Journal of Environmental Management 342 (2023) 118131

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Behavioral responses to offshore windfarms during migration of a declining shorebird species revealed by GPS-telemetry

Philipp Schwemmer[a,*], Moritz Mercker[b], Karena Haecker[a], Helmut Kruckenberg[c], Steffen Kämpfer[d], Pierrick Bocher[e], Jérôme Fort[e], Frédéric Jiguet[f], Samantha Franks[g,h], Jaanus Elts[i], Riho Marja[i,j], Markus Piha[k,l], Pierre Rousseau[m], Rebecca Pederson[a], Heinz Düttmann[n], Thomas Fartmann[d,o], Stefan Garthe[a]

[a] *Research and Technology Centre (FTZ), University of Kiel, Hafentörn 1, 25761 Büsum, Germany*
[b] *Bionum GmbH – Consultants in Biological Statistics, 21129, Hamburg, Germany*
[c] *Institute for Wetlands and Waterbird Research e.V., Am Steigbügel 3, 27283, Verden, Germany*
[d] *Department of Biodiversity and Landscape Ecology, Osnabrück University, Barberstraße 11, 49076, Osnabrück, Germany*
[e] *Littoral Environnement et Sociétés (LIENSs), UMR 7266 La Rochelle University - CNRS, 2 Rue Olympe de Gouges, 17000, La Rochelle, France*
[f] *UMR7204 CESCO, Museum National D'Histoire Naturelle, CNRS, Sorbonne Université, 43 Rue Buffon, CP135, 75005, Paris, France*
[g] *British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, United Kingdom*
[h] *Wash Wader Research Group, The Old School House, Terrington St Clement, PE34 4H, UK*
[i] *BirdLife Estonia, Veski 4, 51005, Tartu, Estonia*
[j] *'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, Centre for Ecological Research, Alkotmány u. 2-4, 2163, Vácrátót, Hungary*
[k] *Natural Resources Institute Finland, Latokartanonkaari 9, 00790, Helsinki, Finland*
[l] *Finnish Museum of Natural History, University of Helsinki, P. Rautatiekatu 13, 00101, Finland*
[m] *National Nature Reserve of Moëze-Oléron, LPO Ligue pour la Protection des Oiseaux, Plaisance, 17780, Saint-Froult, France*
[n] *Heinz Düttmann, Am Bleißmer 25, 31683, Obernkirchen, Germany*
[o] *Institute of Biodiversity and Landscape Ecology (IBL), An der Kleimannbrücke 98, 48157, Münster, Germany*

ARTICLE INFO

Handling Editor: Jason Michael Evans

Keywords:
Marine spatial planning
Eurasian curlew (*Numenius arquata*)
Flight altitude
Collision risk
Biologging
Avoidance behavior

ABSTRACT

EU member countries and the UK are currently installing numerous offshore windfarms (OWFs) in the Baltic and North Seas to achieve decarbonization of their energy systems. OWFs may have adverse effects on birds; however, estimates of collision risks and barrier effects for migratory species are notably lacking, but are essential to inform marine spatial planning. We therefore compiled an international dataset consisting of 259 migration tracks for 143 Global Positioning System-tagged Eurasian curlews (*Numenius arquata arquata*) from seven European countries recorded over 6 years, to assess individual response behaviors when approaching OWFs in the North and Baltic Seas at two different spatial scales (i.e. up to 3.5 km and up to 30 km distance). Generalized additive mixed models revealed a significant small-scale increase in flight altitudes, which was strongest at 0–500 m from the OWF and which was more pronounced during autumn than during spring, due to higher proportions of time spent migrating at rotor level. Furthermore, four different small-scale integrated step selection models consistently detected horizontal avoidance responses in about 70% of approaching curlews, which was strongest at approximately 450 m from the OWFs. No distinct, large-scale avoidance effects were observed on the horizontal plane, although they could possibly have been confounded by changes in flight altitudes close to land. Overall, 28.8% of the flight tracks crossed OWFs at least once during migration. Flight altitudes within the OWFs overlapped with the rotor level to a high degree in autumn (50%) but to a significantly lesser extent in spring (18.5%). Approximately 15.8% and 5.8% of the entire curlew population were estimated to be at increased risk during autumn and spring migration, respectively. Our data clearly show strong small-scale avoidance responses, which are likely to reduce collision risk, but simultaneously highlight the substantial barrier effect of OWFs for migrating species. Although alterations in flight paths of curlews due to OWFs seem to be moderate with respect to the overall migration route, there is an urgent need to quantify the respective energetic costs, given the massive ongoing construction of OWFs in both sea areas.

---

* Corresponding author. University of Kiel (FTZ), Hafentörn 1, 25761, Büsum, Germany.
E-mail address: schwemmer@ftz-west.uni-kiel.de (P. Schwemmer).

https://doi.org/10.1016/j.jenvman.2023.118131
Received 7 February 2023; Received in revised form 5 May 2023; Accepted 7 May 2023

1. Introduction

All EU member countries have set a goal to decarbonize their energy systems by committing to significant reductions in greenhouse gas emissions (European Commission, 2021). To achieve this goal, offshore renewable energy is currently becoming a core component of Europe's energy mix (Wind Europe, 2021). There are currently (2022) 717 wind turbines in the Baltic Sea, including the Kattegat, covering a total of 437.8 km^2 and providing a capacity of 2,787 MW (Helcom – Baltic Marine Environment Protection Commission and Helsinki Commission, 2021; Offshore, 2021), with six times as many turbines in the North Sea (including the English Channel), i.e. 4,321 turbines covering an area of 3,226 km^2 with a capacity of 21,953 MW (Zhang et al., 2021; Offshore, 2021). The five largest overall offshore windfarm (OWF) areas are currently in the UK (1,700 km^2), Germany (886 km^2), Denmark (457 km^2), The Netherlands (432 km^2), and Belgium (170 km^2) with plans to extend the numbers and areas of offshore windfarms in both sea areas significantly (Rusu, 2020; Offshore, 2021).

However, birds may be especially vulnerable to the energy infrastructure required to promote this energy transition (Gauld et al., 2021). In this respect, birds are impacted by the installation of OWFs in various ways, including potential loss of foraging and resting habitats, disturbance during construction, barrier effects and collisions during foraging, dispersing, or migrating (Drewitt and Langston, 2006; Allison et al., 2008; Masden et al., 2012). However, collisions of birds with OWFs cannot be quantified by empirical data because collision victims at sea cannot be found, and the technical methods needed to record collisions are not yet sufficiently developed. Collision risk models are therefore an important tool for assessing the impact of vertical structures at sea on migrating birds, and detailed knowledge of the spatial and temporal patterns of bird migration are essential input variables for these models (Brabant et al., 2015; Masden and Cook, 2016; Kleyheeg-Hartman et al., 2018). In addition, collision risk estimates still lack flight altitude data (Furness et al., 2013), the inclusion of flight altitudes (Cleasby et al., 2015; Khosravifard et al., 2020) and site-specific flight speed data (Fijn and Gyimesi, 2018; Masden et al., 2021) has been shown to produce more robust models. Finally, the individual behavior of migrating birds approaching windfarms is a core component that is still lacking in collision risk models (Chamberlain et al., 2006; Fox et al., 2006). However, these behavioral responses may have a substantial impact on collision risk, and migrating birds that cross an OWF will be at higher risk than birds that exhibit avoidance behaviors, such as horizontal or vertical changes in their flight tracks that allow them to circumvent an OWF (Fox et al., 2006).

Although radar recordings have provided some important insights into the behavioral responses of migrating birds at single wind farms (Masden et al., 2009, 2012; Fijn et al., 2015; Skov et al., 2018), they cannot usually record species-specific data and importantly cannot track the bird's entire migration route across a given sea area (which might include multiple OWFs). High-resolution Global Positioning System (GPS) telemetry now offers a valid tool for recording individual data at high temporal and spatial resolutions, thus enabling individual responses and avoidance/attraction behaviors to be recorded. This approach has been applied successfully in previous studies of foraging seabirds (Hull and Muir, 2013; Fijn and Gyimesi, 2018; Schaub et al., 2020; Vanermen et al., 2020) and terrestrial birds (Johnston et al., 2022), but its use in migrating individuals is still lacking.

In the current study, we used GPS-tracking to assess individual responses to OWFs of migrating Eurasian curlews (*Numenius arquata;* hereafter curlews) that crossed the North and Baltic Seas. Curlews are rated as near-threatened and show a negative population trend across the East Atlantic Flyway (van Roomen et al., 2019; BirdLife International, 2022). They are also regarded as a sensitive species with respect to collisions with OWFs (Leopold et al., 2015; Jiguet et al., 2021). Previous studies found that curlews spend a high proportion of time migrating across the sea (Pederson et al., 2022; Schwemmer et al., 2021) and at rotor level (Schwemmer et al., 2022), which significantly increases their collision risk with OWFs.

