.* 2012a). We used movement probabilities between 0.97 and 0.98, minimum stopover durations of 1–2 days, and combined stopover locations that were between 200 and 500 km from each other. The calibration method and movement probability values were chosen based on the most accurate breeding locations for birds in Cumbria, or wintering locations for those in Senegal. A distance filter prevented birds moving at more than 75 km per hour (Lisovski *et al.* 2012b).

We removed all position data 10 days either side of the autumn and spring equinoxes, because location estimates are inaccurate during this period (Lisovski *et al.* 2012b), and averaged all the location estimates during the non-breeding season in Africa to obtain a single wintering location for use in plots and for the analysis of wind assistance (see below). The dates of the non-breeding season were defined by the first and last location estimate within West Africa as determined by the ‘ChangeLight’ function. These arrival and departure dates to and from West Africa were also used to identify the autumn and spring migration periods. Positional data were twice smoothed for plotting purposes (Carneiro *et al.* 2019), kernel density estimation and the analysis of wind assistance.

### Geolocator data analysis (Scotland)

To understand differences in the migration routes and wintering locations between birds tagged in Cumbria, Senegal and Scotland, we used the data from Summers *et al.* (2019a) downloaded through the Movebank Data Repository (Summers

*et al.* 2019b). We re-analysed their data using the methods described above (and a light intensity threshold value of 3) to ensure comparability between populations. To validate our methods, we compared the results of our analyses of the geolocator data from Scottish birds with those of Summers *et al.* (2019a), who analysed their data using the package FLIGHTR (Rakhimberdiev *et al.* 2017). For each Scottish bird, we compared the timing of the departure from the breeding grounds, arrival at the wintering grounds, departure from the wintering grounds and arrival at the breeding grounds. The results from the two analyses were strongly correlated, validating our analyses (Pearson correlations,  $r_{\text{breeding departure}} = 0.90$ ,  $P_{\text{breeding departure}} < 0.001$ ;  $r_{\text{winter arrival}} = 0.98$ ,  $P_{\text{winter arrival}} < 0.001$ ;  $r_{\text{winter departure}} = 0.91$ ,  $P_{\text{winter departure}} = 0.002$ ;  $r_{\text{breeding arrival}} = 0.71$ ,  $P_{\text{breeding arrival}} = 0.05$ ). Full details of the timings of departure and arrival of each bird for their wintering locations can be found in Table S1.

### Breeding locations of Senegal-tagged birds

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

### Migratory connectivity (kernel density and overlap)

To identify the overlap in the stopover sites and wintering distributions of Common Sandpipers from the different tagging locations, we analysed kernel densities using the package ‘adehabitatHR’ (Calenge 2019). We were primarily interested in stopover sites throughout Europe, and we therefore assumed that birds had reached the breeding grounds after crossing certain latitudes, depending on their tagging location. For Cumbria, this threshold was 50 degrees north latitude; for the Scottish population it was 52 degrees north latitude; and for the Senegalese birds it was 57 degrees latitude.

We excluded positions that were above these thresholds for the analyses of overlap during the autumn and spring migration periods.

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

#### *Migratory connectivity during winter*

We determined the amount of mixing between breeding populations on the wintering grounds using Mantel correlation tests. These were used to determine whether the distances between individuals on their breeding and wintering grounds were correlated (i.e. whether birds that breed close together also winter close together), using a scale ranging between  $-1$  and  $1$ . Low Mantel coefficients indicate a high degree of mixing, while high coefficients indicate low mixing (Ambrosini *et al.* 2009). This was done for individuals from Scotland and Cumbria, but not for the individuals tagged in Senegal because of the small sample size.

