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Research

Bird migration in space and time: chain migration by Eurasian curlew *Numenius arquata arquata* along the East Atlantic Flyway

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Migration patterns in birds vary in space and time. Spatial patterns include chain, leap-frog and telescopic migration. Temporal patterns such as migration duration, number, and duration of stopovers may vary according to breeding latitude, sex, and season. This study aimed to verify these patterns in a long-distance migrant, the Eurasian curlew *Numenius arquata arquata*, and to provide a synopsis of spatio-temporal migration patterns in this species of concern throughout the East Atlantic Flyway. We tagged 85 adults with GPS-data loggers in Germany, Poland, France and Estonia between 2013 and 2019. We computed the distance flown, linear loxodromic distance, duration, stopover number, total stopover duration, mean stopover duration, departure time and arrival time for 177 out of 187 tracks. On average (\pm standard deviation), spring migration occurred from 4 to 14 April (10.2 ± 8.4 days), curlews flew 3.623 ± 1.366 km, and had 5.8 ± 3.6 stopovers, with a duration of 29.4 ± 38.2 h per stopover, while autumn migration occurred from 18 to 29 June (10.9 ± 9.9 days), curlews flew 3.362 ± 1.351 km, and had 5.4 ± 4.0 stopovers, with 31.8 ± 32.3 h per stopover. Curlews displayed chain migration because wintering curlews maintained the latitudinal sequence to their breeding sites. Southern curlews had a longer nesting period due to their earlier arrivals. While spring arrival at breeding sites did not differ between the sexes, in autumn females departed earlier than males. Migration duration and distance, as well as stopover number and duration, showed a significant increase with breeding site latitude but did not differ between the sexes or between spring and autumn migrations, suggesting that curlews took a comparable amount of time migrating during both seasons. The high site faithfulness in curlews suggests that rapid autumn migration allows them to return to defend their winter foraging areas.

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Introduction

Migration drives the seasonal redistribution of birds in general (Alerstam 1990). There are three main patterns regarding bird migration. 1) Chain migration occurs when bird populations at their wintering sites are arranged in a latitudinal sequence similar to their breeding sites; i.e. birds breeding at higher latitudes tend to migrate to more northerly wintering areas, while birds breeding at lower latitudes migrate to more southerly wintering areas (Nilsson 1858, Lundberg and Alerstam 1986, Newton 2010). 2) Leapfrog migration results in a latitudinal sequence of wintering sites that is the reverse of the breeding areas, with populations of a species that breed farther north having wintering sites farther south (Palmén 1874, Lundberg and Alerstam 1986, Newton 2010). The leapfrog migration pattern tends to be more common than chain migration, though some species may use a combination of both (Salomonsen 1955, Lundberg and Alerstam 1986). 3) Telescopic migration occurs when different populations all migrate to the same latitudinal location, such that different populations meet for one season during their annual migration (Newton 2010, Chapman et al. 2014).

Besides these possible spatial patterns, the temporal component of migration is also essential. Usually, birds breeding in northern latitudes start their spring migration later than birds breeding farther south because conditions in the breeding areas (such as food peaks, temperature, snow cover etc.) enabling a successful reproduction are met later in the year (Reneerkens et al. 2016, Saalfeld et al. 2019). This might lead to a later departure from wintering grounds in individuals breeding in higher latitudes (Amélineau et al. 2021, Schwemmer et al. 2021). Furthermore, the time spent at breeding grounds is often longer in southern latitudes as the conditions for reproduction last longer than in northern latitudes (Wyndham 1986). Finally, migration speed might differ significantly between the seasons (i.e. between spring and autumn migration): Nilsson et al. (2013) found in their compilation study that birds had higher flight speeds and shorter migration durations during spring migration rather than autumn migration due to the competition pressures at the breeding sites. However, a faster spring migration does not hold true for all bird species, e.g. Kölzsch et al. (2016) found a faster autumn than spring migration in white-fronted geese *Anser albifrons*. Similar results were also found in Icelandic whimbrels *Numenius phaeopus islandicus* (Carneiro et al. 2019).

Sex can also be a reason for the variation of migration behavior when males and females display different methods in migration (Cristol et al. 1999, Morbey and Ydenberg 2001). One example of this variation is protandry where males arrive earlier to breeding sites than females, or protogyny where the females arrive earlier than the males (Morbey and Ydenberg 2001). Departure timing from the breeding site can also differ between the sex such as in offspring desertion when one

parent may leave its offspring before it becomes independent (Fujioka 1989). In shorebirds, it is most common that the females will desert earlier than males (Székely and Reynolds 1995).

Although information on migration patterns is an essential prerequisite for ensuring conservation, the migration period remains a crucial, but poorly studied part of the annual cycle for many bird species. It is also important to have a good understanding of the migration behaviors of individual populations and different sexes, which could differ from those of the species as a whole. Migratory birds are less-well protected due to the need to consider multiple sites with different habitat uses (Runge et al. 2015, Pearce-Higgins et al. 2017). It is therefore important to identify the birds' movements and stopover sites as well as the timing of the start and end of the migration in order to improve their population management and habitat conservation (Palm et al. 2015).

We analyzed the spatial and temporal patterns of the migration of Eurasian curlews (*Numenius arquata arquata*; hereafter named curlews) along the East Atlantic Flyway and explored differences in migration duration, distance flown as well as number and mean duration of stopovers with respect to breeding latitudes, sex, and season (i.e. spring versus autumn migration). Curlews winter along the Atlantic coast from North Africa to the North Sea, and breed from Spain and Ireland to the Ural Mountains and up to the Arctic Circle (Summers et al. 2013, van Gils et al. 2020). Few studies have looked specifically at curlew migration patterns (Palm et al. 2015); however, two studies using GPS tags revealed the migration patterns of curlews wintering in the German Wadden Sea and migrating to western Russia for breeding (Schwemmer et al. 2016, 2021). These studies also showed the feasibility of GPS-tagging of curlews. Based on observations and ring recoveries it has also been implied that curlews might display chain migration (Delany et al. 2009). The current study aimed to extend this knowledge using an extensive dataset of curlew migratory movements recorded by GPS dataloggers, including 85 individuals tagged in different parts of the East Atlantic Flyway. In addition to unraveling the spatial (i.e. chain migration versus leapfrog migration) and temporal patterns (i.e. differences among both migration periods), this study also aimed to describe Eurasian curlew migration patterns across different regions of their global distribution area.

This study tested the following four hypotheses: 1) curlews on the whole East Atlantic Flyway perform chain migration with the northern wintering populations migrating to more northern breeding areas (Nilsson 1858, Lundberg and Alerstam 1986, Delany et al. 2009). 2) Location of the breeding site (i.e. breeding site latitude) has been found to influence the onset of curlew migration (Amélineau et al. 2021, Schwemmer et al. 2021). Therefore, we expected further migration characteristics such as duration of migration, distance flown, number of stopovers and stopover duration to

depend on the location of the breeding site. 3) Based on the available research, migration patterns might differ between spring and autumn migration dependent on the respective bird species (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Kölzsch et al. 2016, Carneiro et al. 2019). Therefore, we will test for seasonal differences in curlew migration patterns. 4) Finally, we expected females to leave their breeding sites earlier than males, based on previous findings for curlews and other shorebird species (Currie et al. 2001, Krupa et al. 2009, Sanders and Rees 2018).