The overall aim of this study was to quantify the potential horizontal and vertical responses of curlews approaching OWFs separately for their spring and autumn migrations as behavior and spatio-temporal migration patterns might differ between seasons (Hüppop et al., 2006). We also aimed to quantify the distance from OWFs at which potential behavioral responses occurred. This is an important prerequisite for modelling energetic constraints for migrating birds related to the barrier effects of vertical structures at sea (Fox et al., 2006). Moreover, we aimed to quantify the proportion of birds that showed avoidance behavior *versus* individuals that crossed the OWFs (and were consequently exposed to higher collision risks). Finally, the large high-resolution, long-term GPS dataset used in this study enabled us to explicitly assess the temporal and spatial patterns (i.e. flight altitudes, flight speeds, as well as diurnal and seasonal differences) of curlews that crossed, rather than avoided OWFs on their migration tracks.

2. Methods

2.1. Study area and curlew tagging

We compiled an international set of curlew tracking data ranging from the southernmost wintering grounds in the southern Iberian Peninsula to the Arctic breeding grounds in western Russia (Fig. S1). Crossings of the North and Baltic Seas by curlews during spring and autumn migrations were recorded in an area south of 66° 0′ 0′′ N, north of 50° 0′ 0′′ N, east of 02° 0′ 0′′ W, and west of 30° 0′ 0′′ E (Fig. 1). All birds were equipped with solar-powered GPS Global System for Mobile Communications data loggers (Ornitela, Lithuania). The entire dataset contained 259 migration tracks recorded between 2017 and 2022, comprising an offshore portion (90 during spring and 169 during autumn migration), for 143 individuals equipped in seven countries (Germany: n = 103, France: n = 16, UK: n = 10, Estonia: n = 6; Finland: n = 6, the Netherlands: n = 1, Russia: n = 1) during either the breeding or wintering period (see Table 1 for an overview of the number of tracks and individuals per tagging location and season; note that many individuals recorded data in consecutive years). The 143 tagged birds included 136 adults and seven juveniles as well as 78 males and 65 females. The devices weighed 10 g (n = 115), 15 g (n = 22), and 20 g (n = 6), respectively. Different types of data loggers were used as lighter versions became available during the course of the study. None of the tags was >3.5% of the bird's body mass (Phillips et al., 2003). The data loggers recorded geographical position, time (UTC), speed (m/s), and flight altitude (m above sea level). Data were stored in the online portal Movebank (Kays et al., 2021).

Curlews were caught in their wintering grounds using mist nets or cannon nets, or during the breeding period while incubating using walk-in-traps or clap nets. All devices deployed in Germany, Estonia, and Russia were fitted with breast harnesses (Guillaumet et al., 2011), while individuals in the other tagging locations were fitted with leg-loop harnesses (Mallory and Gilbert, 2008). Harnesses consisted of 6 mm Teflon cord, 1 mm braided Teflon cord, or silicone elastic tube (diameter: 2.1 mm; Reichelt Chemietechnik GmbH, Germany). Curlews were sexed either genetically using feather samples (Tauros Diagnostics, Berlin, Germany) or based on bill length (Summers et al., 2013). Age was classified according to plumage characteristics (Prater et al., 1977).

2.2. Compilation of OWF data

Data on the statuses of OWFs (as of May 2022) in the North and Baltic Seas were obtained from Offshore, 2021, Helcom – Baltic Marine Environment Protection Commission and Helsinki Commission (2021), and Zhang et al. (2021), as well as from multiple sources provided by the different North and Baltic Sea countries (Table S1). On the basis of single turbines, we used the tool "Concave Hull (k-nearest neighbor)" in QGIS (version 3.2.4.0; QGIS Development Team, 2022) to convert the area of each windfarm to polygons, using the positions of the turbines at the edge of the respective windfarm. We also added a buffer of 85 m (i.e. maximum rotor radius of all wind turbines in the dataset), because the rotors might extend the border of the windfarm to a maximum of their radius. Finally, we calculated the resulting OWF area (km^2) (see Table S1).

2.3. Data analyses and statistics

2.3.1. Data preparation

All maps were created using QGIS. All statistical analyses were conducted using R (version 4.2.2; R Development Core Team, 2022). Each GPS track was visualized in the GIS and all fixes that were not recorded in flight (i.e. positions at stopovers, breeding or wintering grounds that could be identified by flight speed and low distances between consecutive fixes) were removed. Flight speeds were recorded using doppler shift which is known to be a very precise measurement enabling easy classification between stop-overs and in-flight positions. The remaining in-flight positions were assigned as recorded over sea or land using the R package *spData* (Bivand et al., 2021) and R package *sf* (Pebesma, 2018). Furthermore, each position was classified as "*day*" (i.e. from calculated morning to evening civil twilight) or "*night*" (i.e. from evening to morning civil twilight) using the R package *suncalc* (Thieurmel and Elmarhraoui, 2019).

To study the avoidance responses of curlews approaching OWFs on a fine spatial scale, it was necessary to collect in-flight fixes with a high temporal resolution. We therefore programmed "geofences" covering the North and Baltic Seas, and when a tagged curlew entered this area, the device started recording data at resolutions of 1, 60, or 300 s intervals, according to the battery state. GPS-based altitude measurements show stochasticity, with the magnitude of scatter around the true

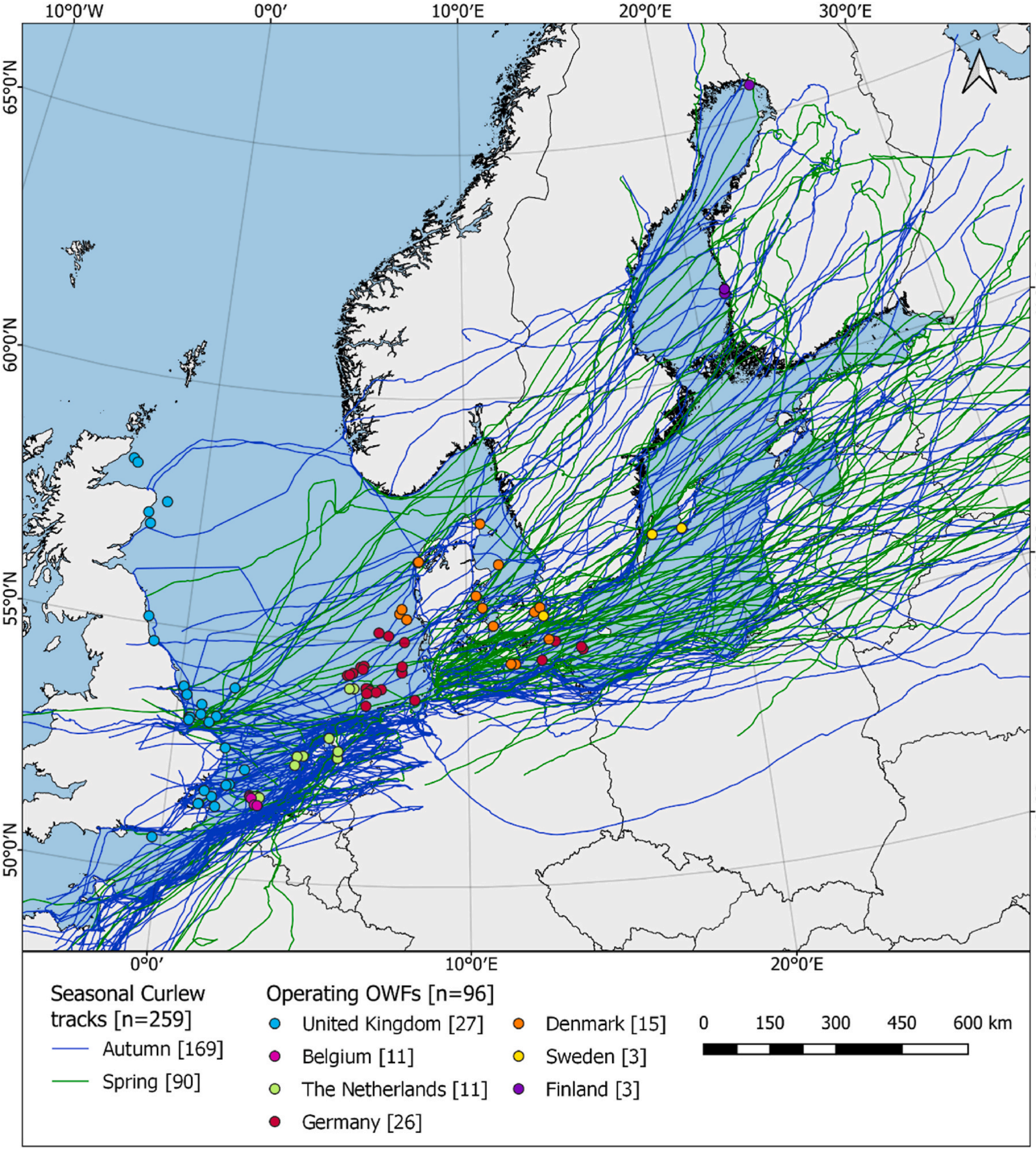

Fig. 1. Location of the 259 tracks recorded from 143 individual curlews crossing the North and Baltic Seas during spring (green) and autumn migrations (blue) between 2017 and 2022.

altitude value being strongly associated with the logging interval of the devices (i.e. coarser schedules produce a higher degree of uncertainty compared with high-resolution schedules towards both positive and negative divergence from the true value; Poessel et al., 2018; Péron et al., 2020; Schwemmer et al., 2021, 2022; Lato et al., 2022). In accordance with Schwemmer et al. (2022), we therefore removed all altitude values with a difference of >500 m between consecutive fixes within 300 s, accounting for 4,344 fixes (0.84% of all recorded data). The flight altitude recordings of the devices used were calibrated for a previous study on flight altitude in curlews (Schwemmer et al., 2021) and showed an inaccuracy of ±55 m (Schwemmer et al., 2022). The measurement inaccuracy of flight altitudes is a non-systematic error (i.e. scattering to the same degree below and above the true value). Thus, although there is some degree of uncertainty in the data, the interpretation drawn from the models using flight altitude records stays valid. Besides flight altitude, the GPS position is known to show a potential bias of up to 25 m (Ornitela pers. com.). Given the range of the spatial analyses used in the study (see below), this bias does not affect the results.