#### **Analysis of wind assistance**

To understand whether birds used wind to support their migratory journeys, we compared the wind costs experienced by migrating birds to those of randomly simulated migrations. Costs were determined by the speed and direction of wind, as described below. We used the package 'RNCEP' to obtain daily gridded (2.5-degree resolution) model-derived 'U' and 'V' wind components at 00:00 AM, 06:00 AM, 12:00 PM and 18 h PM Coordinated Universal Time from the NCEP/NCAR R-1 re-analysis datasets (Kemp *et al.* 2012). We downloaded data for 1000, 925, 850 and 700 millibars which correspond approximately to: 0, 780, 1500 and 3100 m above sea level, respectively. We do not currently know the altitude at which Common Sandpipers migrate, and these altitudes correspond to the range in which most avian migration occurs in radar data (Kemp *et al.* 2013, Kranstauber *et al.* 2015). For the autumn and spring migration periods of each individual in our dataset, we obtained the daily wind conditions

across the entire Afro-Palaeartic flyway at a 0.5-degree spatial resolution, disaggregated from 2.5 degrees using the 'terra' package (Hijmans 2022). We converted the 'U' and 'V' wind components into wind direction and speed, and calculated the mean wind direction and speed values for each migration at each of the altitudes considered. This produced a gridded map of the average conditions across the entire flyway for the autumn and spring migration periods of each individual tracked with a geolocator, at each of the altitudes described above. The birds in our study were tracked over a number of different years, in which wind conditions could have differed between locations. To ensure that differences between locations did not affect our analyses, we plotted the wind speeds and directions at each altitude for each individual. There was considerable overlap in the distributions of both wind speed and direction for all of the individuals in the study, suggesting that wind conditions across the flyway were broadly similar for each tracked individual across all years.

We then used the gridded maps of the average conditions to calculate the transition probabilities between every cell in the flyway, for each altitude separately, with movement into headwinds allowed, but incurring a greater cost penalty than movement with tailwinds (Fernández-López & Schliep 2018). These 'costs' are conductance values between cells, and are determined by the direction and speed of wind conditions rather than referring to the physiological costs associated with bird flight (Fernández-López & Schliep 2018). This provides an index of the costs to movements due to the wind conditions that birds are confronted with during migration.

#### *Observed migratory tracks*

For each spring and autumn track of an individual, we calculated the cost of moving between sequential positions based on the transition probabilities using the 'costDistance' function from the package 'gdistance' (van Etten 2017). During migration, birds are likely to change their flight altitude to find favourable wind conditions (Kranstauber *et al.* 2015). Therefore, we calculated the cost of moving between sequential positions for each of the altitudes listed above. From these, we selected the altitude at which there was the lowest movement cost, thereby mimicking the ability of birds to change flight altitude in search of favourable wind conditions. Our analysis assumes that birds

will always fly at the optimal altitude with respect to wind conditions. This may not always be true because there are likely to be physiological costs associated with changing flight altitude. Therefore, the actual wind costs faced by birds are likely to be higher than those we have estimated. The costs of all movements between sequential locations identified by the geolocator analyses in the migratory track were summed and divided by the total number of relocations to obtain a 'cost index'. This equates to the average cost of movement per relocation. This was needed because the number of locations estimated by the geolocators was different for each individual as they travelled different total distances. This made the migration costs calculated for each bird comparable across tagging locations and between the observed and simulated tracks.

#### *Simulated migratory tracks*

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

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

spring migration. The random tracks were twice smoothed.

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

In order to determine the differences in wind costs experienced during autumn and spring migrations, we fitted models for observed and simulated tracks separately. For observed birds, we fitted a linear model with cost index as the response variable and the migration period (autumn or spring) as the only explanatory variable. For simulated tracks, we fitted a linear mixed effects (LME) model from the package 'lme4' (Bates *et al.* 2015) using the same variables, but included individual identity as a random intercept to control for repeated simulated tracks for the same observed individual. We then fitted a separate set of LMEs to test whether Common Sandpipers used winds to facilitate their autumn and spring migrations. For each tagging location and each migration separately, we fitted the cost index as the response variable and whether the cost was that of an observed or simulated track (hereafter 'bird type') as the sole explanatory variable. We also included individual identity as a random intercept, again to control for repeated simulations for the same observed individual. Locations were defined as the tagging locations. We did not test for within-site differences in the cost of migrations between seasons because small sample sizes would have made any results questionable. We validated all models by plotting the distribution of the residuals and the residuals versus fitted values.

