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Assessing potential conflicts between offshore wind farms and migration patterns of a threatened shorebird species

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Abstract

Installation of offshore wind farms (OWFs) is becoming increasingly important to ensure a reduction in greenhouse gas emissions; however, OWFs also pose a threat to migrating birds and other wildlife. Informed marine spatial planning is therefore crucial, but individual-based high-resolution data on bird migration across the sea are currently lacking. We equipped 51 individuals of the near threatened Eurasian curlew *Numenius arquata* with GPS tags (118 flight tracks) across multiple years and countries to assess their four-dimensional migration routes across the Baltic Sea (i.e. flight tracks, altitudes, phenology and diurnal patterns), to inform collision-risk models and assess potential conflicts with current and future OWFs. Despite a broad-front migration, we identified core migration areas in the south-western Baltic Sea (and adjacent mainland), largely overlapping with already operating OWFs. Generalized linear models based on a resampling procedure to overcome autocorrelation of tracking data showed that flight altitudes across the sea and during autumn (median: 60 m) were significantly lower than those across land (median: 335 m) and during spring (median across sea: 150; median across land: 576 m). Across the sea, curlews spent 74.8% and 62.2% of their migration times below 300 m during autumn and spring, respectively, indicating a potentially high collision risk with OWFs. The mean flight speed was 56.3 km/h (±20.3 km/h). Migration intensity was highest at night over a 10-day period during April, suggesting that restricted turbine operation for several days might be a possible management measure. Our study showed that, even for broad-front migrants, it is possible to identify particularly sensitive sea areas deserving special protection enabling a sound marine spatial planning. This is a crucial finding also for various other shorebirds on the East Atlantic Flyway. Further studies are needed to assess the behavioural reactions of migrating birds with respect to OWFs using high-resolution tracking data.

Introduction

Wind energy is the largest contributor and driving force behind the clean-energy transition. Major accelerations in the development of onshore and offshore wind installations in Europe are therefore currently underway (European Commission, 2021), and most EU member states plan to substantially increase their offshore wind energy generation (Henderson *et al.*, 2003; 4C Offshore, 2021). The Baltic Sea currently (2022) has an installed capacity of nearly 3 GW generated by a total of 717 wind turbines, mostly located in the south-west (mainly Germany and Denmark; Helcom, 2021; 4C Offshore, 2021; Zhang *et al.*, 2021; Supporting Information Figure S1, Supporting Information Tables S1 and S2). However, there are plans to significantly extend the installation of offshore wind farms (OWFs) throughout the

Baltic Sea in the near future, from 417.7 km^2 to >27 000 km^2 (Rusu, 2020; 4C Offshore, 2021; Supporting Information Figure S1, Supporting Information Table S1).

Renewable energy installations usually occupy large areas, with profound effects on landscapes, potentially leading to habitat loss for a high number of species, including some endangered ones (Segan, Murray, & Watson, 2016; Pratiwi & Juerges, 2020), and are often at odds with protecting biodiversity (Gasparatos *et al.*, 2017). Informed spatial planning is therefore crucial for resolving this dilemma.

The installation of OWFs has been identified as a threat to birds (Fox & Petersen, 2019), through habitat loss for resting and foraging species (e.g. Mendel *et al.*, 2019; Mercker *et al.*, 2021*b*) and impacts on migrating birds (Hüppop *et al.*, 2006; Brabant *et al.*, 2015). Collision-risk models for migrating birds are an essential tool to inform spatial planning (e.g. Brabant *et al.*, 2015); however empirical collision-risk models often lack precise spatial and temporal bird-migration data (Kleyheeg-Hartman *et al.*, 2018). There is thus an urgent need for more information on locations of migration tracks as well as flight direction and speed (1st and 2nd dimensions of bird migration) and flight altitudes (3rd dimension), which have been shown to be crucial for assessing collision risks (Furness, Wade, & Masden, 2013; Khosravifard *et al.*, 2020). More data are also needed on temporal patterns such as seasonal differences in migration patterns, including phenology and diurnal differences in migration intensity (4th dimension; Lindström *et al.*, 2021). Information on flight speeds (Masden *et al.*, 2021) and potential behavioural responses to anthropogenic structures (Schaub *et al.*, 2020) are ultimately essential for accurate collision-risk analysis. All these parameters can be recorded using high-resolution miniaturized Global Positioning System (GPS) devices.

The Eurasian curlew *Numenius arquata arquata*; hereafter curlew is a near-threatened shorebird species due to large-scale and long-term population declines across the whole East Atlantic Flyway (Delany *et al.*, 2009; van Roomen *et al.*, 2019; BirdLife International, 2022). We therefore collected the above data at high temporal and spatial resolutions for curlews as a model species, and compiled an extensive tracking dataset using data from four countries collected over four consecutive years. Curlews reportedly show a broad migration front in the Baltic Sea (Schwemmer *et al.*, 2021); however, it is easier to inform marine spatial planning (and take appropriate measures) if distinct bird-migration corridors can be identified (e.g. Oloo, Safi, & Aryal, 2018; Pearse *et al.*, 2018). We hypothesized that sea areas with high migration intensity could be identified based on a large number of flight tracks recorded at high spatial and temporal resolutions. Although breeding curlews avoid interactions with onshore wind farms (Pearce-Higgins *et al.*, 2009), migrating curlews have been reported to be threatened by coastal wind farms (Jiguet *et al.*, 2021). Furthermore, Leopold *et al.* (2015), ranked curlews among the most-threatened migrating birds with respect to collision risk with OWFs, with expected strong negative population effects. Potential interactions with OWFs are thus likely to increase the overall threat to this declining shorebird species.

High-resolution tracking data are associated with the problem of severe temporal and spatial autocorrelation (Mercker *et al.*, 2021*a*). We therefore developed a statistical approach based on a resampling procedure of thinned data to overcome these problems. Using this statistical approach, we examined differences in flight altitudes and flight speeds of migrating curlews between spring and autumn seasons, diurnal and nocturnal flights and marine areas and land masses.

This study aimed to analyse four-dimensional high-resolution spatio-temporal data on curlew-migration patterns in relation to OWFs in the Baltic Sea. In addition to generating basic data for collision-risk models and developing a novel statistical approach for analysing autocorrelated tracking data, the study aimed to directly inform management by identifying migration hot-spots, assessing overlap with OWFs (with respect to spatial distribution of flight tracks and flight altitude) and revealing temporal aspects of migration, such as periods with the highest migration intensity throughout the year (phenology) and diurnal patterns.

This information is crucial to inform spatial planning regarding the suitability of planned OWF sites, and for identifying potential time periods for restricted turbine operation during the critical phases of migration as a possible mitigation measure (Marques *et al.*, 2014).

Materials and methods

Study area and telemetry

Flight paths, altitudes and timing of migration were investigated across the Baltic Sea and adjacent mainland in an area south of 66° N, north of 53° N, east of 8.5° E and west of 35° E (rectangle in Fig. 1).