2.3.2. *Responses in the vertical plane*

Wind farm avoidance reactions by birds take place at different spatial scales (i.e. micro-, meso- and macro-avoidance; May, 2015; Skov et al., 2018). While our tagging data are not appropriate to analyze the immediate risk reaction (i.e. micro-avoidance), we focus on meso- and macro-avoidance. Therefore, we analyzed potential avoidance responses in the vertical plane on two different spatial scales: (1) within 1.5 km surrounding the OWFs (subsequently referred to as small-scale approach) and (2) within 30 km surrounding the OWFs (subsequently referred to as large-scale approach). In the small-scale approach, the relative intensity of use at distances of 0–1 km was compared with that at 1–1.5 km, while for the large-scale approach, we compared the relative intensities of use at 0–15 km and 15–30 km. For the small-scale approach, these choices were based on observed reaction scales in our flight-height analysis, which suggested no effect at distances >1 km. In addition, we validated this choice empirically by varying these values and confirming that this choice showed the most distinct response. In contrast, the large-scale choice was based on previous studies demonstrating that long-range effects of OWFs can reach beyond 10 km (Mendel et al., 2019), suggesting that 15–30 km distance can be considered as unaffected. Totals of 928 approaches to OWFs by 130 individuals and 201 approaches by 76 individuals were included for the large-scale and the small-scale analyses, respectively (Table 1). The respective GPS locations are shown in Fig. 2. Prior to the analyses, GPS positions within both radii around OWFs were classified as intersecting with *land* and *sea*, respectively and this classification was used as an additional predictor in the subsequent modelling approaches (see below), in line with a previous study showing significant differences in flight altitudes of curlews across land and sea (Schwemmer et al., 2022). We included the variable *sea/land* as a binary variable as curlews are known to abruptly change their flight altitudes when crossing the coastline (Schwemmer et al., 2022). To avoid problems caused by negative values of flight altitudes during regression analyses (in the context of negative-binomial distributed altitude data), all flight altitude data were increased by a constant to make all altitude values ≥ 0. Because regression techniques only evaluate relative changes, this shift affected the intercept but not the regression coefficients related to the investigated predictors.

We analyzed the flight altitudes of curlews approaching OWFs using generalized additive mixed models (GAMMs; Hastie and Tibshirani, 1990; Zuur et al., 2009; Wood, 2017) using the R package *mgcv* (Wood, 2022). Specifically, both the appropriate probability distribution (testing a negative-binomial (Lindén and Mäntyniemi, 2011), a normal, and a Tweedie-distribution (Kokonendji et al., 2004), as well as the choice of predictor variables were selected based on the Akaike information criterion (AIC; Akaike, 1973). The predictors *season*, *land/sea* (see above), and *day/night* were tested in all possible subsets/combinations/interactions, along with a smooth dependency on the distance to the nearest OWF (*Dist OWF*). We also tested via AIC if the smooth dependency of flight altitudes on *Dist OWF* differed between seasons and between day and night, respectively. Temporal autocorrelation was accounted for by introducing lagged variables on the predictor scale (i.e. as a Markov process; Mercker et al., 2021a), because autoregressive models failed to converge. In addition, bird ID was introduced as a random intercept to account for the nested data structure (Hurlbert, 1984; Zuur et al., 2009).

2.3.3. *Responses in the horizontal plane*

Avoidance behavior in the horizontal plane was analyzed using integrated step selection methods (iSSMs; Avgar et al., 2016), which were recently shown to outperform other regression techniques (such as spatio-temporal point process models) with respect to statistical power and false-positive rates when analyzing habitat selection based on animal tracking data (Mercker et al., 2021b). It was necessary to use iSSMs instead of GAMMs to model behavioral reactions in the horizontal plane, because there is a fundamental difference to the behavior reactions in the vertical plane: in the latter case, all possible heights are equally available in 3D space, whereas in the case of the distribution of 2D-variables (like nearest distance to an OFW), the situation is much more complex, since “habitat”-availability strongly varies in space (e.g., the area of each distance class quadratically increases with the distance to the OWF, which is even more complicated in a scenario with multiple turbines). More details are given in Mercker et al. (2021b).

Given that data recorded at 1 s intervals comprised too few individuals close to the OWFs, we only included individuals with data that could be regularized to 60 s and 300 s intervals for small-scale, and 300 s and 1500 s for large-scale analyses. The interval size was thus adapted to the spatial scale of the considered problem; too-small intervals (such as

Table 1
Spring and autumn migration data for curlews tagged at different locations.

	Spring migration								Autumn migration							
	DE (W)	DE (B)	FR (W)	UK (W)	FI (B)	EE (B)	NL (B)	RU (B)	DE (W)	DE (B)	FR (W)	UK (W)	FI (B)	EE (B)	NL (B)	RU (B)
Number of tracks	36 (23)	22 (22)	16 (14)	10 (10)	4 (4)	2 (2)	–	–	29 (17)	96 (80)	15 (15)	10 (10)	9 (6)	8 (6)	1 (1)	1 (1)
Number of approaches - 30 km large scale	96 (21)	95 (18)	36 (10)	80 (10)	13 (4)	4 (1)	–	–	50 (13)	356 (70)	38 (10)	81 (9)	42 (6)	32 (6)	5 (1)	–
Number of approaches - 3.5 km small scale	11 (6)	26 (7)	5 (3)	17 (9)	2 (1)	–	–	–	5 (4)	89 (42)	6 (3)	23 (6)	10 (4)	6 (4)	1 (1)	–
Number of crossings	7 (5)	10 (7)	1 (1)	8 (6)	1 (1)	–	–	–	6 (3)	24 (21)	2 (1)	12 (6)	3 (3)	1 (1)	–	–
Proportion of crossings on all tracks (%)	19.4	45.5	6.3	80.0	25.0	–	–	–	20.7	25.0	12.5	120.0	33.3	12.5	–	–

Number in brackets depict the number of individuals. (W) = curlews tagged at wintering sites; (B) = curlews tagged at breeding sites.