#### *Geolocation error*

Positional data obtained from geolocators are relatively inaccurate because of shading (e.g. from cloud cover, vegetation or feathers) and their reliance on differing day lengths globally (Lisovski *et al.* 2012b). To understand how this error could have affected the results of our wind assistance analyses, we simulated 100 tracks for each migration period of an individual. For each position of an observed individual, we sampled a random, new position from two normal distributions, one

for latitude and another for longitude. We used the latitude and longitude values from the track of the corresponding observed bird as the means of the distributions, with standard deviations of 2 degrees for latitude and 1 degree for longitude. These values were chosen because they approximate the errors in geolocator position estimates; 250 km for latitude and 100 km for longitude (Lisovski *et al.* 2012b). We determined the cost indices for each of the 100 tracks using the wind conditions at the same altitude as the associated observed individual; these tracks differed from the real tracks in their two-dimensional location only (i.e. only in longitude and latitude, not altitude). These were analysed using LMEs. For each tagging location and each migration separately, we fitted the cost index as the response variable and whether the cost was that of an observed track, a geolocation error or a simulated track as the sole explanatory variable. We also included individual identity as a random intercept to control for repeat sampling of individuals. There were no important differences between the migration costs when accounting for geolocator error and those from the raw tracks of individuals (Fig. S2, Table S2).

## RESULTS

In Cumbria in 2018, we recovered 11 geolocators after resighting 13 tagged individuals at the study site (13/22). In Senegal in 2019, we recovered four geolocators, but resighted eight tagged birds in total (8/10). There were no significant differences between the return rate, body condition or reproductive success of birds with geolocators compared with those carrying only rings (Mondain-Monval *et al.* 2020). Additionally, the raw light data of the birds tagged in Senegal showed light patterns indicative of incubation, meaning that they were all breeding individuals. The Scottish study retrieved

10 geolocators (10/28, Table 1), but there were no comparisons with a colour-ringed control group (Summers *et al.* 2019a). This resulted in 25 tracks of autumn migration and 22 for spring migration, as three geolocators had failed on the wintering grounds (two from birds in Scotland and one from a bird in Cumbria).

Common Sandpipers tagged with geolocators in Cumbria used similar migration routes and wintering grounds to the Scottish birds (Summers *et al.* 2019a; Fig. 1, Table S1). In autumn, the birds from Cumbria used southern England, northern France and the western half of the Iberian Peninsula as stopover sites, before wintering in the southern half of West Africa (all south of 18° =N). In spring, individuals also stopped in Morocco and, compared with autumn migration, used sites further inland on the Iberian Peninsula and throughout France (Fig. 1). The four Common Sandpipers tagged in Senegal all bred in Scandinavia but in different regions, ranging from approximately 59°N in southern Sweden to approximately 70°N in Arctic Norway (Fig. 1, Table S1). In autumn, birds from Senegal used northern Europe (Denmark, the Netherlands and northern Germany), western France and the east coast of the Iberian Peninsula as stopover sites. In spring, these birds used sites similar to those used by the birds from Cumbria, although these stopover sites also extended to northern Europe (Fig. 1). Table S1 provides a full summary of each individual's migratory schedule as determined by the geolocator analyses, including breeding and wintering locations, and the number of stopover sites and days during each migration.