Methods

Study area and tagging of curlews

We tagged 85 adult curlews (43 males, 42 females) across six different programs in Europe between 2013 and 2019 (three German, one Polish, one French and one Estonian; green triangles for breeding curlews and green rectangles for wintering curlews in Fig. 1, Table 1). For detailed information about each curlew, see Supporting information. The curlews were caught using either a scoop or cage on the nest (breeding curlews), or with a mist net (wintering curlews). Four different brands of GPS tags including eight different types of solar tags were used to track the curlews, all weighing within 4–5% of the bird's body mass (Phillips et al. 2003): three tag types were manufactured by Ecotone, Poland (Sterna (7.5 g), Saker L (17 g) and Skua (17 g)), three by Ornitela, Lithuania (OT-10 (10 g), OT-15 (15 g) and OT-20 (20 g)), one by Milsar, Poland (M-9 (16 g)) and one by e-obs, Germany (e-obs (20 g)). Fifty-eight tags were attached using breast-harnesses (Guillaumet et al. 2011) and the remaining 27 were attached using leg-loop harnesses (Mallory and Gilbert 2008). Tag intervals ranged from 1 min to 12 h. All curlews were weighed and ringed, and their biometrics were recorded (i.e. wing, tarsus and bill length). Curlews were sexed either morphologically ($n=49$) (after Summers et al. 2013) or genetically through blood samples ($n=36$) (Tauros Diagnostics, Berlin, Germany).

Mapping of tracks and designation of breeding and wintering sites

The GPS latitude and longitude were mapped for each curlew, using ArcGIS 10.6.1 (Environmental Systems Research Inst. (ESRI) 2018). GPS data were represented as points and then converted to lines to show the migration routes taken by each curlew. Based on these maps, curlews that did not migrate (either because tags malfunctioned or the curlews stayed in their wintering grounds over summer) and curlews with incomplete tracks were excluded (for sample sizes see Table 1). Seventy-four curlews performed at least one complete migration trip, and 23 birds had migration data for consecutive years, with a maximum of four years. We thus obtained a total of 187 migration tracks, including 90 complete spring migration tracks, with 49 tracks being a single

migration (Table 1), and 97 complete autumn migration tracks, with 48 tracks being a single migration (Table 1). Wintering and breeding sites were identified for each curlew and were used to calculate migration dates and distances. We visually identified the main high tide roost at each wintering site, corresponding to the highest concentration of points outside the tidal range area for the whole wintering period. The mean latitudes and longitudes of these main roosts were calculated to define the wintering locations of the curlews.

Locations of nest sites were either recorded directly in the field (if the curlew was caught while incubating) or calculated (if the curlew was tagged while wintering) using R (ver. 3.5.3) (<www.r-project.org>). First, we took account of all the GPS points to create a subset for the breeding season, based on the curlew's rough arrival and departure times. From this subset, we defined the most likely location of the nest site using a latitudinal and longitudinal grid (cell size $0.0001^\circ \times 0.0001^\circ$) over the area visited by the curlew, by counting the number of positions in each cell within the breeding period. The grid cell centroid containing the most positions was then defined as the breeding site and showed a maximum error of 5 km, which is of a negligible magnitude for the spatial scale of this study (Amélineau et al. 2021).

The start and end dates for each migration were established when the curlew entered and exited 20 km from either the breeding or the wintering site, respectively. This limit was chosen because the curlews can be vagrant around the defined breeding or wintering locations, and it helped to avoid the inclusion of stops outside the breeding or wintering sites as stopovers. We then used the start and end dates and times to calculate the duration of each migration.

Statistical analysis

Migration parameters were computed using the statistical open-source software R (<www.r-project.org>). The raw tracking data were combined into one data frame, and we then calculated the temporal (dt) and spatial (dx) differences between the subsequent tracking points, and an approximation of the speed (dx/dt). The histogram showed a distinct bimodal pattern (Supporting information), corresponding to the two behavioral modes 'flight' versus 'resting'. Although values lower than 24 km h^{-1} might also appear during flight (and values higher than 24 km h^{-1} may appear during short flights within resting periods), the minimum between the two distinct 'behavioral modes' suggests that the likelihood of incorrect attribution is lowest when using approximately 24 km h^{-1} as a threshold, which has been slightly corrected up by visual checks of classified tracking points within known resting and migration areas. The different time intervals of the tags from geofencing using Ornitela devices (i.e. increasing the number of tag intervals within a given area, battery level or setting preference) resulted in major differences in fix intervals, leading to potential biases in the calculation of migration parameters: e.g. tags with a shorter fix interval would produce a more accurate spatial resolution of the migration route and stopovers. To account for this bias, we