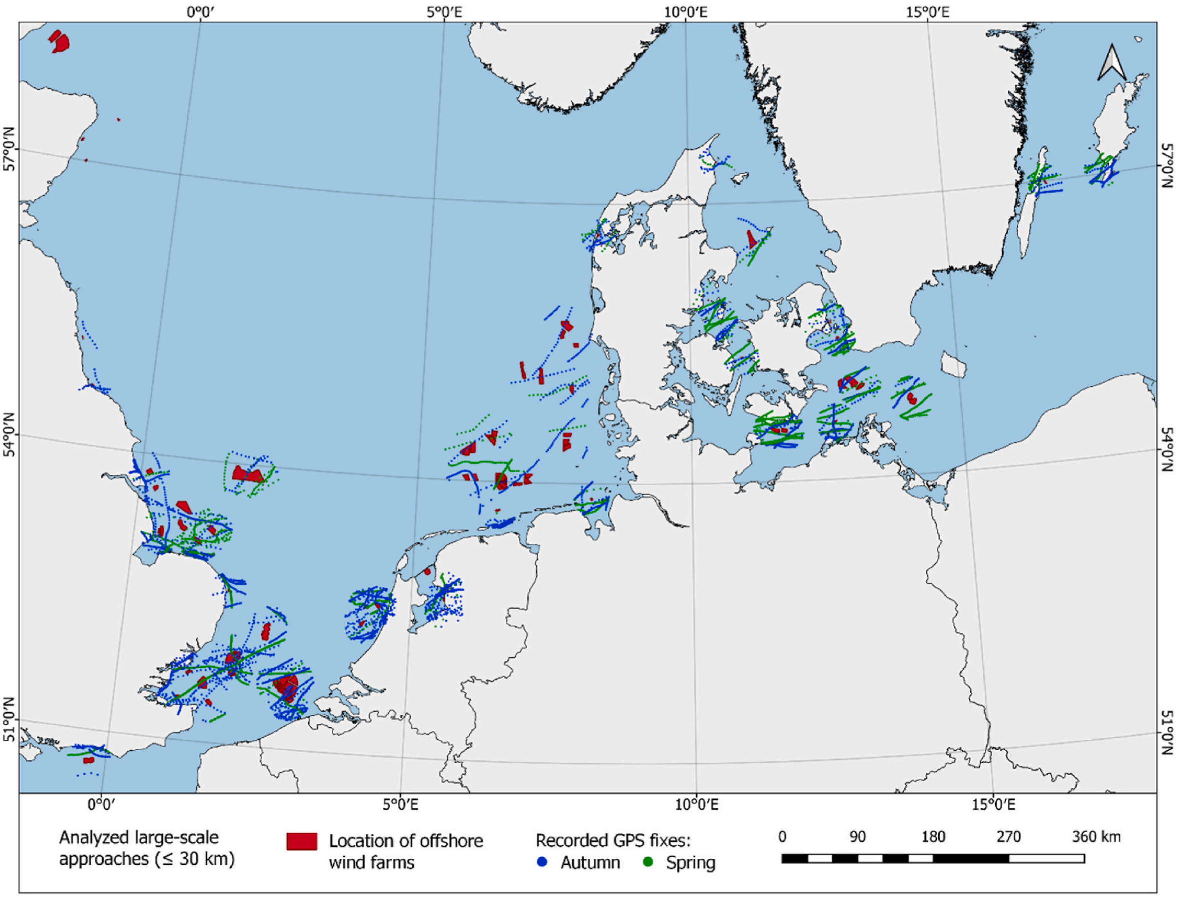

Fig. 2. Location of OWFs in the North and Baltic Seas (red polygons) and location of GPS fixes of curlews during spring (green dots) and autumn (blue dots) recorded within the 30 km surrounding each OWF used in the modelling approach. Map shows section containing most of the analyzed data.

1 s data) would lead to an underestimation of effects (since available steps will fall into similar OWF-distance classes – c. f., below), whereas too-large intervals would lead to sparse data and strong stochasticity. Regarding iSSM predictors, we used the logarithm of the spatial distance to the previous tracking point *log(dx)* (as a proxy proportional to flight speed) as well as the cosine of the turning angle *cos(ta)* (Avgar et al., 2016). These two movement-dependent predictors integrate the possibility to allow the movement characteristics to feed back on habitat selection, extending “step selection models” to “integrated step selection models”. Indeed, a simulation-based study reveals that this further increases the statistical power respectively minimizes type I error rates (Mercker et al., 2021b). Data regularization and generation of available steps (n = 10 per tracking point, were carried out based on the R-package *amt* using the *issf* function (Signer et al., 2019). To consider OWF avoidance, the binomial predictor *Dist OWF* was also included, defining a ring/belt with X ± 50 m distance (small-scale) or X ± 250 m (large-scale) from the nearest OWF, and contrasting the relative selection strength (i.e. changes in turning angle and flight speed) of this belt area with the area outside the belt (up to 1.5 km distance for small scale and up to 30 km for large scale). The relative selection strength of belts of 100 m (500 m) width and with an average OWF distance of X m were thus compared with the relative selection strength of areas outside the outermost belt. Thus (and similar in all presented iSSM-based results), the relative selection strength of areas close to OWFs is compared to habitat selection of areas which are assumed to be not influenced by OWFs, the latter represented by a value of 1 (i.e., values < 1 indicate a relative avoidance, values > 1 a concentration of birds relative to the non-influenced areas). Notably, we performed separate iSSM analyses for X values ranging from 50 to 1050 m. This original iSSM approach ignored the pseudoreplication (Hurlbert, 1984) caused by multiple observations of the same individual. We therefore also performed mixed iSSMs in the framework of Bayesian techniques (R package *R-INLA*; Rue et al., 2009; Zuur et al., 2017), as recently proposed by Muff et al. (2018). Using this approach, mixed iSSMs can be formulated in the framework of GAMMs (Hastie and Tibshirani, 1990; Zuur et al., 2009) and smooth (non-linear) dependencies can therefore be investigated. In particular, cubic regression splines with 10 knots (Zuur et al., 2017) were used to model the smooth dependency of relative selection strength depending on the distance to the nearest OWF. To account for the nested structure, random slopes with respect to the linear predictor *Dist OWF* were also considered, adapting the approach of Muff et al. (2018). We performed four different modelling approaches for the small-scale analysis, i.e. using GPS fixes recorded at 60 s and 300 s intervals, respectively, and using the standard iSSM as well as the INLA-based mixed additive iSSM analyses. While the latter model describes the nested data structure more appropriate, the former is assumed to lead to more robust results (i.e. serving as an additional validation of the INLA-based iSSM). In contrast, only two standard iSSM approaches (with 300 s and 1500 s regularized data, respectively) were applied for the large-scale analysis.

In both, the GAMM and iSSM approach described above, avoidance is defined as active/intentional avoidance as both analysis types quantify changes in vertical respectively horizontal movements by contrasting it to movements without active avoidance behavior that takes place outside the areas influenced by OWFs.

2.4. *Crossings*

Among all the tagged curlews that approached OWFs during their spring and autumn migrations, we created a subset of individuals that crossed the windfarms or windfarm clusters (including a buffer zone of eight times the rotor diameter; i.e. between 312 m and 1,336 m, depending on the turbine type). In total, we recorded 75 crossings of OWFs or wind farm clusters by 45 of the 143 equipped individuals (44 during the day and 31 during the night; 27 during spring and 48 during autumn migration) (Table 1). We computed the mean speeds and mean flight altitudes during each crossing. We also assessed the altitude changes (delta *h*) within the OWF by computing the difference in flight altitude of the bird when it entered and left the OWF. We used linear mixed effect models (lme) using bird ID as a random factor (Venables and Ripley, 2002) to test for differences in flight altitude and flight speed between day and night and between seasons, respectively.

3. Results

3.1. Avoidance responses in the vertical plane

For the small-scale analysis, a negative-binomial distribution was preferred, including a significant interaction term between *season* and *land/sea.* This indicated that flight altitudes across the land were significantly reduced, particularly during spring ($p < 0.01$). Flight altitudes were also reduced by 32% during the day compared with the night ($p < 0.01$) (Fig. 3). Notably, GAMM analyses (Fig. 3) and raw data plots (Fig. 4) indicated a distinct vertical avoidance response of curlews when approaching OWFs that was more pronounced on a smaller spatial scale in autumn than in spring, and which was strongest at 0–500 m from the OWF (Fig. 3). Different examples of individual avoidance reactions of curlews approaching OWFs in the vertical plane by increasing flight altitudes at short distances to OWFs are presented in the supplement (Fig. S2). In most cases, the birds returned to their original flight altitudes after crossing the OWF above rotor levels (Fig. S2).

No GAMM-based prediction was made for the large-scale approach because the general flight-altitude behavior related to land *vs.* sea probably confounded the results relating flight altitudes to distance from OWFs. However, raw-data plots indicated an increase in flight altitudes at 1–10 km from OWFs, compared with larger distances (Fig. 5).

3.2. Avoidance responses in the horizontal plane

In the small-scale analysis, all the investigated combinations of methods (i.e. iSSM and INLA-based mixed additive iSSM analyses) and datasets (i.e. 60 s and 300 s GPS fix schedules) showed a generally consistent picture, with the relative intensity of use becoming <1.0 between 0 m and approximately 300 m from the OWFs (indicating a significant small-scale horizontal avoidance behavior). This was followed by values > 1 at approximately 450 m distance, indicating that birds were locally concentrated by aiming to circumvent the turbines (Fig. 6). The only difference between the two methods was an increase in selection strength in the 300 s dataset compared with a decrease in the 60 s dataset. Notably, the relative selection strength decreased continuously down to about 30% from approximately 450 m onwards with decreasing distance to the OWFs (Fig. 6), suggesting that about a third of the birds did not respond to the OWFs. In contrast to the analyses in the vertical plane, *season*, *land/sea*, and *day/night* had no significant effect on the selection strength.

For large-scale analyses regarding the horizontal plane, no large-scale avoidance effect was detected for either of the two approaches, except for a reduction in the relative selection strength in the immediate

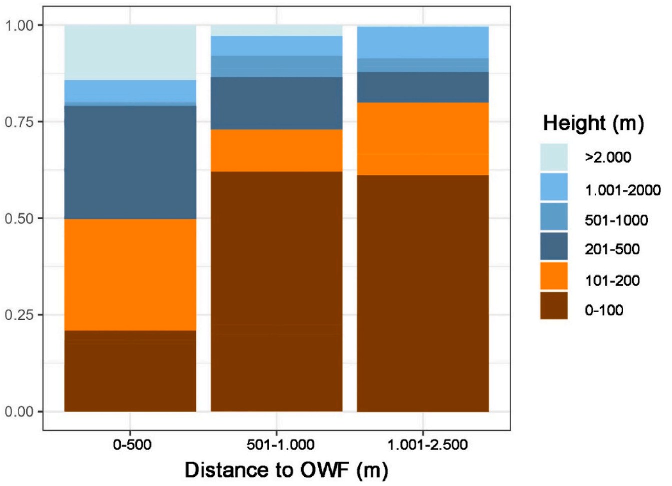

Fig. 4. Proportion of GPS fixes in different flight altitude classes (height in m) and distance classes to OWFs (small-scale analyses).