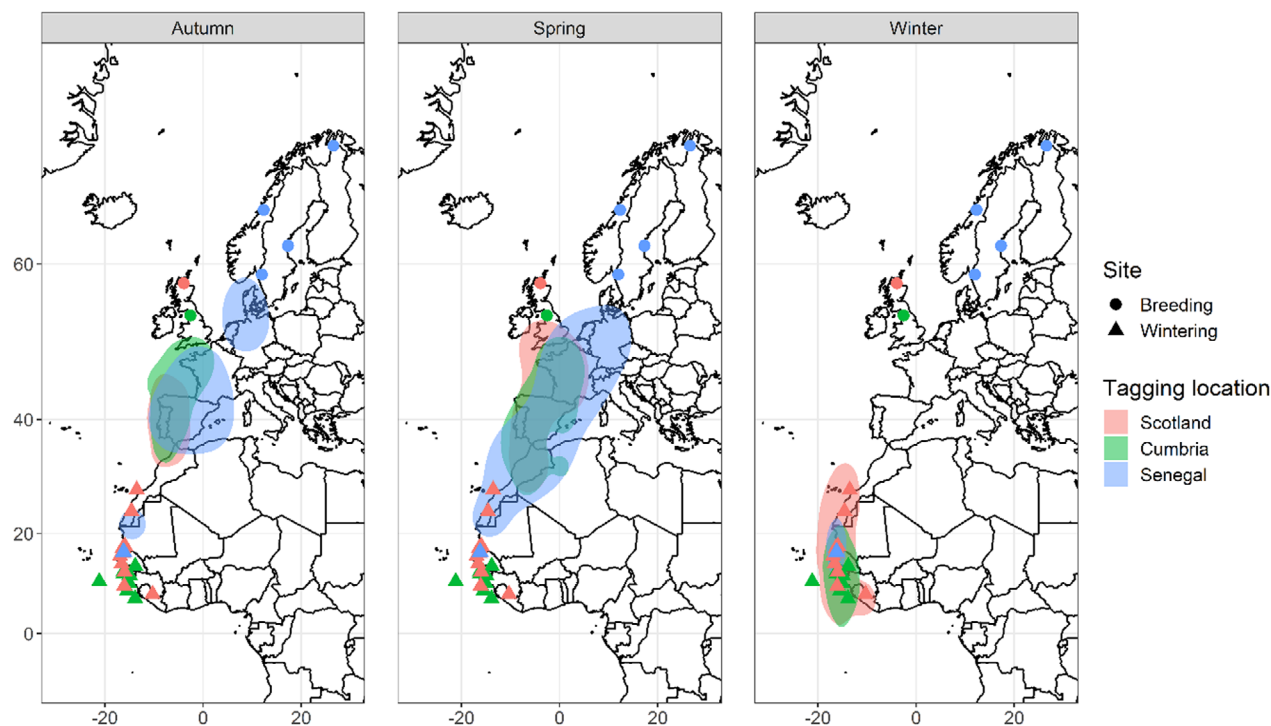
### Migratory connectivity (kernel density and overlap)

The migration routes and wintering locations of birds from the three different tagging locations

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

Location	Number of birds tagged	Mean tagging long	Mean tagging lat	Median tagging max distance	Tagging median distance	Final mean long	Final mean lat	Final max distance	Final median distance	Median migration distance
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

Abbreviations: lat, latitude; long, longitude; max, maximum.



**Figure 1.** The distribution of the wintering sites of individuals from the three tagging locations and their stopover sites during autumn and spring migrations. The shaded regions represent the 75% kernel densities of the utilization distribution of individuals from different tagging locations. Closed circles are breeding locations and closed triangles are wintering locations.

overlapped considerably, with the proportion of overlap between the British populations being highest. The proportion of overlap between the Senegal-tagged birds and the British birds was lower in autumn than in the spring migration (Table 2). This is because the Senegal-tagged birds flew further east before crossing the Pyrenees in autumn. In spring there was more overlap between the Senegalese and British birds than in autumn, as the latter used stopover sites throughout France. In winter, there was considerable overlap in the kernel density distributions between individuals from the different tagging locations, suggesting a low level of migratory connectivity between breeding and wintering areas (Fig. 1). However, a Mantel correlation coefficient of 0.26 ( $P = 0.001$ ) suggests some connectivity; i.e. tagged birds that bred close together also wintered relatively close together, and vice versa. The median distances between wintering individuals from the Scotland and Cumbria populations were 800 and 290 km, respectively (Table 1).