In a study by Pederson *et al.* (2022), a total of 85 curlews were equipped with solar-powered Global Positioning System (GPS) Global System for Mobile Communications (GSM) data loggers to assess their general migration patterns along the East Atlantic Flyway. For the current study, we selected a subset of n = 51 individuals from this dataset which had recorded data at sufficiently high temporal resolution to allow for accurate altitude measurements (Poessel *et al.*, 2018, Péron *et al.*, 2020; Schwemmer *et al.*, 2021; see below) and which at the same time crossed our study area. These birds were equipped with GPS-GSM data loggers (Ornitela, Lithuania) weighing 10 g (n = 24), 15 g (n = 22) or 20 g (n = 5) respectively. The devices recorded time (UTC), geographical position, speed (m/s), acceleration (m/s^2) and flight altitude (metres above sea level). Data transfer was enabled via GSM connection and the data stored in the online portal Movebank (Kays *et al.*, 2021).

Curlews were tagged from 2018 to 2021 in four different countries: Germany (Wadden Sea; n = 23), France (Atlantic coast; n = 14), Estonia (n = 6) and Finland (n = 8) (Fig. 1). Curlews were either caught with mist nets at coastal high tide roosts during winter (Germany and France), or with walk-in traps on nests (Estonia, Finland). The GPS data loggers used in Germany and Estonia were attached by breast harnesses (Guillaumet *et al.*, 2011), while leg-loop harnesses

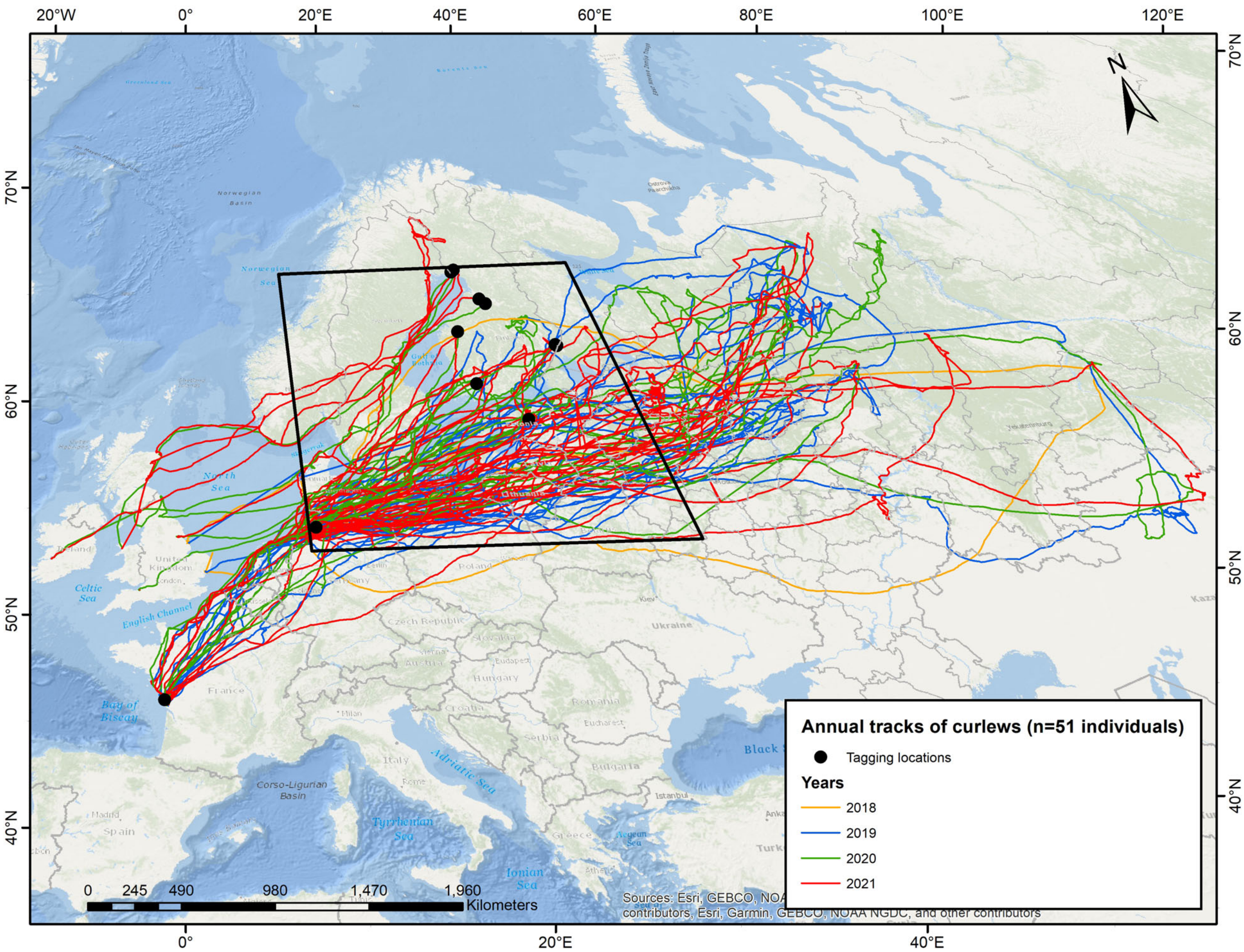

Figure 1 Flight tracks of 51 Eurasian Curlews equipped with GPS data loggers from 2018 to 2021 at different tagging locations (black dots). Black polygon indicates the study area.

were used in the other tagging locations (Mallory & Gilbert, 2008). Both harnesses were made of Teflon ribbon and silicone elastic tube (diameter 2.1 mm; Reichelt Chemietechnik GmbH, Germany). None of the tags were > 4% of the bird's body weight (Phillips, Xavier, & Croxall, 2003). All individuals were ringed and biometrics (bill and wing length) were recorded to the nearest mm. Sex was determined using genetic markers (Tauros Diagnostics, Berlin, Germany) or biometry (Summers *et al*., 2013). Age was classified according to plumage characteristics following Prater, Marchant, & Vuorinen (1977).

Altogether there were 20 females and 30 males tagged (the sex could not be determined in one individual), including 37 adult and 14 first-year birds. We recorded a total of 118 tracks from the 51 birds across the study area, including 106 517 GPS fixes (n = 57 tracks and n = 46 933 fixes during spring migration; n = 61 tracks and n = 59 584 fixes during autumn migration; see Table 1 for details of numbers equipped and fixes per individual among the years, seasons and capture locations).