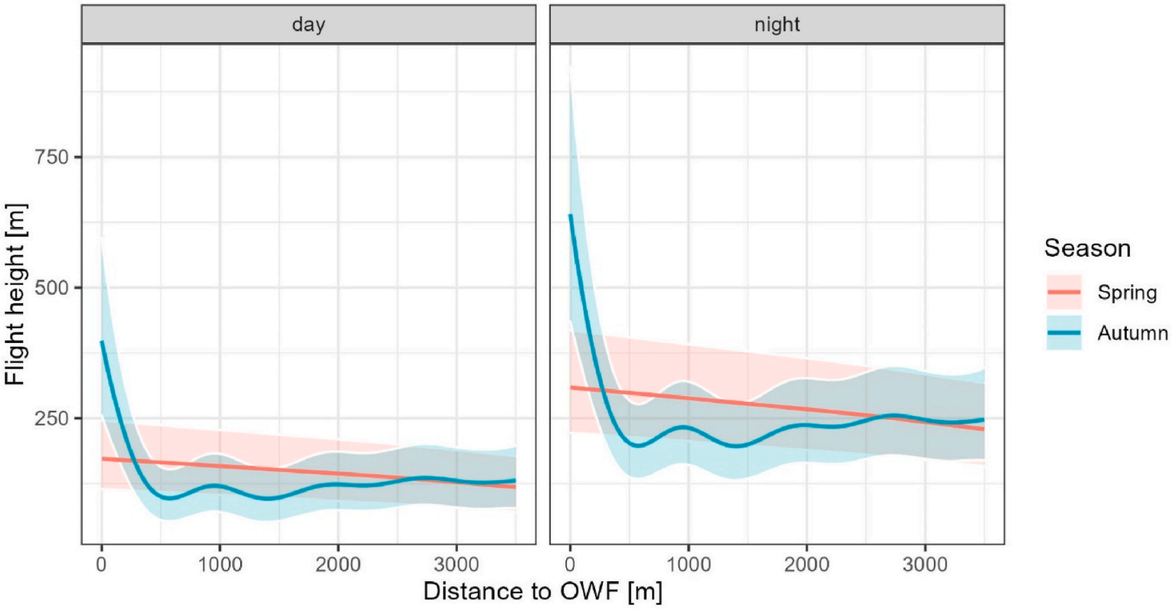

Fig. 3. GAMM-based predictions of flight altitudes (vertical plane) during spring (red) and autumn (blue) with respect to distance from the nearest OWF (solid lines). Shaded areas depict 95% confidence intervals.

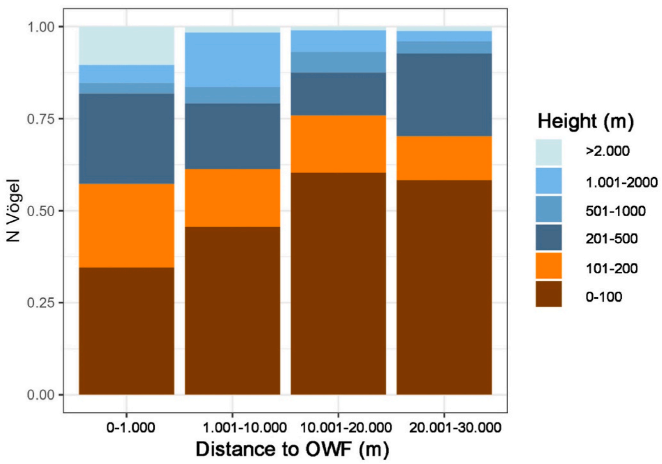

Fig. 5. Proportion of GPS fixes in different flight altitude classes (height in m) and distance classes to OWFs (large-scale analyses).

surroundings of the OWFs, which was larger in the 1500 s approach than in the 300 s approach (Fig. 7).

Different examples of individual avoidance reactions of curlews approaching OWFs in the horizontal plane by changing flight directions at short distances to OWFs are presented in the supplement (Fig. S3).

3.3. *OWF crossings*

A total of 75 of the 259 recorded tracks (29%) and 45 of the 143 tagged individuals (31.5%) crossed OWFs at least once during their migrations, in line with the horizontal avoidance analyses (see above). On the 45 individuals, 23 crossed OWFs once, 17 individuals crossed twice, two individuals crossed three times, and three individuals crossed four times. Curlews wintering in the UK showed the highest crossing rate of all tagged individuals, with 80% of all recorded tracks crossing OWFs at least once during spring and up to 120% during autumn (the value exceeding 100% is caused by multiple crossings by the same individuals) (Table 1).

The median flight altitudes during crossings ranged from 78 m during the day in autumn to 531 m during the night in spring (Table 2). Flight altitudes within OWFs were significantly higher during spring than during autumn (lme: $\chi^2 = 22.47$, df = 1, $p < 0.01$), but did not differ between day and night (lme: $\chi^2 = 0.45$, df = 1, $p = 0.5$; Fig. 8). Accordingly, for curlews crossing OWFs, the proportion of flight altitudes that overlapped with rotor levels (considering rotor levels 20–200 m above sea surface; Table S1) differed significantly between autumn (50%) and spring (18.5%) migrations, whereas there was only a small difference between day (40%) and night (34.4%).

The median difference in flight altitude between leaving and entering the OWF ranged from −39 m during the day in spring (i.e. decrease in altitude) to 86 m during the night in autumn (Table 2). No consistent pattern of flight altitude changes for curlews crossing OWFs could be detected.

Flight speeds were significantly higher during spring than during autumn (lme: $\chi^2 = 4.33$, df = 1, $p = 0.037$) but did not differ between day and night (lme: $\chi^2 = 0.08$, df = 1, $p = 0.78$) (Fig. 8; Table 2). The median crossing distance was lowest in spring during the day (6.6 km) and highest during autumn in the night (13.7 km) (Table 2). Finally, the median crossing duration ranged from 5.7 min during the night in spring to 13.9 min during the night in autumn (Table 2).

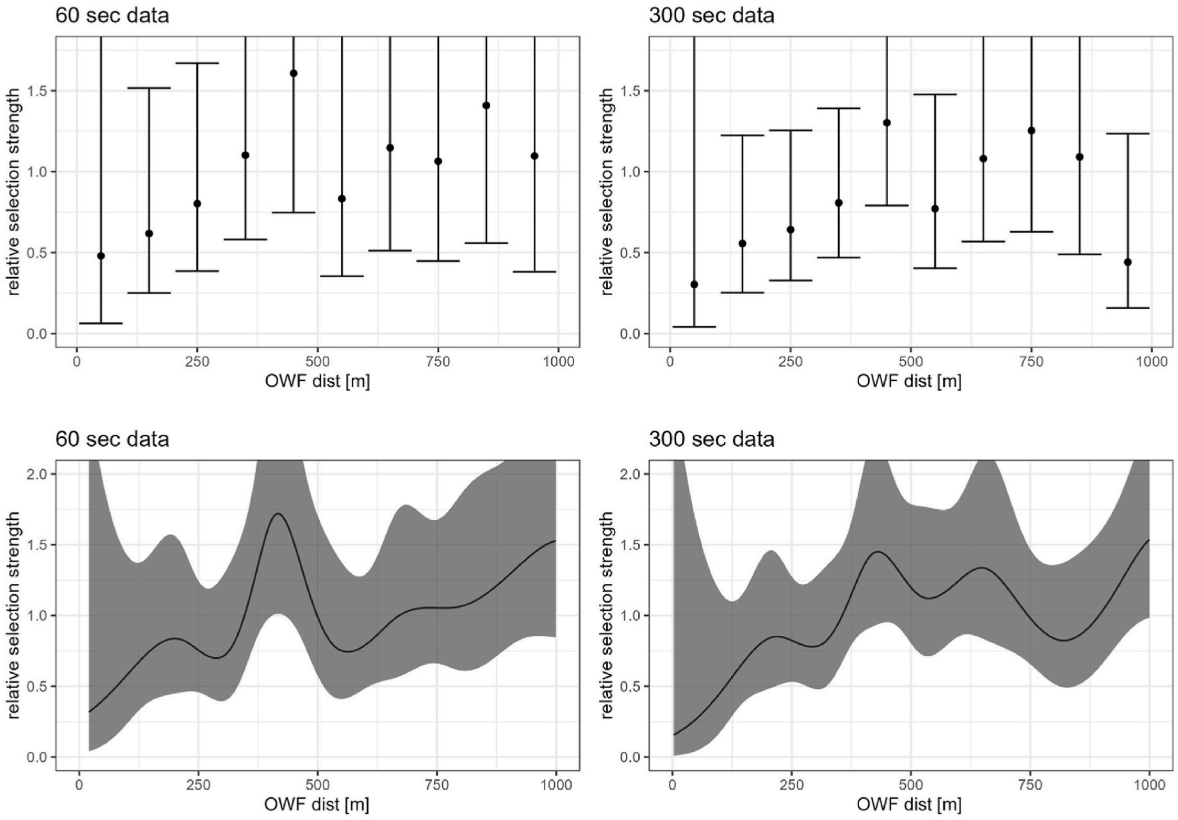

Fig. 6. Regression-based analysis of OWF avoidance by curlews in the horizontal plane (small-scale analysis). Upper panels: standard iSSM analyses; lower panels: INLA-based mixed additive iSSM analyses. Both methods were applied for GPS intervals of 60 s and 300 s, respectively. Values < 1.0 indicate relative avoidance and values > 1.0 indicate local concentration. Error bars (upper panels) and shaded areas (lower panels) indicate 95% confidence limits. For clarity, error bars were cropped beyond a relative selection strength of 1.8 (upper panels).