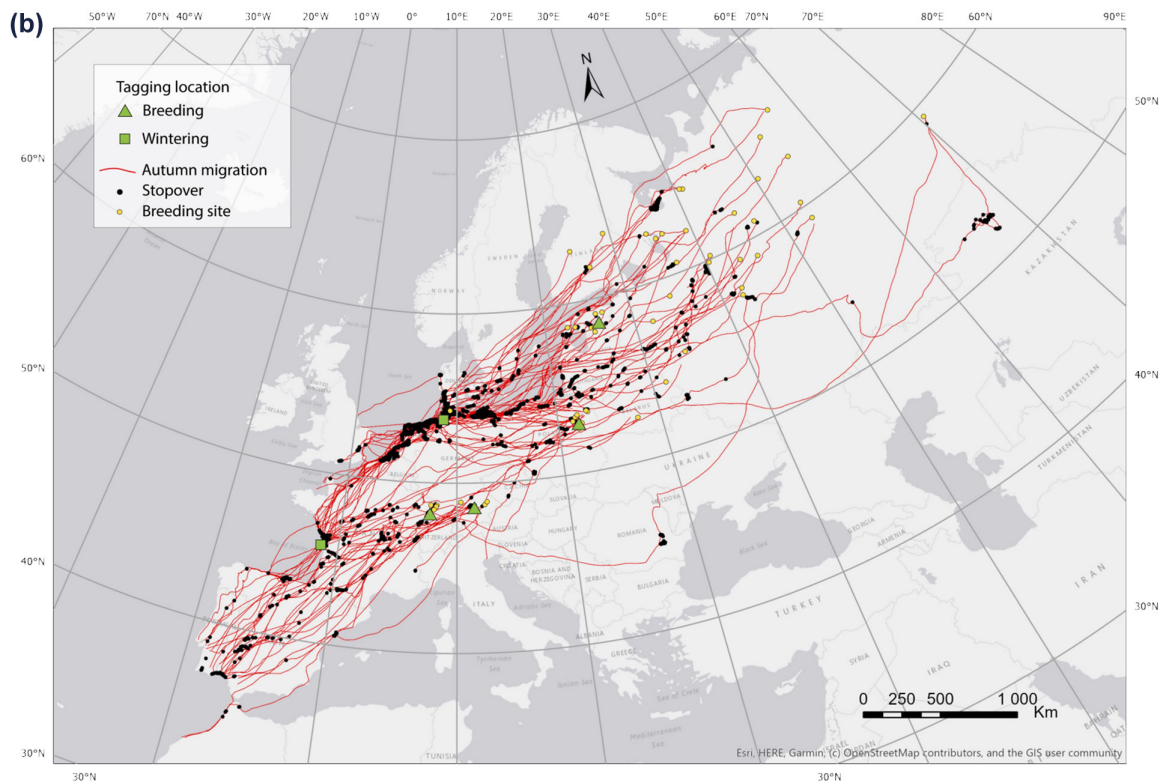
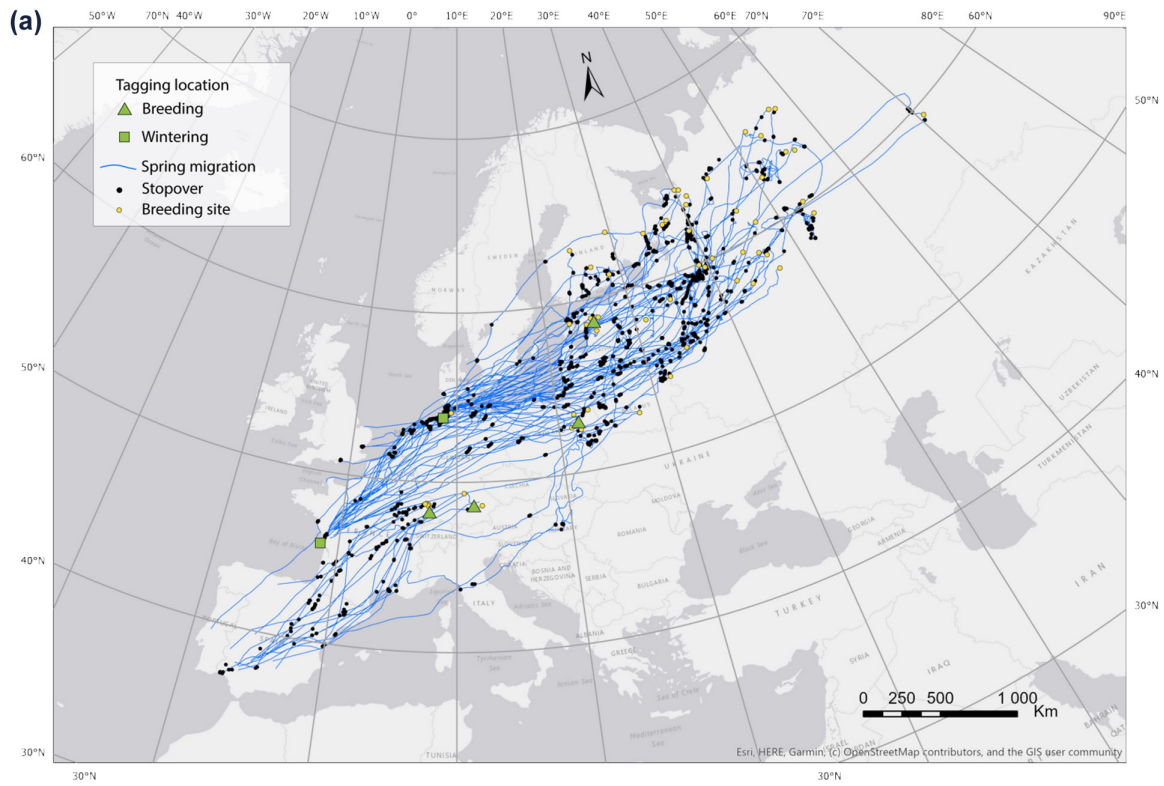


Figure 1. Migration tracks with stopovers (black) and breeding sites (yellow) based on (a) spring and (b) autumn periods. Green triangles: curlew caught at breeding sites, green rectangles: curlew caught at wintering sites.

Table 1. Overview of tagging information.

	Tagged adults	Males	Females	n*	Spring migration	Autumn migration	Device type	Time interval range (min)	Study period	Attachment method	Sexing method	Catching method
Germany North	26	13	13	22	31	26	Skua, OT-10, OT-15, OT-20	1-480	2014-2019	Breast	Genetic	Scoop and mist net
Germany South	7	5	2	6	6	9	Saker L	1-360	2016-2019	Breast	Morphology, genetic	Cage trap on nest
Germany West	7	4	3	7	11	13	e-obs OT-20	180	2014-2019	Breast	Morphology	Cage trap on nest
France	24	11	13	22	29	25	Sterna OT-10	1-240	2015-2019	Leg-loop, breast	Morphology, genetic	Mist net on roost
Estonia	10	6	4	6	5	6	e-obs, OT-15, OT-20	1-720	2015-2019	Breast	Morphology	Caught on nest
Poland	11	4	7	11	8	18	Milsar	5-120	2013-2019	Leg-loop	Morphology	Cage trap on nest
Total	85	43	42	74	90	97						

*Number of individuals that completed at least one full migration.

only included migration tracks from individuals with average time intervals < 100 min. We also discarded data for individuals with tracks including single gaps of > 24 h. Therefore, we discarded 10 of the originally 187 tracks and used an overall sample size of 177 tracks for our analyses. Finally, the data were further processed to redefine a 'rest' period as a period ≥ 60 min long, a similar approach was applied to 'migration'. We defined this 'rest' period as 'stopover' based on Warnock's (2010) definition of stopovers. We produced several visualizations of stopover lengths and stopover versus flight for additional visual validation, e.g. checking that only migration behavior was observed offshore and that a high proportion of resting occurred in well-known resting areas, such as the Wadden Sea. We then pooled the data on a daily basis (separately for each individual) and applied it to different appropriate regression models (generalized additive mixed models; Wood 2006, Zuur 2012) using the R package 'mgcv' (Wood 2006). This regression analysis was performed to detect possible bias due to the varying interval length dt. In particular, we systematically checked for dependencies between dt and several variables of interest (used as outcome variables in generalized linear mixed effect model (GLMM) analysis), namely daily track length, rest number, average rest length and total rest length. These first three models showed significant relationships, and the variables of interest were corrected correspondingly (based on the inverse of the predicted correlation). There was no significant relationship between dt and total rest length per day, and correction for this parameter was therefore unnecessary. Finally, we temporally pooled the corrected daily data down to the level of individual migration tracks, to calculate the unbiased number of stopovers, duration of stopovers, mean duration of stopovers, distance flown and linear distance per individual and migration, to provide a database that was comparable among the different types of devices with different fix intervals. Linear distance was defined as the Haversine (great circle) distance between the start and end points of each migration route.