Programming of tags and recordings of flight altitudes

To record high-resolution four-dimensional migration patterns of curlews crossing the Baltic Sea region, we programmed a so-called 'geofence' covering the study area. When a curlew entered this defined area, the attached device started recording data at very high temporal resolution (1–5 min, depending on battery charge). However, this schedule drained the battery quickly and could therefore not be maintained all year round. This high temporal resolution allowed us to track the birds precisely and to estimate overlaps between the flight tracks and the existing OWFs in the Baltic Sea. GPS-based altitude measurements are known to involve a certain stochasticity, the magnitude of the scatter around the true altitude value being strongly associated with the logging interval of the devices (i.e. coarser schedules produce a higher degree of uncertainty compared to high-resolution schedules in terms of both positive and negative divergence from the true value; Poessel *et al*., 2018; Péron *et al*., 2020;

Table 1 Number of GPS fixes (and number of individual Eurasian Curlews) per season, year and catching country

	Spring				Autumn			
Year	Germany	France	Estonia	Finland	Germany	France	Estonia	Finland
2018	1010 (2)	0	0	0	660 (1)	0	2401 (2)	0
2019	11 113 (10)	4824 (6)	335 (1)	0	14 191 (8)	4450 (5)	1108 (1)	0
2020	7642 (8)	898 (4)	1575 (1)	0	9943 (6)	1310 (4)	1527 (2)	2094 (7)
2021	16 843 (15)	1442 (6)	0	1251 (4)	16 550 (13)	1357 (5)	2857 (3)	1136 (4)
Sum	36 608 (35)	7164 (16)	1919 (2)	1251 (4)	41 344 (28)	7117 (14)	7893 (8)	3230 (11)

Only GPS schedules with a temporal resolution ≤5 min were used.

Schwemmer *et al.*, 2021; Ornitela pers. com.). In accordance with Schwemmer *et al.* (2021), we therefore excluded all migration tracks of curlews with fix intervals >5 min (Table 1). A comparison of the GPS-based altitude recordings with altimeter recordings from an airplane flying at different heights revealed a mean non-systematic error of ±55 (calibration done for the study by Schwemmer *et al.*, 2021). Outliers are a common phenomenon in GPS altitude recordings and rely on the dilution of precision (DOP; relative value that estimates the bias of the GPS fix according to the number of satellites and their positions relative to the GPS device; Theobald, 2007). We therefore scanned the whole dataset for inconsistencies in flight-altitude records. Altitude values with a difference of >500 m between consecutive fixes within 5 min and a high DOP were excluded, accounting for 497 fixes (0.46% of all recorded data). Due to the known non-systematic error of GPS-based altitude recordings that scatters above and below the true value, tags of curlews flying very low above the water surface may show negative altitude values (Poessel *et al.*, 2018; Péron *et al.*, 2020). In the case of our dataset, 9139 negative values (8.6% of the overall dataset) were included, ranging from −244 m to −1 m. Based on the median (−11 m), these values were strongly right-skewed and large negative values were the exception. In accordance with Péron *et al.* (2020), we did not exclude these negative values because this would have significantly reduced low-altitude records, resulting in a bias towards higher flight altitudes. We therefore used the median rather than the mean flight altitudes.

Home ranges

We identified areas with different migration intensities across the Baltic Sea (and adjacent mainland) by computing home ranges (i.e. 25, 50, 75 and 95 utilization distributions (UDs)) of the flight tracks (excluding stop-over positions) using the R package 'adehabitatHR' (Calenge, 2006). Prior to home-range analyses, we excluded all data from stop-over locations of curlews by exploring each migration track in the GIS, that is only in-flight fixes were included, to ensure that home ranges were only computed for active migration tracks. Differences in some of the GPS tracking schedules led to different fix resolutions (i.e. between 1 and 5 min according to battery charge), and we therefore interpolated tracks between different stop-over sites to 1-min intervals using the R package 'sula' (Lerma, 2021). Finally, the home ranges were visualized to identify hot spots of spring and autumn migrations, and flight altitudes of <250 m and ≥250 m to separate fixes on and above turbine level respectively.

Data analyses and statistics

Flight tracks and altitudes were plotted on maps using ArcGIS (version 10.3; Environmental Systems Research Institute (ESRI), 2011). All other analyses were carried out using R (Version 3.5.3; R Development Core Team, 2021). Each in-flight GPS position was assigned as recorded over either sea or land using the R package 'spData' (Bivand *et al.*, 2021) and R package 'sf' (Pebesma, 2018), and from morning to evening civil twilight ('day') or from evening to morning civil twilight ('night') using the R package 'suncalc' (Thieurmel & Elmarhraoui, 2019). We then tested if flight altitude differed between spring and autumn, between day and night and across land and sea using generalized linear mixed models (GLMMs; Zuur, Leno, & Saveliev, 2017; Korner-Nievergelt *et al.*, 2015), with bird ID as a random factor.

The current study aimed to use all the available information to produce a dataset with high temporal and spatial resolution, including even small-scale behaviours, such as sudden adjustments in flight altitude when the birds crossed from sea to land. We therefore did not conduct simple thinning out, pooling or smoothing of the data (as often found in telemetric studies of flight altitudes; e.g. Poessel *et al.*, 2018), but instead applied a combination of thinning and resampling to account for spatial and temporal autocorrelation of the high-resolution tracking data. The main aim was to reduce autocorrelation by temporally thinning the data before applying regression methods, to repeat this process several times with the newly generated thinned data-resamples, and eventually to jointly analyse the regression results from all the resamples. We initially created 2000 thinned resamples of the original data. For each resample, we randomly chose a tracking point within each available individual/date/hour combination. Each resample was then used to fit two regression models, a negative-binomial and a Tweedie distribution, using the log-linear predictors 'land' (1 = flight across mainland, 0 = flight across the sea), 'day' (1 = day, 0 = night) and 'season' (1 = spring vs. 2 = autumn). The Tweedie-distribution is an alternative probability distribution to the negative binomial distribution in order to describe possibly overdispersed count data, and it performs particularly well if the mean count data values are close to zero (Kokonendji *et al.*, 2004*a*,*b*). The variable 'year' of the migration track was also considered as a factor variable, and curlew ID as a random intercept. Finally, third-order temporal autocorrelation was considered on the predictor scale as a Markov process (Mercker *et al.*, 2020). A GLMM with a temporal autocorrelation structure was thus applied to the data. Based on the Akaike Information Criterion (Akaike, 1973), we selected the most appropriate model with respect to the two above probability distributions. Finally, based on the selected model, a random normal resample was drawn for each regression coefficient (on the linear scale), using the estimated regression coefficient as the mean value and the estimated standard error as the standard deviation (SD). The latter process thus reflected the uncertainty in the regression coefficient estimate from the regression model itself, whereas the variability in regression results between the models applied to the different data resamples reflected the uncertainties with respect to the (random) thinning. Based on a total of 2000 regression coefficient resamples (comprising the two above-mentioned sources of uncertainties), the final results were calculated based on the appropriate quantiles. The same statistical procedure was applied to test for differences in flight speeds between sea/land, day/night and autumn/spring.

Flight-altitude data were used to compute the relative time that migrating curlews spent at turbine level. The collision risk of birds with OWFs is highest at the rotor level (the tallest turbine currently installed has an overall height of 188 m); however, the rotors may extend down to 20 m above sea level (Iberdrola, 2021; Vattenfall, 2021). In light of different rotor diameters among turbine types and the measuring inaccuracies of the GPS devices, we presented different scenarios of proportional overlap between flight altitudes and turbines for turbine heights of <150 – <300 m (the latter being the projected height of future turbines; Vattenfall, 2021), both for the entire turbine (i.e. starting at water level) and for the rotor (i.e. excluding data <20 m).