**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.

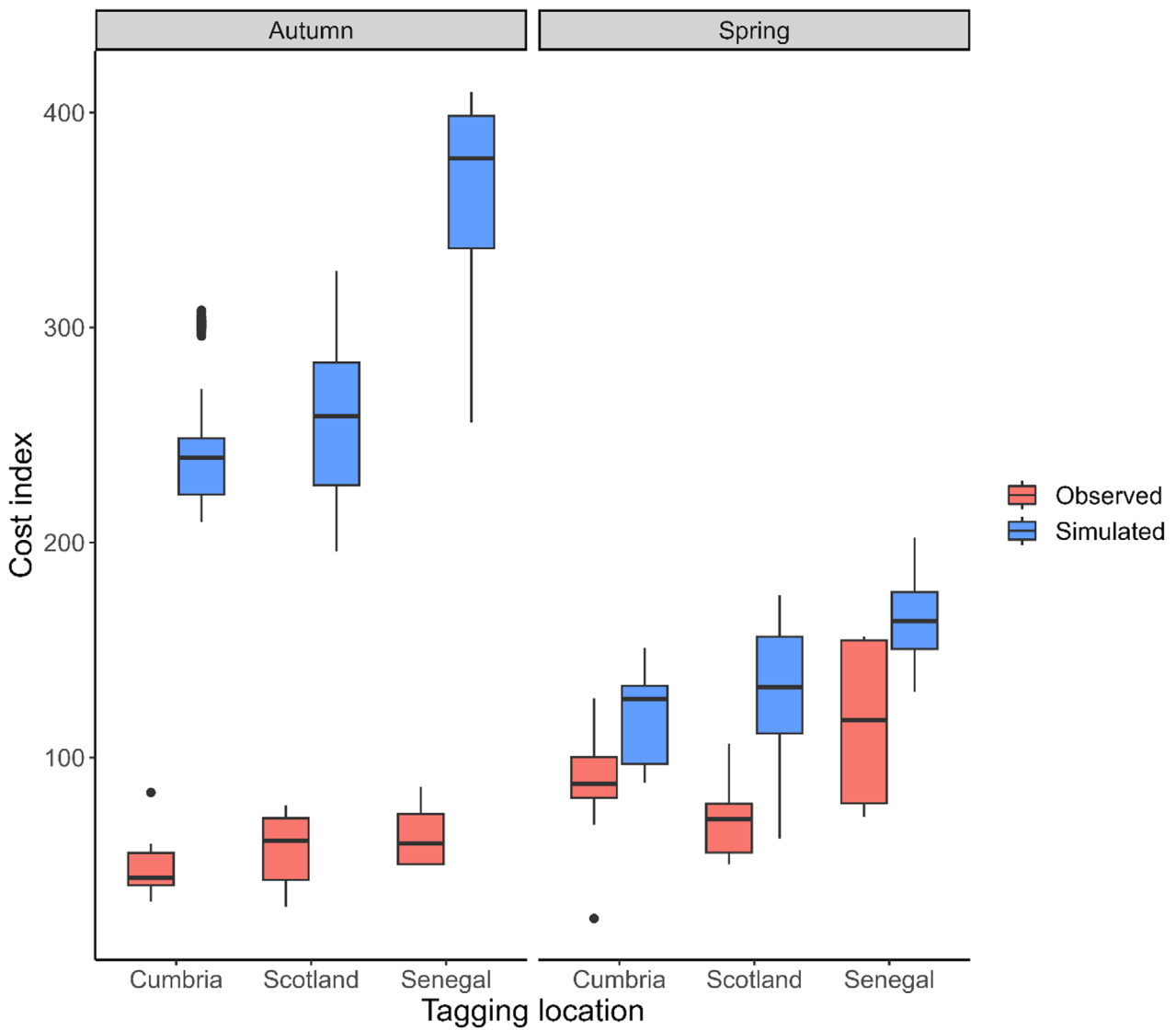
	Scotland	Cumbria	Senegal
Scotland	–	0.83, 0.83, 0.46	0.78, 0.82, 0.15
Cumbria	0.55, 0.83, 0.97	–	0.76, 0.88, 0.23
Senegal	0.26, 0.40, 1	0.37, 0.50, 0.77	–