Based on the above calculations, each GPS fix was assigned to one of four categories: 1) wintering, 2) spring migration, 3) breeding or 4) autumn migration. The four categories were plotted for each curlew and year of migration based on the breeding latitude, to illustrate differences in phenological patterns across a gradient from south to north.

We analyzed the effect of the migration season (i.e. spring versus autumn migration), sex and breeding site latitude on the four outcome variables (migration duration, flown distance, number of stopovers and mean stopover duration) using GLMMs. Furthermore, we determined if the spring and autumn departure dates were significantly related to breeding site latitude, and if there were differences between the sexes with regard to the spring and autumn departure dates. Bird-ID was included as a random intercept in the GLMM models, to prevent pseudo-replication due to multiple observations of the same individual. The most appropriate probability distribution (Gaussian, Tweedie or Negative Binomial) was selected, based on the Akaike information criterion (Akaike 1973). Tweedie distribution was used for all the variables,

except for mean stopover duration, where Negative Binomial was used. Flown distance and linear distance were compared separately for both migrations. All plots were visualized using the R package 'ggplot2' (Wickham et al. 2010).

Results

Spatio-temporal migration patterns

The tagged curlews exhibited a large migration range across the East Atlantic Flyway, from as far west as north-western Africa (Morocco) to east of the Ural Mountains (Russia) (Fig. 1). Stopover sites were located in all parts of the migration range (Fig. 1). Many stopover sites during spring migration were in the eastern part of the range, with a high proportion around the southern Baltic coast, the southern North Sea (including the Wadden Sea) and the Atlantic coast during autumn migration. This connectivity was also present, but less prominent, during spring migration. There was a significant relationship between wintering site latitude and breeding site latitude, with the latter increasing on average by approximately one degree for each increased degree in wintering latitude ($p < 0.001$; Fig. 2). This relationship clearly showed that the curlews performed chain migration. The spatial and temporal migration patterns of migrating individuals throughout the study sites are shown in Supporting information. While individuals tagged in northern Germany migrated in a broad front across the Baltic Sea and exclusively bred in western Russia (Supporting information), curlews tagged in the breeding colonies in southern and western Germany migrated to the Iberian Peninsula by crossing the Pyrenees (Supporting information). The majority of curlews tagged in

the wintering site of the French Atlantic coast followed the coastline of the southern North Sea and crossed the Baltic Sea in a similar way to the individuals tagged in northern Germany (Supporting information). Breeding curlews tagged in Estonia crossed the Baltic Sea and the southern North Sea and mainly wintered in the UK (Supporting information). Finally, about half of the breeding curlews tagged in Poland followed the southern Baltic Sea coastline and crossed the southern North Sea to winter in the UK or France while the other half of the curlews migrated across central Europe and mainly used the Iberian Peninsula as wintering grounds (Supporting information).

Both migration periods took around 10 days and were therefore very short (Fig. 3, Table 2). Overall, wintering accounted for the longest part of the annual cycle (average $75.83 \pm 5.2\%$ of total time). Curlews that bred farther south and west started their spring migrations approximately 50 days (seven weeks) earlier than individuals breeding farther north and east. However, all curlews left their breeding site for their autumn migration at roughly the same time, irrespective of their breeding latitude (mean: June 18 ± 10.76 days, range: 28 May–19 July). Consequently, curlews breeding farther south spent significantly more time at their breeding sites than curlews breeding farther north ($p < 0.001$; mean: 62.78 ± 18.68 days, range: 18.00–108.63 days; Fig. 4 and also see animation in Supporting information).

Effects of season, sex and breeding location on migration

Migration duration, distance flown, number of stopovers and mean stopover duration did not differ significantly between the two seasons (Table 2, 3; Supporting information), and

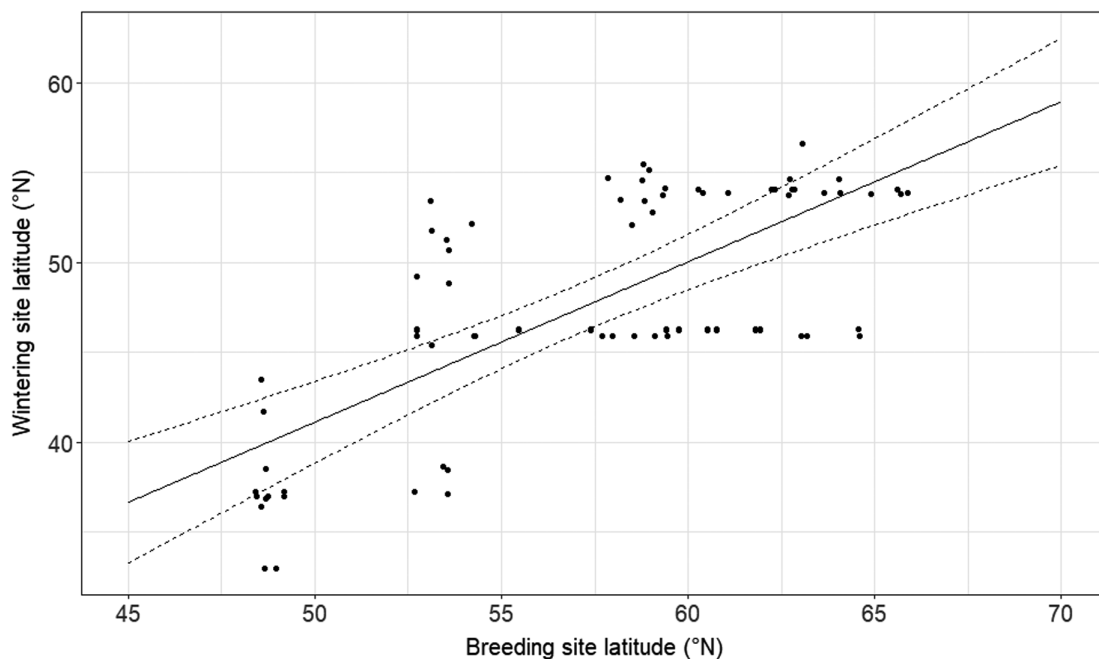


Figure 2. Relationship between wintering and breeding site latitudes. Solid line: model curve, dashed lines: 95% confidence intervals.