In addition to migration maps (1st and 2nd dimensions) and the altitude distribution (3rd dimension), we also assessed the temporal pattern of curlew migration on three different time scales (4th dimension). We aimed to detect seasonal differences in migration intensity across the Baltic Sea by comparing the proportion of time the birds spent migrating across the sea during each crossing of the study area between autumn and spring, using linear mixed-effect models (Venables & Ripley, 2002). We also examined seasonal peaks of migration intensity across the Baltic Sea by summing the number of actively migrating curlews for each day, and summing the number of these migration days for every 5 days (pentad). We then computed the relative values on the total of 116 bird-migration days for spring and 137 bird-migration days for autumn for each pentad. Furthermore, we assessed the diurnal patterns of migration across the Baltic Sea by summing the time curlews spent migrating across the sea for each hour of the day during spring and autumn migration respectively. We then calculated the total time of migration across the sea for each track. We finally computed the relative time spent migrating across the sea for each hour of the day and eventually calculated the mean values and SDs of all tracks within each hour, for spring and autumn migration separately. Tracks with <100 GPS fixes at sea were excluded because the time spent over the sea was considered too low to compute mean values. This resulted in the total of 47 tracks for spring migration and 38 for autumn migration.

Results

Migration patterns across the Baltic Sea

Curlews showed a broad migration front across the whole Baltic Sea (Fig. 1). Migration patterns of most individuals tagged at the French Atlantic coast tended to be channelled across the northern inland France or along the English Channel and southern North Sea coast; however, after staging in the Wadden Sea area, those individuals continued their migration in a broad front across the Baltic Sea, as did the birds caught at the other tagging locations (Fig. 1). Only seven tracks (5.9%) crossed the mainland without a marine passage.

Although the single tracks suggested an unfocussed broad-front migration across the Baltic Sea (Fig. 2), home-range analyses revealed the most intensive migration along the southern and western Baltic Sea coasts, particularly during autumn migration (Fig. 3a and b), as well as the adjacent mainland area in the coastal parts of Germany, Poland and the Baltic states (Supporting Information Figure S2). There was considerable overlap between curlew tracks and operating OWFs in the western part of the Baltic Sea (Fig. 2), and most wind turbines, 717 in total currently installed in the whole Baltic Sea, were located in the core curlew-migration area (i.e. within the 25% or 50% UDs) during spring migration and for birds migrating at altitudes <250 m (Table 2; Fig. 3). Key core curlew migration areas were located in the southern Baltic Sea in a strip from northern Germany to the Baltic states during autumn (Fig. 3a), but this area shifted towards the western part of the Baltic and to more offshore zones during spring (Fig. 3b). Core migration areas of altitudes <250 m were located in the southern Baltic Sea (Fig. 3c), whereas altitudes ≥250 m occurred infrequently and mainly in the western Baltic Sea between northern Germany, Denmark and southern Sweden (Fig. 3d).

Flight altitudes

Curlews migrated across the Baltic Sea at significantly lower altitudes than across the adjacent mainland (Fig. 2; Table 3). The GLMMs showed that the average flight altitude increased by 31% (95% confidence interval (CI): 26%–35%) from sea to land (Table 3; Figs. 2 and 4). Furthermore, the average flight altitude increased by 9% during spring compared with autumn (CI: 6%–13%; Table 3; Fig. 4). In contrast, there was no significant difference in average flight altitudes between day and night (Table 3).

Flight altitudes were lowest during autumn and across the sea (median: 60 m; SD: 604 m; maximum: 4350 m). Between 64.5% and 74.8% of migrating time was spent at

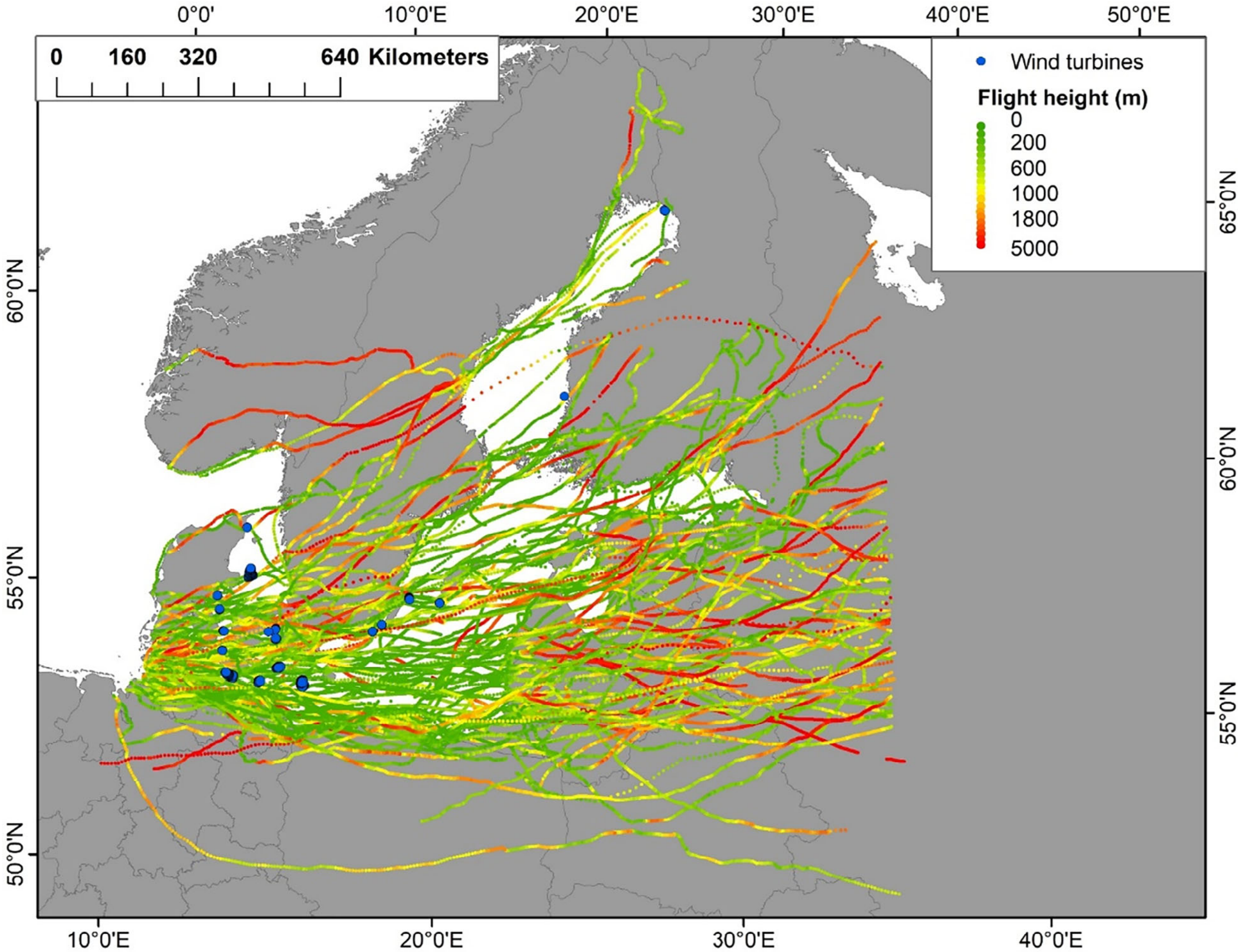

Figure 2 Total of 118 tracks from 51 Eurasian Curlews tagged between 2018 and 2021. Different colours represent different flight altitudes. Blue dots indicate operating offshore wind farms.