## Analysis of wind assistance

### Wind costs in autumn and spring

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





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

**Table 3.** Results of a generalized linear model (GLM, for observed birds) and a linear mixed effects model (LMM, for simulated tracks) 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 *F*<sup>2</sup> value is not shown for the model of the observed birds because this did not have mixed effects.

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

### Wind assistance during migration

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

## DISCUSSION

Our simulations suggest that the migration of Common Sandpipers is facilitated by wind, with the evidence indicating that this effect is stronger in autumn than in spring. In spring, the wind costs associated with their migratory journeys were higher than the costs in autumn, but still lower than expected at random. The wind costs of simulated migrations were actually significantly lower in spring than in autumn on average, suggesting a decrease in wind speed or more tailwinds, perhaps due to changes in prevailing wind direction leading to generally more favourable conditions (Kemp *et al.* 2010, Nussbaumer *et al.* 2022). Therefore, it appears that the migrations of Common Sandpipers are less affected by prevailing wind conditions in autumn than in spring. Indeed, we found that autumn migration lasted on average 18 days, whereas spring migration lasted only 15 days, perhaps because individuals were able to pause and

wait for favourable conditions (Table 2). These findings could suggest that the timing of autumn migration is under weaker selection pressure than spring migration. In spring, early arrival at the breeding grounds is important for reproductive success (Morrison *et al.* 2019) and individuals may therefore migrate more quickly or take the most direct route, irrespective of wind conditions (McNamara *et al.* 1998, Nilsson *et al.* 2013, Gutierrez Illan *et al.* 2017). In autumn, individuals could be under reduced time pressure, allowing them to select the optimal migratory routes that involve more tailwinds or fewer crosswinds and headwinds (Nilsson *et al.* 2013, Duijns *et al.* 2017). It is also possible that individuals are in poorer body condition in autumn following reproduction, meaning they are less able to fly during adverse wind conditions. In our study, the time window available for migration was the same for the observed and simulated tracks, meaning that any differences in wind costs between the two were due to differences in route and flight speed only. In reality, individuals can also change the total duration of migration by waiting at stopover sites for adverse wind conditions to pass (Watts *et al.* 2021). Our results show that Common Sandpipers face higher wind costs during spring migration, as suggested by Summers *et al.* (2019a), and as shown for other species (Lok *et al.* 2015, Loonstra *et al.* 2019).

The physiological cost of migration is likely to be high for many species, especially when making large desert or ocean crossings (Alerstam *et al.* 2003, Klaassen *et al.* 2014, Lok *et al.* 2015). The simulated costs for birds during autumn migration were very high, meaning that failure to adapt to flight altitude and to adapt general migration behaviour to these conditions could have resulted

**Table 4.** Results of the linear mixed effects models comparing the cost indices of observed and simulated tracks 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 tracks cost index (intercept)	Simulated tracks cost index (estimate)	Standard error (estimate)	$\chi^2$	<i>P</i> value	Marginal $R^2$	Conditional $R^2$
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

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

We are the first to report the migration routes and wintering distributions of Common Sandpipers breeding in England. Although our Mantel test revealed some connectivity between tagging and wintering locations, the birds tagged in England, Scotland and Senegal had overlapping and widespread distributions on migration and during winter, as determined by the kernel density analysis. This could be because of the biases associated with Mantel correlations when analysing small samples and from few discrete sites (Vickers *et al.* 2021). However, if the overlap of individuals determined by our kernel density analyses reflects connectivity more broadly, it could potentially buffer distinct breeding populations from habitat change in non-breeding areas (Taylor & Norris 2010, Finch *et al.* 2017, Summers *et al.* 2019a).