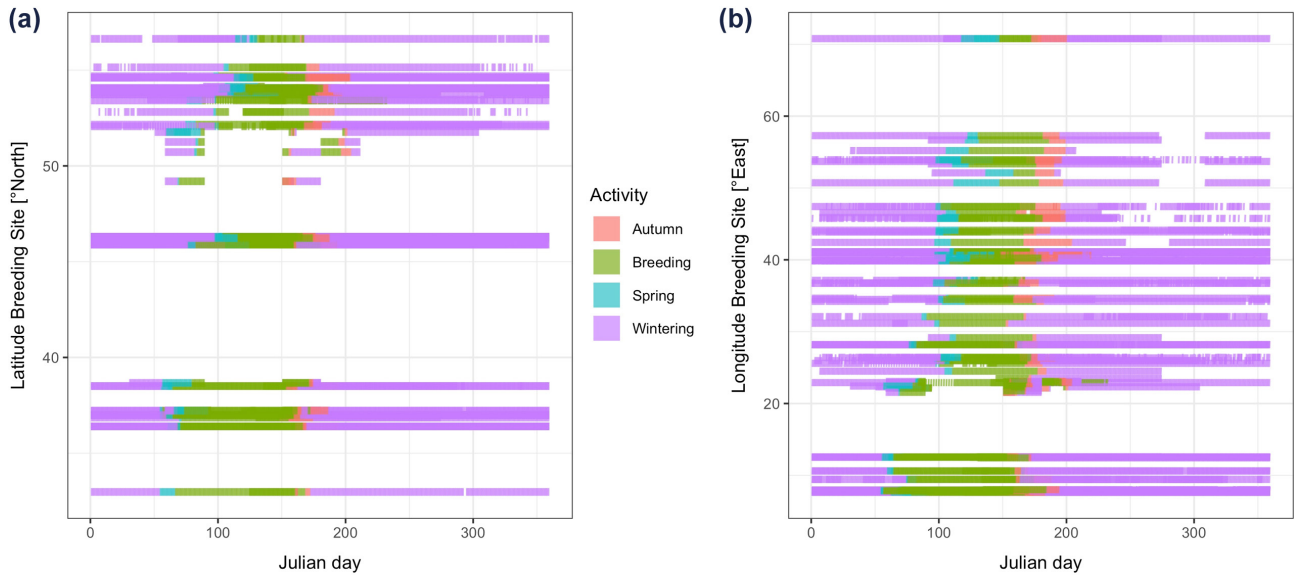


Figure 3. Phenology of annual cycle per individual ($n=85$) according to (a) breeding latitude and (b) breeding longitude.

between males and females (Table 3; Supporting information). In contrast, migration duration, distance flown and stopover number, but not mean stopover duration, showed significant positive linear relationships with breeding latitude (Fig. 5, Table 3). The ratio between distance flown and linear distance decreased significantly with increasing breeding site latitude (Fig. 5e).

The ratio of distance flown to linear distance was similar in the spring and autumn migrations (Supporting information). The distance flown exceeded the linear distance by $> 33\%$ during both migrations (flown distance exceeded linear distance by $38.0 \pm 10.8\%$ and by $37.1 \pm 11.0\%$ during spring and autumn migrations, respectively). The correlation between flown and linear distances was high in both seasons (both $p < 0.001$; Supporting information).

Spring migration-departure time did not differ significantly between the sexes ($p=0.876$, Fig. 6a); however, autumn migration-departure time did ($p=0.041$; Fig. 6b), with males staying at the breeding sites for an average of 3.83 days longer (females: mean 16 June ± 10.26 days, range 28 May–16 July; males: mean 20 June ± 11.08 days, range 28

May–19 July). However, there was no significant difference in departure times during spring migration (females: mean 5 April ± 18.57 days, range 25 February–5 May; males: mean 4 April ± 22.52 days, range 25 February–17 May). Spring departure dates from the wintering sites were positively and highly significantly related to breeding site latitude for both females and males (both $p < 0.001$), showing similar patterns (Fig. 7a). The same was true for autumn departure dates from breeding sites for both females ($p < 0.001$) and males ($p=0.012$), although this relationship showed broader confidence intervals as compared to spring departure date (Fig. 7b).

Discussion

Potential tag biases

It is important to look critically at potential time interval biases associated with the different tag types used. We accounted for those biases by correcting our data with GLMM predictions, which produced reliable overall values of migration parameters.

Table 2. Characteristics of spring and autumn migrations of tagged curlews. Data represent mean values, standard deviation and ranges.

	Spring			Autumn		
	n=82	Standard deviation	Range	n=95	Standard deviation	Range
Start date	April 4	20.5	25 Feb.–18 May	18 June	10.8	28 May–19 July
Midpoint	April 9	21.6	25 Feb.–28 May	23 June	11.5	29 May–20 July
End date	April 14	23.5	26 Feb.–7 June	29 June	14.1	31 May–24 July
Duration (days)	10.2	8.4	0.8–41.7	10.9	9.9	0.8–48.4
Linear distance (km)	2210	803	523–3906	2082	822	563–3910
Distance flown (km)	3623	1366	961–7423	3362	1351	810–7684
Number of stopovers	5.8	3.6	0.0–19.0	5.4	4.0	0.0–26.2
Stopover duration (days)	7.9	8.1	0.0–39.9	8.7	9.4	0.0–49.0*
Mean stopover duration (h)	29.4	38.2	0.0–290.5	31.8	32.3	0.0–164.9
Mean stopover duration (days)	1.2	1.6	0.0–12.1	1.3	1.3	0.0–6.9

*Due to correction of the calculations to account for tag bias, a few stopover durations were greater than the duration of the whole migration.