potentially risky heights, between the water surface and 300 m; however, these proportions were reduced to 27%–37.3% after excluding heights below the rotors (Table 4). The median flight altitude during spring and across the sea was 150 m (SD: 652 m; maximum: 3763 m) and 50%–62.2% of time was spent migrating at <300 m (22%–34.2%, excluding below-rotor heights; Table 4).

In contrast, the median flight altitude during autumn and across the land was 335 m (SD: 1154 m; maximum: 5742 m) and only 25.6%–46.8% of migration time was spent <300 m (Table 4). Flight altitudes were highest during spring and across the land, with a median altitude of 576 m (SD: 809 m; maximum: 4815 m), and only 15.7%–31.3% of time was spent at <300 m (Table 4).

Temporal patterns

There was no significant difference in the proportion of time that curlews spent migrating over the Baltic Sea between spring and autumn migration (linear mixed-effect model: $\chi^2 = 2.36$, d.f. = 1, $P = 0.124$; Fig. 5).

Migration intensity across the sea peaked from the 16th to 25th of April, which included 59% of all spring migration days (Fig. 6). In contrast, the main time-window during autumn migration was about three times longer, covering 4 weeks from mid-June to mid-July (Fig. 6).

Migration across the sea showed distinct diurnal patterns during spring and autumn (Fig. 7). During both periods, migration intensity was highest during the evening and at night, with a second peak during early morning in spring and from 10:00 to 12:00 (UTC) in autumn. The overall mean flight speed was 56.3 km/h (SD: 8 km/h; range: 5–182 km/h) and the frequency distribution was slightly right-skewed showing a range of comparably high speed values, particularly during spring (Supporting Information Figure S3). According to the GLMs, flight speeds were significantly higher during spring (mean: 60.9 ± 23.1 km/h) than during autumn migration (mean: 52.7 ± 16.8 km/h) (Table 5). Curlews flew slightly but significantly faster at night (mean: 57.4 ± 22.0 km/h) than during the day (mean: 55.87 ± 19.5 km/h). In contrast, there was no significant difference in flight speeds between sea and land (Table 5).

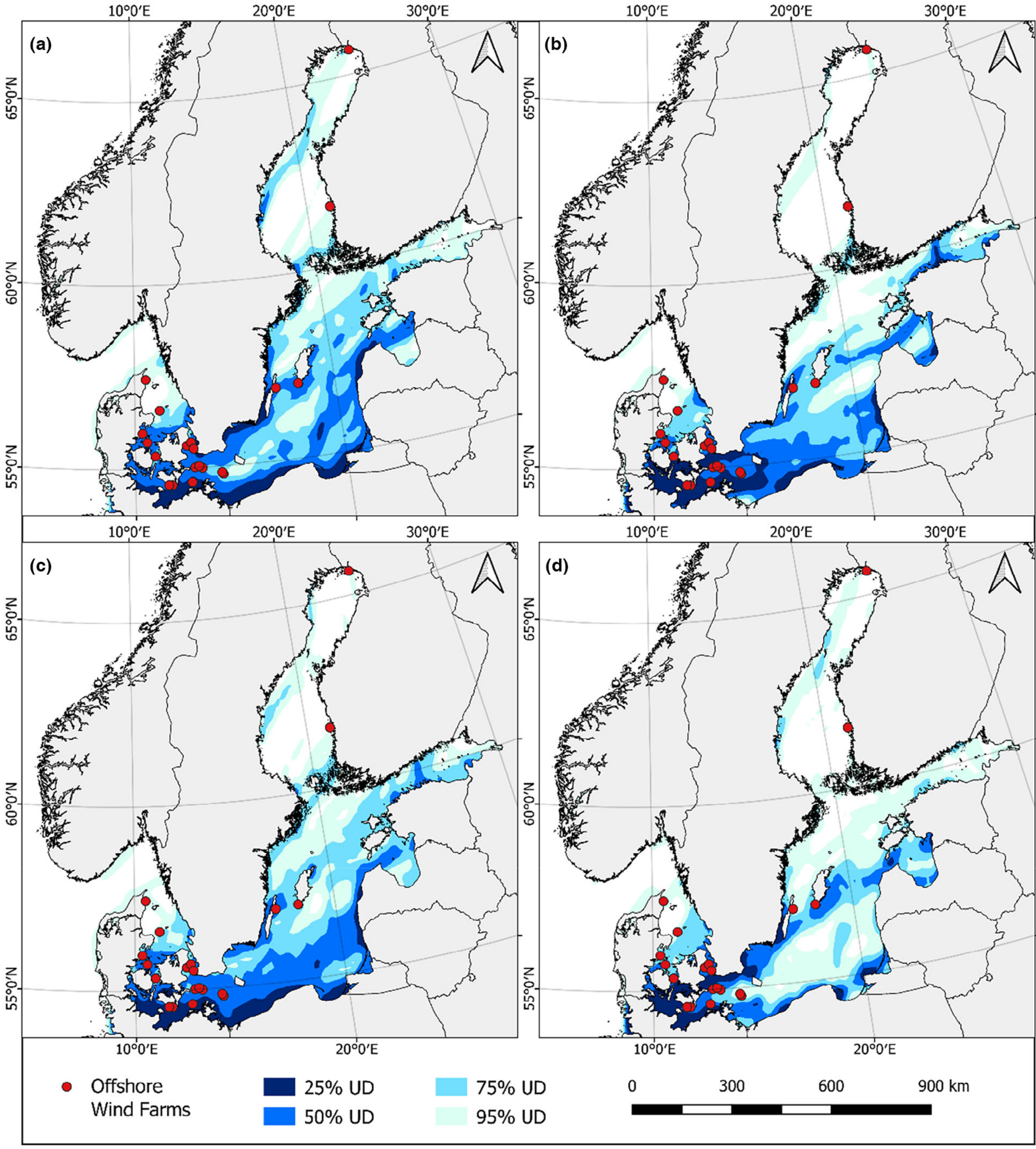

Figure 3 Home ranges of migrating Eurasian Curlews during (a) autumn and (b) spring. Flight altitudes (c) <250 m and (d) ≥250 m (during spring and autumn). Red dots indicate operating offshore wind farms.