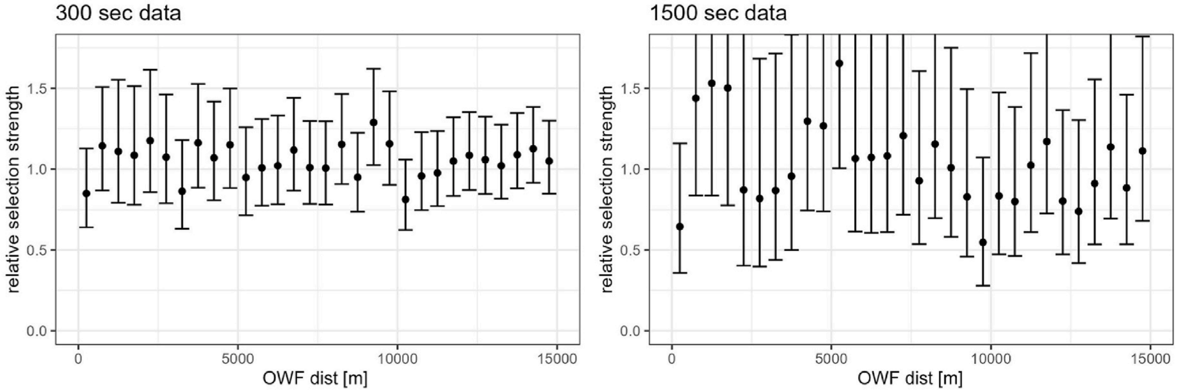

Fig. 7. Regression-based analysis of OWF avoidance by curlews in the horizontal plane (large-scale approach) based on standard iSSM analyses. Error bars indicate 95% confidence limits. For clarity, error bars were cropped beyond a relative selection strength of 1.8 (right panel).

Table 2
Flight characteristics of curlews crossing OWFs.

	Autumn migration		Spring migration	
	Day	Night	Day	Night
Mean flight altitude (m)	78 ± 342.9	133.6 ± 100.4	501 ± 596.9	531.8 ± 756.7
Flight altitude change (m)	11 ± 338.9	86.0 ± 92.9	−39 ± 108.3	32.5 ± 43.0
Mean speed (km/h)	52.0 ± 15.1	58.0 ± 12.6	67.0 ± 29.4	60.6 ± 26.1
Crossing distance (km)	6.7 ± 6.9	13.7 ± 6.4	6.6 ± 5.2	7.1 ± 3.7
Crossing duration (min)	7.7 ± 8.2	13.9 ± 7.0	5.9 ± 5.9	5.7 ± 5.0

Values given as median (± standard deviation).

4. Discussion

Avoidance responses of birds to OWFs have been described for various species; however, most studies have been restricted to seabirds during foraging flights (e.g. Cook et al., 2018; Schaub et al., 2020; Vanermen et al., 2020; Johnston et al., 2022). To the best of our knowledge, the present study is the first to investigate small-scale individual-based behavioral responses to OWFs in a non-pelagic migratory species, thus providing important information for collision risk assessments (Fox et al., 2006). We analyzed high-resolution GPS-data for multiple curlew sub-populations along the East Atlantic Flyway, and showed that a high proportion of migrating curlews exhibited behavioral responses on a small spatial scale when approaching OWFs, both by increasing their flight altitude and by circumventing the turbines. This avoidance behavior is likely to reduce the collision risk but may also increase the energy expenditure due to the need to adjust flight altitudes and/or fly around wind farm clusters (e.g. Cook et al., 2018). However, a significant proportion of curlews entered OWFs and did not show avoidance responses, thus increasing their risk of collision. We also found significant seasonal differences in vertical avoidance responses and complex interactions with the predictor *sea/land*. Below, we discuss the avoidance responses in the vertical and horizontal planes and provide a rough estimate of the proportion of curlews at increased risk during migration.

4.1. Avoidance responses in the vertical plane

In accordance with two recent studies on flight altitudes (Galtbalt et al., 2021; Schwemmer et al., 2022), we found significant differences in flight altitudes across the land and sea in both small-scale and large-scale avoidance analyses. In contrast however, flight altitudes in the areas surrounding OWFs were lower across the land than across the sea, particularly during spring migration. This general difference is likely to be due to the fact that all the GPS data intersecting with land were located close to the coast where curlews often either start, end, or interrupt their migration, which would lead to a significant decrease in flight altitudes (Schwemmer et al., 2021). Additionally, flight altitudes may depend on the distance to the next stop-over location (H. Düttmann pers. comm.) Notably, the more pronounced avoidance response during autumn migration (curlews generally approaching from the sea) compared with spring (curlews often departing from the coast) might be explained by these topographic issues. In addition, the covariate effects revealed by the GAMM analyses might not reflect the general flight behavior of curlews, but may rather represent the distinct local situations in the surroundings of the OWFs, which are generally located close to the coast and thus might interact strongly with coast- and season-related flight altitude patterns (Schwemmer et al., 2021). This shows the importance of testing additional predictors (such as season and land/sea, as well as their interaction) in the GAMM approach in order to obtain unbiased effects of the *OWF_dist* on flight altitudes, without the confounding effects of local (e.g. near-shore) situations. However, the potential confounding effect was assumed to be much stronger in the large-scale approach (including data for up to 30 km from the OWFs) than in the small-scale approach (up to 3.5 km), because a higher proportion of GPS fixes intersected with the land. The results of the large-scale approach with respect to avoidance responses in the vertical plane should thus be interpreted with caution. For this reason, we decided to only present a descriptive bar-plot of flight altitudes and to not perform a GAMM-based prediction for flight altitude changes. Separate from these potential confounding effects, our large-scale approach indicated an increase in flight altitudes at 1–10 km compared with >10–30 km from OWFs, which corresponded well with the orders of magnitude of avoidance distances previously described for OWF avoidance effects in other species (Mendel et al., 2019; Peschko et al., 2020; Garthe et al., 2023).

In addition to an effect of *land/sea*, we found clear seasonal differences, with curlews exhibiting much stronger small-scale avoidance responses during autumn than in spring. This is likely due to generally lower flight altitudes during autumn (Schwemmer et al., 2022), which were found to depend on the overall wind regime (Dokter et al., 2013; Schwemmer et al., 2021). Curlews might tend to react more strongly to OWFs when they are migrating at turbine level (as shown in lesser