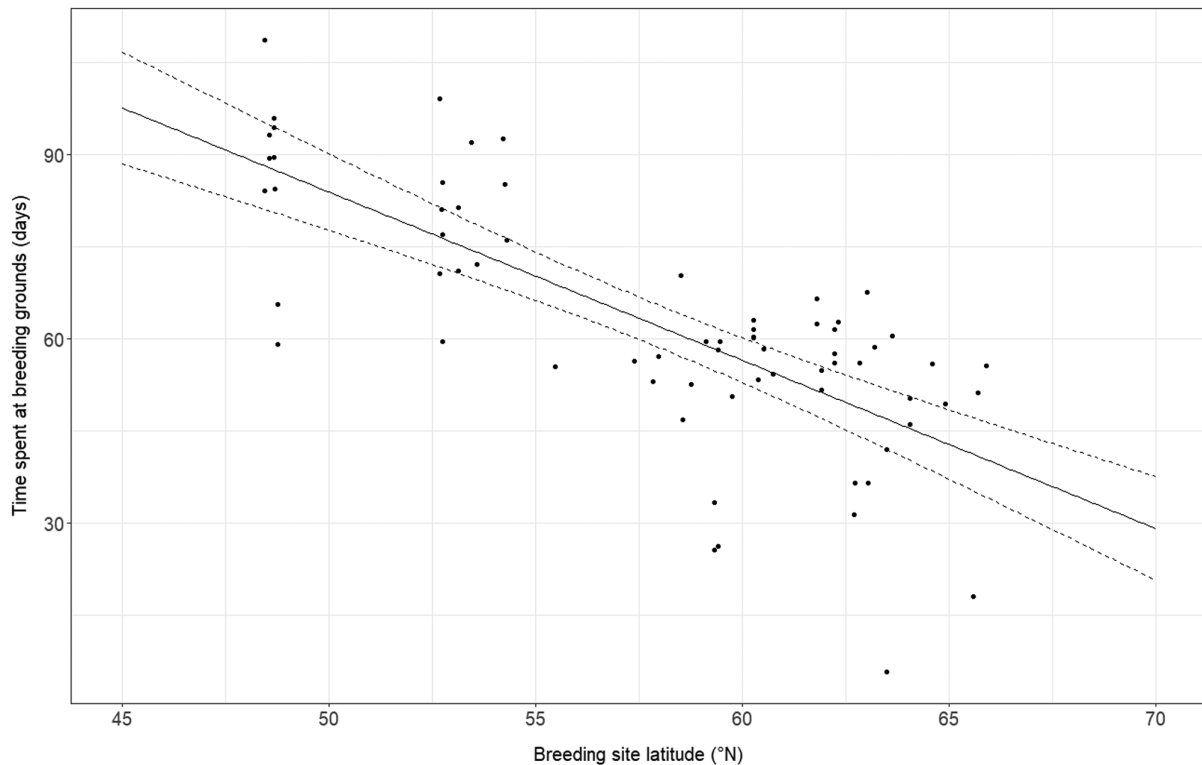


Figure 4. Relationship between time spent at breeding grounds (days) and breeding site latitude. Solid line: model curve, dashed lines: 95% confidence intervals.

However, this process led to outliers for some individuals, as seen in a few individuals for which the total stopover duration exceeded the overall migration duration. Using a threshold of 24 km h^{-1} to separate resting from flying may also have led to errors. Although this method was the best statistical solution, this algorithm mistook a series of GPS fixes in the curlews, and sometimes indicated that they were considered to be resting were actually flying, because they were travelling below the 24 km h^{-1} threshold, making these phases difficult to classify. However, such cases were rare and were therefore assumed to have no effect on our results and conclusions.

Spatial and temporal patterns of curlew migration

The results of this study showed that curlews exhibited chain migration throughout the East Atlantic Flyway, with individuals wintering at more southern latitudes breeding farther south, and individuals wintering at higher latitudes breeding farther north and east. Our results might be slightly biased due to site effects (for instance tagging multiple individuals within the large wintering area of the Wadden Sea where there is an increased chance of catching individuals from breeding sites in northern latitudes). However, recent unpublished data from curlews tagged in Finnish (Jiguet et al. unpubl.) and Russian (Schwemmer et al. unpubl.) breeding sites confirmed the chain migration pattern found in this study. Site effects are hard to be avoided in tagging studies. This is the first study that tried to minimize this potential bias by including multiple individuals of populations across the entire East Atlantic

Flyway. Furthermore, our findings are in agreement with observations and ring recoveries that suggest chain migration (Delany et al. 2009). Our GPS data showed that curlews along the East Atlantic Flyway migrated along a broad front across the whole of Europe. Although migration was channeled along the North Sea coast and across the Baltic, many tagged individuals chose inland routes and were able to fly over mountain ranges, such as the Alps and the Pyrenees.

Curlews also breeding further north showed a lower ratio between distance flown and linear distance, which suggest a straighter route for the birds with northern breeding latitudes. Our data also showed that curlews breeding at lower latitudes left their wintering sites approximately 50 days earlier than individuals breeding at higher latitudes, confirming previous findings for curlews wintering in northern Germany (Schwemmer et al. 2021). This is probably a consequence of the timing of favorable conditions at the breeding site, given that snowmelt starts later at higher latitudes and food resources will thus also be expected to be available later (Reneerkens et al. 2016, Saalfeld et al. 2019). Shorebirds that started breeding as early as possible are known to increase the chance of reproductive success, due to higher invertebrate availability (Saalfeld et al. 2019). Earlier breeding was also found to increase the chances of producing a second clutch, mainly among shorebirds with a failed first nest, but also allowing shorebirds to renest if the conditions were favorable (Gates et al. 2013) and particularly in lower latitudes where the breeding period is longer since all the curlews left their breeding sites around the same time (this study).

Table 3. Regression results of five migration parameters with respect to breeding site latitude, season (spring / autumn) and sex. Estim. std.: Estimated standard deviation.

	Duration of migration (days)			Distance flown (km)			Number of stopovers			Mean stopover duration (h)			Distance flown:linear distance							
	Estim. std.	Error	t-value	p-value	Estim. std.	Error	t-value	p-value	Estim. std.	Error	t-value	p-value	Estim. std.	Error	t-value	p-value				
Breeding site latitude	0.05	0.02	3.36	< 0.001	0.02	0.01	2.84	0.005	0.04	0.01	3.65	< 0.001	0.028	0.02	1.69	0.092	-0.01	0.00	-3.08	0.003
Spring/autumn	-0.16	0.12	-1.38	0.17	0.00	0.03	-0.08	0.931	0.01	0.08	0.10	0.927	-0.17	0.14	-1.20	0.229	0.03	0.02	1.1	0.271
Sex	0.23	0.16	1.40	0.163	0.11	0.09	1.18	0.240	0.12	0.12	0.99	0.320	0.04	0.18	0.40	0.689	0.02	0.04	0.55	0.586
R ²	0.27			0.80	0.37				0.10								0.38			

Differences between spring and autumn migrations

In theoretical and empirical findings, the duration of spring migration is shorter than that of autumn migration in some migrating bird species (Kokko 1999, Nilsson et al. 2013). Birds are also under pressure to reproduce within a short period of time and have to optimize their migration through time, fuel and risk, especially considering the shorter time frame for birds breeding at higher latitudes (Marcström and Mascher 1979, Alerstam and Lindström 1990, Kokko 1999). In black-tailed godwits *Limosa limosa limosa*, Senner et al. (2019) found that spring migration was shorter than autumn both within individuals and across populations over multiple years. In contrast, our study revealed no significant differences in migration duration, distance flown, number of stopovers and mean stopover duration between the spring and autumn migrations of our overall dataset. Also including an interaction term between season and breeding site latitude led to insignificant results in all of the four outcome variables. However, speed and duration of migration are not necessarily the primary factors for indicating time constraints or migratory strategies that the birds display, environmental factors are key as well: The Icelandic whimbrels *Numenius phaeopus islandicus* had a faster autumn migration than spring migration (Carneiro et al. 2019). The authors suggest that unfavorable wind patterns during spring migration could have caused the birds to stop more during spring. It is also theorized that the birds stopped more just before arriving to their breeding site to increase their reserves (Carneiro et al. 2019). The white-fronted goose *Anser albifrons* also showed a faster autumn migration than spring migration, even though their speeds were similar. This difference seemed to be due to the fact that these geese follow the green wave of spring growth that influence their timing for spring (Kölzsch et al. 2016).