Discussion

Conflicts between curlew migration patterns and OWFs in the Baltic Sea

Using a large, international dataset on GPS-tagged curlews, we found that while curlews migrated across a large band of the Baltic Sea, they had predictable high-use flight areas that overlapped with OWFs. Our flight altitude data showed that curlews were migrating across marine areas that contained OWFs at significantly lower altitudes than across land, suggesting higher collision risks for offshore migrants regardless of time of day.

The nature of the broad migration front of curlews across the Baltic Sea and adjacent mainland was previously

Table 2 Number and proportions of turbines (of the 717 turbines in total currently installed in the Baltic Sea) which fell into the core migration area (i.e. 25% and 50% UD) of curlews during autumn and spring as well as for birds migrating at altitudes <250 and ≥250 m (see Fig. 3 for map)

	UD kernel	Number of turbines	Proportion of turbines
Autumn	25%	136	19.0%
	50%	416	58.0%
Spring	25%	194	27.1%
	50%	566	78.9%
Flight altitude <250 m	25%	203	28.3%
	50%	549	76.6%
Flight altitude ≥250 m	25%	1	0.1%
	50%	315	43.9%

Table 3 Regression results for flight altitudes of Eurasian Curlews

	Beta	Lower CI 95	Upper CI 95	*P*-value
Intercept	4.12	3.46	5.17	<0.001
Year 2019	0.84	0.75	0.94	<0.001
Year 2020	0.86	0.77	0.96	0.01
Year 2021	0.93	0.84	1.03	0.18
Day 1	1.01	0.98	1.03	0.64
Season spring	1.09	1.06	1.12	<0.001
Land 1	1.31	1.26	1.35	<0.001

Beta = regression coefficient, lower/upper CI 95 = 95% confidence limits of beta.

described by Schwemmer *et al.* (2021). However, despite the broad migration front, we now identified migration hot spots (particularly in the south-eastern Baltic Sea), highlighting important sea areas for marine spatial planning.

Lower flight altitudes across the sea than across the land were recently confirmed in related species (Galtbalt *et al.*, 2021; Lindström *et al.*, 2021). Some shorebirds are known to migrate at high altitudes to avoid overheating and to take advantage of favourable wind conditions (Senner *et al.*, 2018), however the reason why curlews migrate so low across the Baltic Sea remains unknown.

We found significantly higher flight altitudes during spring compared with autumn, in accordance with the observation of flight altitudes in the vicinity of curlew wintering sites at the Wadden Sea, which were related to different wind regimes (Schwemmer *et al.*, 2021). Galtbalt *et al.* (2021) found median flight altitudes of 538 m over land and 156 m over sea for Far Eastern curlews *Numenius madagascariensis* during north-bound migration. Interestingly, this was similar to the range for spring migration in our study, while our study showed significantly lower flight altitudes during autumn.

The current study revealed that up to 74.8% of flight time was spent at heights prone to collision with OWFs (though this proportion was reduced to 37.3% when data <20 m were excluded). However, even considering only data for >20 m and < 150 m (i.e. the actual rotor level), without accounting for measurement inaccuracies, still resulted in 27% of flight time spent within the rotor height during autumn migration across the sea. Potential avoidance reactions of the birds when approaching OWFs, such as documented in geese using radar observations (Desholm & Kahlert, 2005), where not in the focus of the current study but will be an essential contribution to quantify collision risk in the future.

Including flight altitude in addition to two-dimensional tracking data can greatly reduce the estimated risk in collision-risk models, because flight altitudes may often exceed turbine heights (Khosravifard *et al.*, 2020). However, the current study suggests that the two-dimensional tracks alone could provide a good estimate of the areas with potentially high collision risks for curlews, because of the high proportion of low-altitude values (particularly across the sea).

Flight speeds were shown to have a significant impact on collision rate estimates with OWFs: birds flying at higher speeds were at a significantly higher risk to collide (Fijn & Gyimesi, 2018). As curlew flight speeds were significantly higher during spring, our study suggests higher collision risks during this season. Furthermore, the current study revealed major spatial and temporal differences in flight speeds, thus highlighting the need for site-specific flight-speed data to inform collision-risk models (Masden *et al.*, 2021).

Temporal patterns

In contrast to autumn, the condensed spring migration period suggests that restricting turbine operation during this critical time frame might offer a possible management option. The short migration peak during spring suggests that turbine operations would only need to be restricted for a few critical days. Notably, curlew migration, unlike for songbirds or other bird species, is widely independent of local and global meteorological conditions, and migration initiation has been shown to be genetically programmed (Schwemmer *et al.*, 2021). The 10-day period of spring migration for curlews can thus likely be regarded as fixed, which might also facilitate the potential turbine operation restriction. In contrast to other species including landbirds (Oloo, Safi, & Aryal, 2018; Pearse *et al.*, 2018) and geese (FTZ unpublished data), curlews do not exhibit corridor-like migration in the Baltic Sea (in contrast to patterns along the East Atlantic and North Sea coast). This could make restricting turbine operation times more difficult because a wider sea area is involved. However, using high-resolution tracking data, our study showed that, even over a broad migration front, distinct sea areas with peak migration intensity and critical flight altitudes could be identified, such as in the south-western coastal Baltic Sea, indicating the need for spatial planning to consider the high conflict potential between OWFs and migrating curlews in this area and careful operation of the facilities.

Although curlews showed no diurnal differences in flight altitudes, there was a clear trend for higher migration