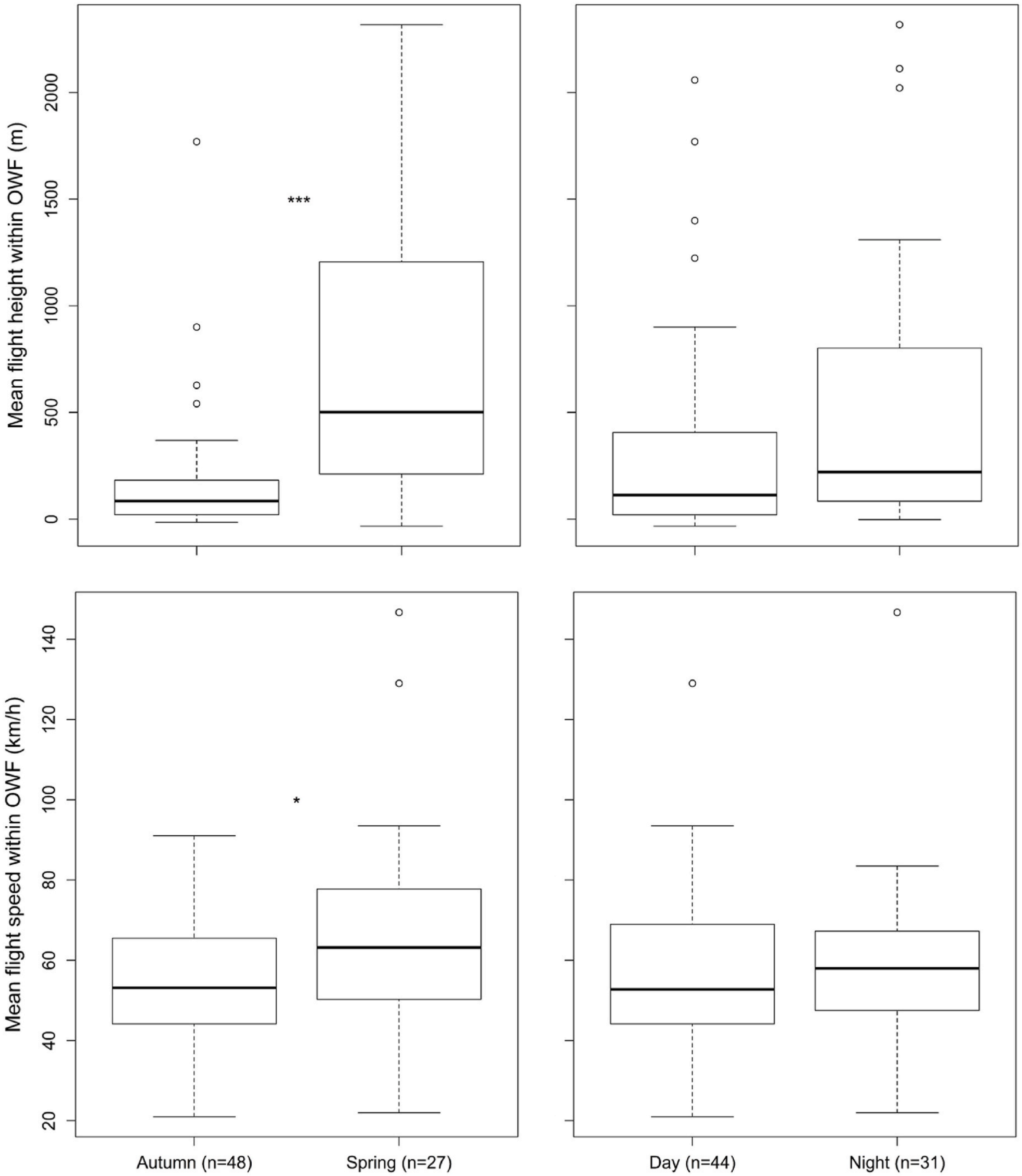

Fig. 8. Flight altitudes and speeds of curlews crossing OWFs during autumn and spring migrations and during day and night. Solid lines: medians; box: quartiles; dashed lines: 95 confidence intervals; dots: outliers; ***$p < 0.001$; *$p < 0.05$.

black-backed gulls, *Larus fuscus*; Johnston et al., 2022), which is more common during autumn than during spring movements. The significant seasonal effect was also reflected by the crossing analysis, which highlighted significantly lower crossing altitudes during autumn compared with spring migrations. Similar seasonal differences were found for flight speed, which is an important factor for improving future collision risk models (Fijn and Gyimesi, 2018; Masden et al., 2021).

4.2. Avoidance responses in the horizontal plane

Horizontal avoidance of wind farms by different bird species has previously been demonstrated by non-species-specific radar studies (Masden et al., 2009, 2012; Fijn et al., 2015; Skov et al., 2018), for foraging raptors at terrestrial sites (Hull and Muir, 2013; Schaub et al., 2019), and for foraging seabirds (e.g. Fijn and Gyimesi, 2018; Vanermen et al., 2020; Johnston et al., 2022). The current study demonstrated similar effects for a long-distance migrant during active migration bouts. The small-scale iSSM approach using different dataset and method combinations consistently revealed a higher density of curlews at about 450 m from OWFs, with a strong peak in selection length reflecting evasion at this distance class followed by avoidance at 0–350 m. However, compared with previous studies on foraging birds, the avoidance distance for migrating curlews was significantly higher, which might indicate both species-specific differences in avoidance distance, as well as significant behavioral differences between foraging and migrating birds with respect to OWFs in general. The distance from OWFs at which curlews demonstrated horizontal avoidance responses might be classified as anticipated meso-to macro-scale evasion behavior (May, 2015; Cook et al., 2018). In addition, individual curlews crossing the OWF did not show any indications of impulsive behavioral in-flight responses within the windfarm, as indicated by the lack of any significant altitude changes during crossing. This indicates that the individuals entering OWFs might either show micro-avoidance on a turbine scale (May, 2015) or do not avoid the turbines at all. However, we observed two cases of curlews that abruptly changed their flight courses within or in the vicinity of OWFs, resulting in a flight path of non-directed circles (Fig. S4), but whether this behavior was caused by the presence of the OWF is unknown.

Similar to the avoidance response in the vertical plane, we found no clear evidence for horizontal avoidance patterns of curlews on larger spatial scales. The decay in selection strength in the direct surroundings of the wind farm observed in both datasets (i.e. data thinned out to 300 s and 1,500 s) again indicates a small-scale horizontal avoidance response close to the OWFs. The approach using 1,500 s data revealed a reduced selection strength of about 30% within the closest (0–500 m) radius of the OWFs, which matched well with the orders of magnitude estimated in the small-scale analysis, where both strong decays and local increases in birds due to evasion of OWFs occurred within the 500 m radius (see above).

4.3. Estimation of proportion of curlews at elevated risk

The two main potential effects of OWFs on migrating birds such as curlews are collisions and barrier effects (Drewitt and Langston, 2006). Our GAMM and iSSM approaches showed that a high proportion of the GPS-tagged migrating curlews exhibited significant horizontal and vertical avoidance responses when approaching OWFs, suggesting that barrier effects might be the key issue. However, not all individuals showed avoidance responses, and GPS-tracking has demonstrated strong interference with wind turbines for curlews (Jiguet et al., 2021a). It is therefore important to estimate the proportion of curlews that migrate at elevated risk, which can be calculated using the following data: according to the crossing analysis, 45 out of 143 individuals crossed OWFs at least once during migration (31.5%), of which 50% and 18.5% crossed the OWFs at rotor level during spring and autumn migration, respectively (these seasonal differences were in accordance with flight altitudes recorded on a larger spatial scale; Schwemmer et al., 2022). These data suggest that about 15.8% and 5.8% of the overall curlew population migrates at elevated risk during autumn and spring, respectively. As flight altitudes and flight speeds of individuals crossing OWFs do not differ between day and night, the proportion of curlews migrating at elevated risk is not expected to differ with respect to time of day. Notably, these values should only be regarded as a general rough estimate and do not reflect spatial differences in elevated risk among sub-populations. According spatial differences in relative collision risks can be revealed by intersecting the flight density of migrating curlews and the location of OWFs (Fig. S5). The resulting map illustrates that the collision risk for curlews is currently highest in the southern North Sea between The Netherlands and the UK (Fig. S6).

Furthermore, as shown for songbirds (Hüppop et al., 2006), the proportions at elevated risk are likely to change substantially during severe weather, such as fog, rain, or storms that reduce visibility.

Regarding flight altitude, the proportion of curlews migrating at increased risk is higher during autumn (Schwemmer et al., 2022; this study). This is corroborated by the fact that a higher overall number and a higher number of inexperienced juveniles migrate during autumn (Sergio et al., 2019). Finally, curlews tend to migrate in flocks (Jiguet et al., 2021b), and the risk perception of OWFs is thus likely to depend on the size of the migrating flock. An analysis of the flocking behavior during migration was beyond the scope of this study, but will be important for further collision risk estimates.

In addition to the proportions of curlews migrating at elevated risk, most individuals avoided crossing OWFs at turbine levels because they showed horizontal and vertical avoidance behaviors. However, this behavior is associated with higher energetic costs resulting from increasing flight altitudes and/or navigating around OWFs. Although these additional distances might be low compared with the overall journey of long-distance migrants (Masden et al., 2009), given that curlews may migrate >3,500 km between their wintering and breeding grounds (Pederson et al., 2022), the high number of planned OWFs between these wintering and breeding grounds (Rusu, 2020; Offshore, 2021) suggests that these energetic costs will rise significantly in the future. Furthermore, long-distance migrants (such as a considerable proportion of the Eurasian curlew population) are known to expend their body reserves to a high degree during migration (e.g. Alerstam, 2001) and any additional barrier effects are thus likely to have negative impacts on their migration performance, such as longer stopover durations (Ramirez et al., 2022), and fitness-related consequences thus cannot be ruled out.

5. Conclusions

The current study demonstrates the existence of intense small-scale horizontal and vertical avoidance behaviors of OWFs in a migratory species using a large and unique international tracking dataset. Our findings clearly show that the majority of the curlew population avoids OWFs both, during the night and day. However, as an important result for marine spatial planning we also found that a considerable proportion of the curlew population might cross OWFs at rotor heights and that the overall proportion of curlews migrating at risk is far higher during autumn than during spring migration. Thus, temporal curtailments of OWFs during periods of most intensive migration and within areas of highest bird migration are a likely mitigation measure for conservation management. Furthermore, the extensive expansion plans for OWFs in the North and Baltic Seas (Rusu, 2020; Offshore, 2021) are likely to increase the overall risk for migrating bird species such as curlews. Our long-term dataset offered the option to check for repeatability of behavioral reactions of the same individuals during consecutive approaches to OWFs. However, we were not able to detect any consistencies which might indicate the lack of habituation to OWF.