Curlews are known to demonstrate high rates of mate and territory fidelity (Cramp et al. 1983, Berg 1994, Currie et al. 2001, Brown 2015). This includes high faithfulness to their wintering sites, as shown by tracking the same individuals over multiple years and by ringing studies (Delany et al. 2009, Brown 2015, Sanders and Rees 2018, see also Schwemmer et al. 2021 for a tagging study on curlews wintering in northern Germany). The northern German curlews tagged for this study tended to forage recurrently in the same places on the mudflats in the Wadden Sea (Schwemmer et al. unpubl.). It is therefore likely that the curlews might need to return quickly in autumn to defend their winter foraging sites and to decrease intraspecific and interspecific competition (the latter has been found in gulls before; Ens et al. 1990), especially given that the birds spend the largest proportion of their life cycle in the wintering grounds (Alerstam 1990, this study). This is in agreement with Cotter (1990) who found that curlews feeding on mudflats formed fixed territories of up to 1 hectare in size (in contrast to individuals that feed inland). However, Townshend (1981) implies that also bill biometry and food availability drive the habitat selection in curlews and that intraspecific and interspecific interactions are not the cause of movement between habitats. Multiple

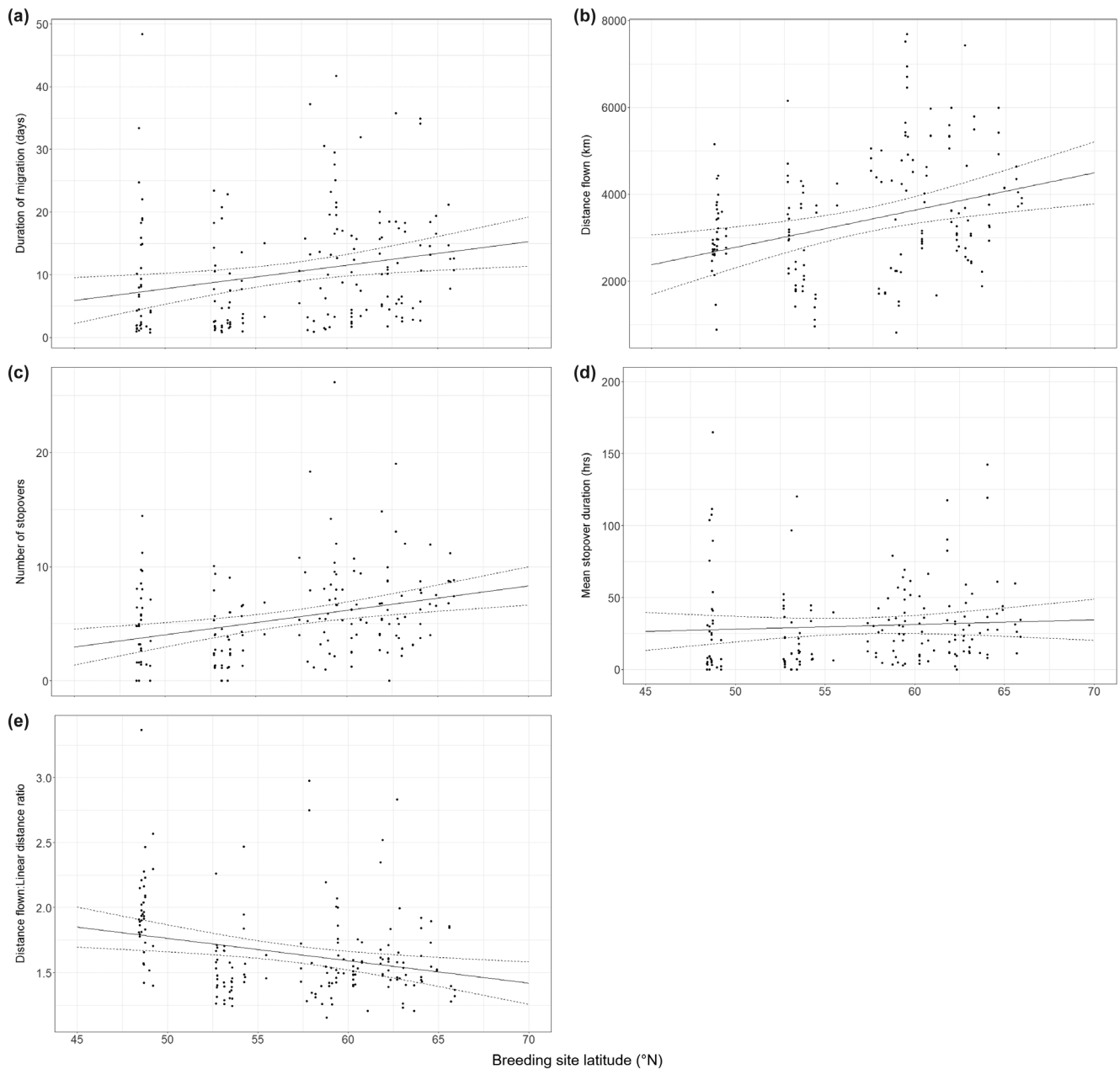


Figure 5. Relationship between breeding site latitude and (a) duration of migration (days); (b) distance flown (km); (c) number of stopovers; (d) mean stopover duration (h); and (e) ratio of distance flown and linear distance. Solid line: model curve, dashed lines: 95% confidence intervals.

studies have shown that curlews with shorter bill size tend to feed predominately in pastures, while birds with longer bill sizes feed on mudflats (Cramp et al. 1983).

As curlews are known to start the molt of their flight feathers already from June to July onwards (Bauer et al. 2005), likely affecting their ability to migrate long distances, an early and short autumn migration can be the consequence. Even though environmental factors were not looked at for this study, the similar migration duration, distance flown, number of stopovers, and mean stopover duration for spring and autumn migration can be the result of similar weather

conditions during spring and autumn. This can also be seen with the similarity in the higher distance flown compared to linear distance in spring and autumn migration, where the higher distance flown shows that a less direct route was taken, which could be due to environmental factors like wind patterns. However, a recent study on GPS-tagged curlews revealed a high repeatability of migration timing for individuals that were tracked in consecutive years, whereas meteorological factors were largely ignored suggesting a high importance of genetic triggers in curlew migration (Schwemmer et al. 2021).