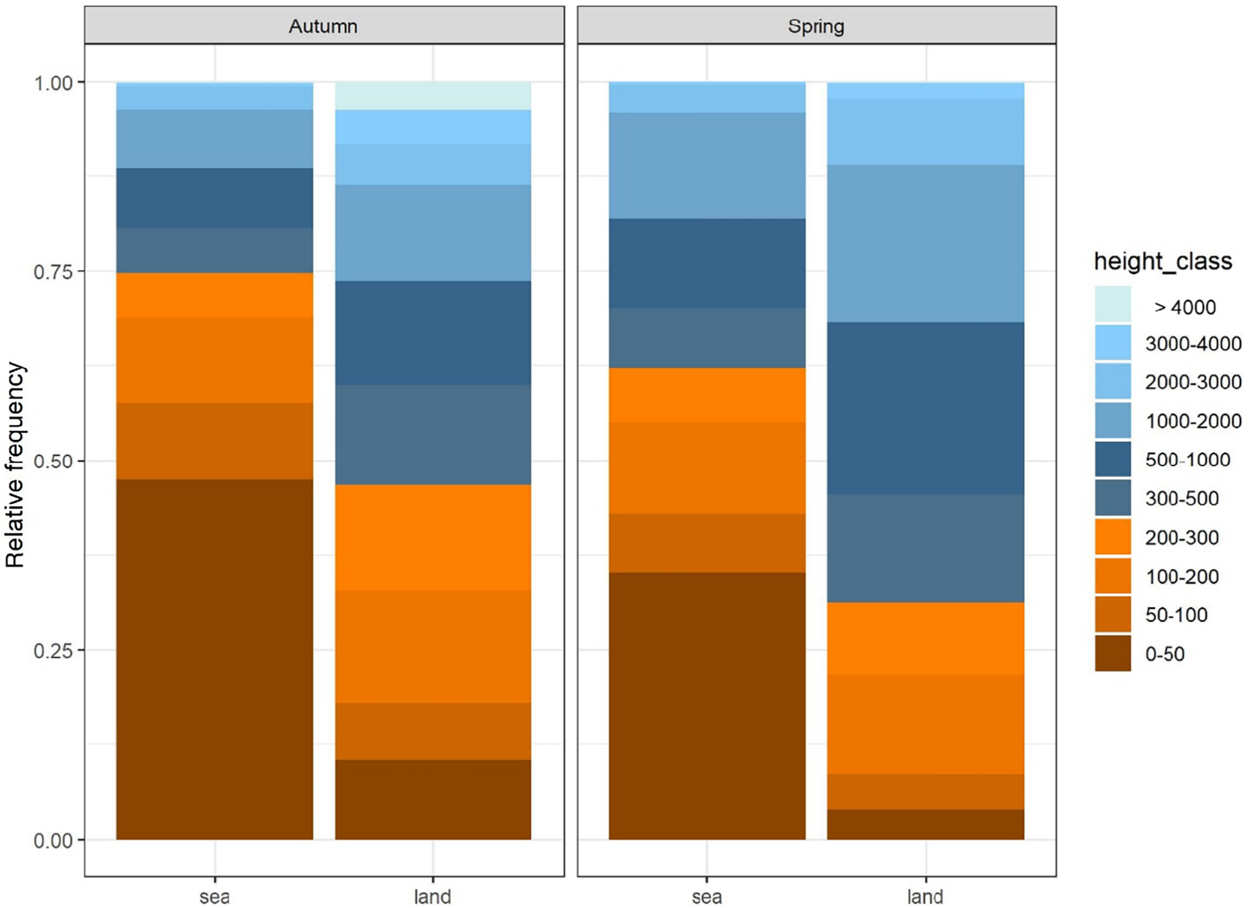

Figure 4 Relative frequencies of flight altitudes of Eurasian Curlews across the sea and the land and during autumn and spring respectively. Brownish colours indicate flight altitudes overlapping with heights of current and projected offshore wind turbines. Blue colours represent altitudes above turbines.

Table 4 Proportions of time spent migrating below different heights in different seasons across sea and land by Eurasian Curlews

	Across the sea		Across the land	
	Autumn	Spring	Autumn	Spring
<150 m	64.5 (27.0)	50.0 (22.0)	25.6 (19.7)	15.7 (13.5)
<200 m	69.0 (31.6)	55.2 (27.1)	33.1 (27.1)	21.8 (19.6)
<250 m	72.2 (34.8)	59.5 (30.9)	40.5 (34.6)	26.8 (24.6)
<300 m	74.8 (37.3)	62.2 (34.2)	46.8 (40.8)	31.3 (29.1)

Values given as % (proportion excluding time spent <20 m, i.e. below rotor height).

intensity across the Baltic Sea at night and in the early morning, suggesting that night-time may be of particular concern, as has been found for songbirds (e.g. Michev *et al.*, 2017). Because most curlews along the East Atlantic Flyway use the Wadden Sea as a wintering or stop-over site (Kleefstra *et al.*, 2019), and curlews leaving the Wadden Sea during spring usually commence their migration during the evening (Schwemmer *et al.*, 2021), they are most likely to

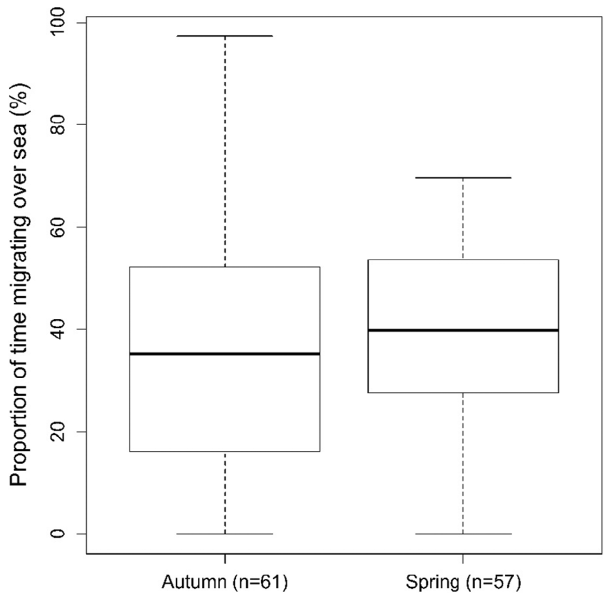

Figure 5 Proportion of time migrating over sea during autumn and spring migration for 118 migration tracks of Eurasian Curlews.

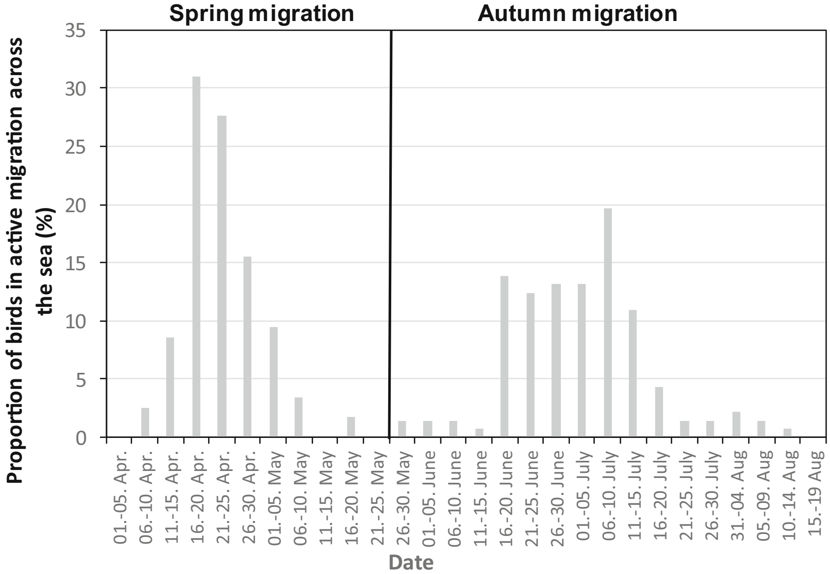

Figure 6 Proportion of migration days of Eurasian Curlews across the sea during spring (n = 116) and autumn (n = 137) shown as pentads (i.e. periods of 5 days) for both migration periods.