The overlap also means that birds from different breeding regions are likely to experience similar wintering conditions; major habitat or climatic changes affecting the whole of the West African coast would therefore be likely to have large-scale impacts across Europe. In West Africa, there has been significant agricultural intensification and a small reduction in the amount of mangrove forest (Vickery *et al.* 2014, Summers *et al.* 2019a). There has been a large expansion of the rice industry in West Africa (Elphick 2000, Wymenga & Zwarts 2010). Although rice fields do provide habitat for foraging waders, these are unlikely to be equivalent to natural wetlands (Wymenga & Zwarts 2010; but see Elphick 2000). Therefore, it is possible that individuals using rice fields could suffer from poor body condition, affecting their ability to perform their spring migration (Duijns *et al.* 2017) or cope with adverse conditions on the breeding grounds (Morrison *et al.* 2013). Patchett *et al.* (2018) found that, in the Afro-Palaeartic flyway, species that are spread over large non-breeding areas are more likely to be affected by habitat change in Africa, as they may be more likely to encounter poor-quality habitats. More work is needed on the wintering grounds to investigate links between changes in habitat and the population trends of migratory species.

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

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

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

We would like to thank the Yorkshire Dales National Park and the local landowners for supporting UK fieldwork. Thanks to Dah Diop and the Direction des Parcs Nationaux, Dakar, for making fieldwork in Senegal possible. We also thank Lucy Magoolagan and Flora Whitehead for help with fieldwork in the UK, and the entire ringing team in Senegal (James Bray, Richard Cope, Ian Hartley, Rob Robinson and Paul Roper). Brian Bates and Brian Etheridge collected the field data with RWS for the Scottish study, and Louise de Raad and Norman Elkins were involved with the original analysis of the Scottish data. Jenny Gill and Andy Wilby provided useful comments on an earlier version of the manuscript.

## AUTHOR CONTRIBUTIONS

**Thomas O. Mondain-Monval:** Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (lead); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Richard du Feu:** Data curation (equal); investigation (supporting); methodology (supporting); writing – review and editing (supporting). **Ron W. Summers:** Data

curation (supporting); investigation (supporting); resources (supporting); writing – review and editing (supporting). **Stuart P. Sharp:** Conceptualization (equal); data curation (equal); formal analysis (supporting); funding acquisition (lead); investigation (supporting); methodology (equal); resources (lead); supervision (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal).

## FUNDING

Natural Environment Research Council (Grant/Award Number: NE/L002604/1).

## CONFLICT OF INTEREST STATEMENT

The authors have no competing interests to declare.

## ETHICAL NOTE

All catching and ringing was performed under British Trust for Ornithology licensing, including special permits for the use and attachment of geolocators.

## CONSENT FOR PUBLICATION

Not applicable.

## Data Availability Statement

All geolocator data will be deposited in the Movebank Data Repository on publication of the paper. All data required to run the analysis are available on figshare, DOI: <https://doi.org/10.6084/m9.figshare.22100108>, except for the position estimates, which will be made available by the authors on reasonable request. All code required to run the analysis is available at: <https://github.com/TMondain/comsa-migration>.

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Received 21 July 2022;

Revision 30 June 2023;

revision accepted 17 July 2023.

Associate Editor: José Alves.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** Map of the Afro-Palaeartic flyway showing the average track across all simulations from each of the tagging locations, Scotland, Cumbria and Senegal, in autumn and spring.

**Figure S2.** Boxplot comparing the cost index of observed and simulated migrations, to those of the observed birds while accounting for geolocation error.

**Table S2.** Results of the linear mixed effects model comparing observed, simulated and observed tracks accounting for geolocation error.

**Table S1.** Summary of the timings and destinations of migration for each of the real birds tracked with geolocators.