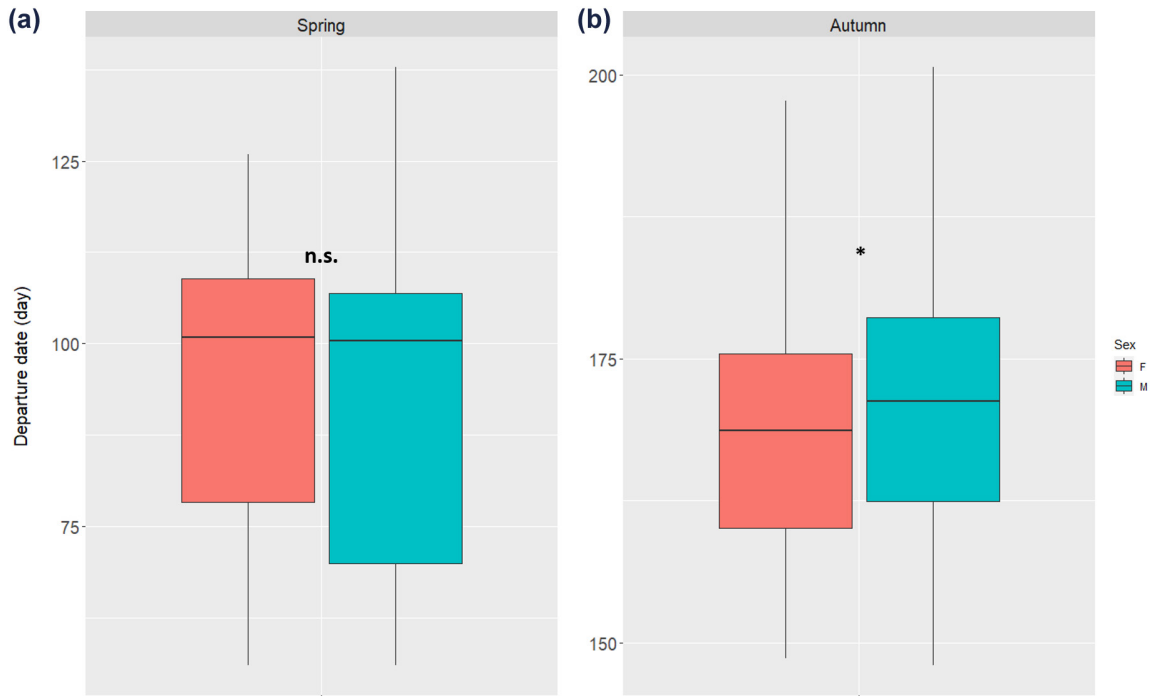


Figure 6. Boxplots of departure dates for female (pink) and male (blue) curlews for the overall dataset. Bold line is the median and the lines extended from the box are the lower and upper quartiles. Departure dates for (a) spring and (b) autumn migration * $p < 0.05$.

Sex-related differences in migration

Our results showed that females left their breeding sites earlier than males, which is in line with previous studies on curlews (Currie et al. 2001, Krupa et al. 2009, Sanders and Rees 2018). There are several hypotheses why females might leave breeding sites earlier than males: 1) Females may be physiologically less able to care for the chicks than males, since the female have higher energy costs due to producing the eggs (Ashkenazie and Safriel 1979, Lenington 1980, Brunton 1988, Gratto-Trevor 1991). Males also showed more aggression before the females left, suggesting that the males could protect the older chicks alone (Currie et al. 2001). However, given the larger body size of female compared with male

curlews, this explanation seems unlikely. It has also been seen in other shorebirds that males spend more time defending their territories than females (Brunton 1988). 2) Several studies found that leaving the breeding site earlier could increase success in future years (Lenington 1984, Jönsson and Alerstam 1990, Székely and Williams 1994). This could explain their haste to return to their wintering sites, which are more food-rich than the breeding sites and birds usually have a reliable knowledge on food availability; early return to the wintering sites could thus increase their likelihood of survival (Alerstam 1990). 3) Finally, the departure decision may be linked to reproductive failure, which we were not able to estimate, with failed breeders returning to their wintering sites earlier. However, this would be likely to cause both

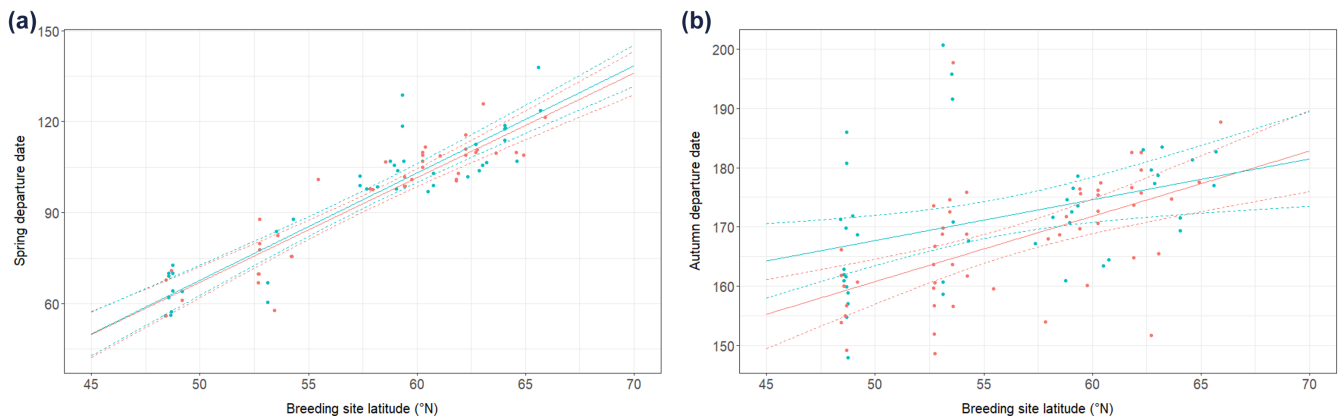


Figure 7. Relationship between breeding site latitude and departure dates for female (pink) and male (blue) curlews for (a) spring and (b) autumn migrations. Solid blue and red lines: model curve, dashed lines: 95% confidence intervals.

members of the affected pairs to depart their breeding sites earlier, rather than just the females. In addition, if the birds breed early enough, there is a good chance that they could try for a replacement clutch if the first one fails (Currie et al. 2001, Verhoeven et al. 2020).

Currie et al. (2001) found that female curlews at northern breeding latitudes deserted their offspring earlier relative to chick age than females at southern latitudes. It is also suggested that at northern latitudes timing of desertion varies due to migratory distance and shorter breeding season. Our results showed that curlew females at lower latitudes left their breeding sites earlier than females at higher latitudes. However, our study only looked at the departure date from the breeding site. This did not take into account the chicks age at time of departure. So, the southern curlews may desert earlier due to being able to breed earlier. It was also shown that females spent more time with broods that hatched earlier, which is a tradeoff for individuals that breed later (Currie et al. 2001).

Outlook and significance of cooperative tracking studies

The current study was able to shed light on spatio-temporal migration patterns of a species of concern along major parts of the East Atlantic Flyway using a large dataset. Therefore, it provides a good example of how the combination of different international telemetry data can help to fill important gaps on the movement ecology of migrating species. The study was a cooperative project conducted throughout Europe with an international consortium of research laboratories and nature associations, which may help to protect the species by involving multiple countries. The extensive cooperation from different organizations means that the current study included one of the largest high resolution migration datasets available among all shorebirds, as well as covering a long timeframe. The study was thus able to create a better overall picture by building on preliminary studies (Schwemmer et al. 2016, 2021) and providing data to fill gaps in our knowledge about the migratory behavior of curlews. The current dataset will also be suitable for the study of inter-individual variability of migration as well as habitat choice within the breeding and wintering habitats, which will hopefully contribute to a better understanding of the life cycle of this long-distance migrant.

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Data availability statement

Data is available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.nk98sf7w6>> (Pederson et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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