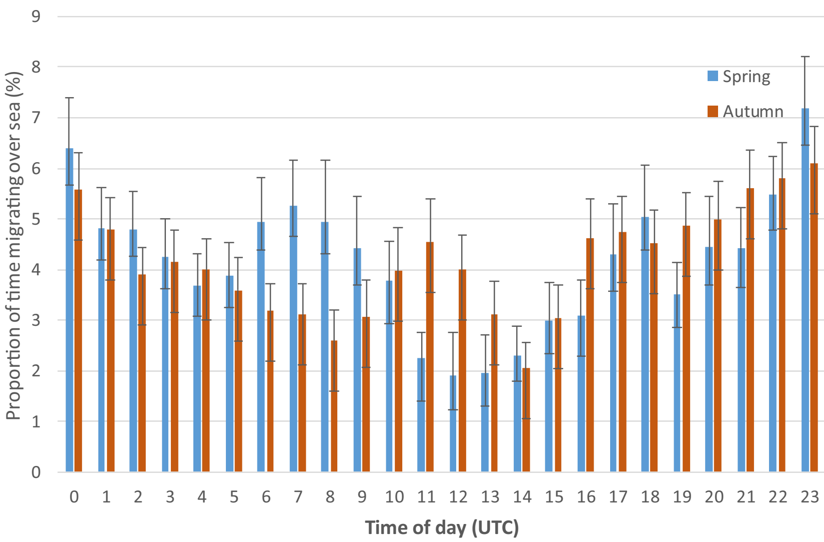

Figure 7 Mean proportions (bars) and standard deviations (black lines) of time spent migrating by Eurasian Curlews across the sea for each hour of the day during spring migration (blue bars, n = 47 tracks) and autumn migration (brown bars, n = 85 tracks). Thirty-three tracks were removed because the birds did not spend sufficient time flying across the sea.

cross the Baltic Sea at night. However, a similar pattern of intense nocturnal migration was true in autumn, suggesting that curlews might decide to cross larger sea areas during darkness. The installation of artificial lights is known to dramatically affect nocturnal bird migration, including changes in behaviour, attraction and increased collision risks (Hüppop *et al.*, 2006; Rodríguez *et al.*, 2017). The installation of illuminated structures in the offshore zone is therefore also likely to affect curlew migration.

Use of GPS telemetry data in improving collision risk models

Telemetry studies have the advantage of collecting individual-based information on migration patterns and allowing their repeatability to be assessed in consecutive years (Battley, 2006; Schwemmer *et al.*, 2021); however, it must be noted that these studies include some bias, because the migration tracks only reflect the sub-population caught at

Table 5 Regression results for flight speeds of Eurasian Curlews

	Beta	Lower CI 95	Upper CI 95	*P*-value
Intercept	5.89	5.05	6.88	<0.001
Year 2019	0.93	0.87	0.99	<0.05
Year 2020	0.96	0.89	1.02	0.19
Year 2021	0.98	0.92	1.05	0.65
Day 1	1.02	1.00	1.04	<0.05
Season spring	1.09	1.07	1.11	<0.001
Land 1	1.01	1.00	1.03	0.17

For further explanations see Table 3.

the tagging location(s). Nevertheless, this potential bias was reduced in this study by using a unique international dataset of tracking data covering a large geographical scale and 51 tracked individuals with 118 flight tracks from different tagging locations.

Our statistical design, based on resampling of temporally thinned data in combination with regression analyses, enabled us to use all the raw data, while if the data were simply pooled or thinned out, information would become blurred or lost respectively. Our novel approach revealed significant differences in flight altitudes between seasons and between land and sea. In contrast, use of hourly pooled data, independent of the method (Frequentist or Bayesian GLMMs with appropriate temporal autocorrelation structures), produced non-significant results for all three variables (land/day/season), indicating how the blurring effect of pooling can hide important effects and demonstrating the importance of high-resolution tracking data.

Another potential bias in the study might have been introduced by the flight altitude data as GPS-based recordings of flight altitudes are known to produce inaccuracies (Poessel *et al.*, 2018; Péron *et al.*, 2020). As the nature of this error is non-systematic, the recorded measurements scatter around the true values (i.e. they deviate in a positive and negative direction). Calibration tests with an altimeter of an aircraft performed for a previous study (Schwemmer *et al.*, 2021) revealed a mean measurement inaccuracy of ±55 m. Thus, although there is a certain uncertainty in the data, due to the non-systematic nature of the measurement inaccuracy, the proportions of time spent migrating at different height classes stay valid.

Conclusions

Even for broad-front migrants like curlews, it is possible to identify high use, low altitude migration pathways through marine areas which will require an ecologically sound planning, placement and management of marine industrial development projects like OWFs. This is also relevant to other shorebirds that use the Wadden Sea to refuel before migrating across the Baltic Sea to their north-eastern breeding grounds. Most OWFs are currently located within the 25% and 50% core home-range UDs (in which curlews spent high proportions of their time migrating at turbine height), and a significant increase in this overlap can be expected if planned future scenarios are realized.

Sensitive sea areas for curlews are located particularly in the nearshore south-western Baltic Sea and the adjacent mainland, although the latter may be of less concern given the significantly higher flight altitudes across the land. Furthermore, this study revealed particularly sensitive and condensed migration periods during spring that should be urgently considered in relation to potential restrictions to turbine operation times.

Given the large areas reserved for offshore wind power generation in the Baltic Sea (and elsewhere), the current study indicates the potential value of high-resolution tracking data for other important bird species in terms of developing robust scenarios for marine spatial planning around OWFs to avoid loss of bird biodiversity (Marques *et al.*, 2014).

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Catching, handling and tagging of curlews complied with European laws. Curlews in Germany were treated according to the permission issued by the Ministerium für Energiewende, Landwirtschaft, Umwelt, Natur und Digitalisierung of the federal state of Schleswig-Holstein (file numbers V 312-7224.121-37(42-3/13) and V 241-35852/2017(88-7/17)) as well as by the Niedersächsisches Landesamt für Verbraucherschutz und Lebensmittelsicherheit of the federal state of Lower Saxony (file number 33-19-42502-04-17/2699). The treatment of curlews in France was in accordance with the permission issued by the Centre de Recherches sur la Biologie des Population d'Oiseaux (file numbers PP336 and PP1083). The animal welfare licence in Estonia was issued by the Matsalu Ringing Centrer, Estonian Environmental Agency (file number 3-2013 and 4-2013 within the 'Program of marking Eurasian curlew'). Curlews in Finland were treated according to the permissions issued by the Centre for Economic Development, Transport and the Environment (file number VARELY/1136/2020 and VARELY/3622/2017).

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Conflict of interest

All authors declare that they have no conflict of interest.

Author contributions

PS and SG drafted the study, PS designed the methodology, PS wrote the manuscript, MM, PS, RP and KH analysed the data, PS, PB, JF, FJ, JE, RM, MP, PR and SG recorded the data. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information

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

Figure S1. Overview of operating and planned offshore wind farms in the Baltic Sea.
Table S1. Area (km^2) of offshore wind farms located in the Baltic Sea by country and current status
Table S2. Overview of operating and decommissioned offshore wind farms located in the Baltic Sea (source: Helcom, 2021; 4C Offshore, 2021; last update: 02/2022)
Figure S2. Homeranges of curlews in the whole study area including areas across the land. Note the high importance of the northern German and Polish coastal zones.
Figure S3. Frequency distribution of flight speeds of migrating curlews during (a) spring and (b) autumn.