Finally, our data clearly show that curlews react strongly to OWFs by altering their flight tracks vertically or horizontally, thus highlighting the significant barrier effects of OWFs. The current and future increases in OWFs in the Baltic and North Seas means that it is necessary to quantify the energetic costs to birds to assess the cumulative barrier effect of OWFs, particularly for long-distance migrants. Using an extended set of tagging data in the future, will allow to draw conclusions on behavioral reactions to OWFs during different weather situations which is needed to assess the options for temporal turbine curtailments during phases of severe weather when avoidance reactions of birds might be reduced.

Author contributions

PS and SG drafted the study; PS designed the methodology; PS wrote the manuscript; MM, PS, RP, and KH analyzed the data; PS, PB, JF, FJ, JE, RM, MP, PR, HK, SK, SF, HD, TF, and SG recorded the data. All authors contributed critically to the drafts and gave final approval for publication. All authors declare that they have no conflict of interest.

Funding

Tagging of curlews in the German Wadden Sea and data analyses were supported by the projects BIRDMOVE (FKZ 3515822100) and TRACKBIRD (FKZ 3519861400) funded by the German Federal Agency for Nature Conservation with funds from the Federal Ministry for the Environment, Nature Conservation and Nuclear Safety and Consumer Protection (BMUV). Tagging of breeding curlews in NW Germany was funded by the German Federal Agency for Nature Conservation (FKZ 3520 53 2052) and the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency (NLWKN) with funds from the Federal Ministry for the Environment, Nature Conservation, Nuclear Safety and Consumer Protection, Niedersächsische Bingo Umweltstiftung, the Senator for Climate Protection, Environment, Mobility, Urban Development and Housing of the State of Bremen, the National Park Administration of the Wadden Sea National Park of Lower Saxony, Niedersächsische Wattenmeer-Stiftung, NRW-Stiftung, Naturschutzstiftung des Landkreises Osnabrück, Naturschutzstiftung Kreis Steinfurt, the districts of Aurich, Cloppenburg, Cuxhaven, Diepholz, Emsland, Grafschaft Bentheim, Leer and Verden. Funding in France was received by the French Ministry of Ecology (project BirdMan) and the Agence Française de Développement, (project Limitrack, grant QUALIDRIS), Contrat de Plan Etat-Région, CNRS (grant ECONAT), Ligue pour la Protection des Oiseaux as well as by the project "Applied research for conservation of the Eurasian curlew" funded by the Estonian Environmental Investment Centre (grant No. 8172). Tagging of wintering curlews in the UK was funded by a donation to the Wash Wader Research Group.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Catching, handling and tagging of curlews complied with European laws. GPS-tagging of curlews in Germany was approved by the Ministerium für Energiewende, Klimaschutz, Umwelt und Natur 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 Lower Saxony State Office for Consumer Protection and Food Safety (LAVES) (file number 33-19-42502-04-17/2699). Approval for tagging Curlews (NW Germany) was obtained from LAVES, Senator for Labour, Women's Affairs, Health, Youth and Social Affairs in Bremen (both AZ 33.19-42502-04-20/3373, dated March 13, 2020, May 06, 2020) and the State Agency for Nature, Environment and Consumer Protection North Rhine-Westphalia (LANUV, AZ 81.April 02, 2020. A097, dated April 02, 2020). 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 license in Estonia was issued by the Matsalu Ringing Centre, 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). Capture, ringing and tagging of curlews in the UK was in accordance with the conditions stipulated by the British Trust for Ornithology and special methods permission (project number 12026).

We thank the many fieldwork helpers for their assistance with bird catching, in particular G (Niko) Nikolaus, T Sveridova, R Kylmänen, T Seimola, P Delaporte, R Vohwinkel, G Müskens, the team from Nature Reserve of Moëze-Oléron, and volunteer members of the Wash Wader Research Group. Furthermore, we would like to thank all people involved in the chick protection programs in Lower Saxony and North-Rhine Westphalia for information about nest locations and general support. We are grateful to Sue Furness for linguistic support.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.118131.

References

4C Offshore, 2021. Global Offshore Map. https://www.4coffshore.com/offshorewind/. (Accessed 13 December 2021).

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: International Symposium on Information Theory. Second Edition 267–281, 1973.

Alerstam, T., 2001. Detours in bird migration. J. Theor. Biol. 209, 319–331.

Allison, T.D., Jedrey, E., Perkins, S., 2008. Avian issues for offshore wind development. Mar. Technol. Soc. J. 42, 28–38.

Avgar, T., Potts, J.R., Lewis, M.A., Boyce, M.S., 2016. Integrated step selection analysis: bridging the gap between resource selection and animal movement. Methods Ecol. Evol. 7, 619.

BirdLife International, 2022. Species Factsheet: *Numenius Arquata*. http://www.birdlife.org. (Accessed 24 October 2022).

Bivand, R., Novosad, J., Lovelace, R., Monmonier, M., Snow, G., 2021. Package "spData". https://cran.r-project.org/web/packages/spData/spData.pdf. (Accessed 13 December 2021).

Brabant, R., Vanermen, N., Stienen, E.W.M., Degraer, S., 2015. Towards a cumulative collision risk assessment of local and migrating birds in North Sea offshore wind farms. Hydrobiol. (Sofia) 756, 633–674.

Chamberlain, D.E., Rehfisch, M.R., Fox, A.D., Desholm, M., Anthony, S.J., 2006. The effect of avoidance rates on bird mortality predictions made by wind turbine collision risk models. Ibis 148, 198–202.

Cleasby, I.R., Wakefield, E.D., Bearhop, S., Bodey, W., Votier, S.C., Hamer, K.C., 2015. Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. J. Appl. Ecol. 52, 1474–1482.

Cook, A.S.C.P., Humphreys, E.M., Bennet, F., Masden, E.A., Burton, N.H.K., 2018. Quantifying avian avoidance of offshore wind turbines: current evidence and key knowledge gaps. Mar. Environ. Res. 140, 278–288.

Dokter, A.M., Shamoun-Baranes, J., Kemp, M.U., Tijm, S., Holleman, I., 2013. High altitude bird migration at temperate latitudes: a synoptic perspective on wind assistance. PLoS One 8 (1), e52300. https://doi.org/10.1371/journal.pone.0052300.

Drewitt, A.L., Langston, R.H.W., 2006. Assessing the impacts of wind farms on birds. Ibis 148, 29–42.

European Commission, 2021. Delivering the European Green Deal. https://ec.europa.eu/info/strategy/priorities-2019-2024/european-green-deal/delivering-european-green-deal_en. (Accessed 24 October 2022).

Fijn, R., Gyimesi, A., 2018. Behaviour related flight speeds of sandwich terns and their implications for wind farm collision rate modelling and impact assessment. Enviro. Amp. Assess. Rev. 71, 12–16.

Fijn, R., Krijgsveld, K.L., Poot, M.J.M., Dirksen, S., 2015. Bird movements at rotor heights measured continuously with vertical radar at a Dutch offshore wind farm. Ibis 157, 558–566.

Fox, A.D., Desholm, M., Kahlert, J., Christensen, T.K., Petersen, I.K., 2006. Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. Ibis 148, 129–144.

Furness, R.W., Wade, H.M., Masden, E.A., 2013. Assessing vulnerability of marine bird populations to offshore wind farms. J. Environ. Manag. 119, 56–66.

Galtbalt, B., Lileyman, A., Coleman, J.T., Cheng, C., Ma, Z., Rogers, D.I., Woodworth, B. K., Fuller, R.A., Garnett, S.T., Klaassen, M., 2021. Far eastern curlew and whimbrel prefer flying low – wind support and good visibility appear only secondary factors in determining migratory flight altitude. Move. Ecol. 9, 32. https://doi.org/10.1186/s40462-021-00267-5.

Garthe, S., Schwemmer, H., Peschko, V., Markones, N., Müller, S., Schwemmer, P., Mercker, M., 2023. Large-scale effects of offshore wind farms on seabirds of high conservation concern. Sci. Rep. 13, 4779. https://doi.org/10.1038/s41598-023-31601-z.

Gauld, J.G., Silva, J.P., Atkinson, P.W., Record, P., Acácio, M., Arkumarev, V., Blas, J., Bouten, W., Burton, N., Catry, I., Champagnon, J., Clewley, G.D., Dagys, M., et al., 2021. Hotspots in the grid: avian sensitivity and vulnerability to collision risk from energy infrastructure interactions in Europe and North Africa. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.14160.

Guillaumet, A., Dorr, B., Wang, G., Taylor, J.D., Chipman, R.B., Scherr, H., et al., 2011. Determinants of local and migratory movements of Great Lakes double-crested cormorants. Behav. Ecol. 22, 1096–1103.

Hastie, T., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman and Hall, London, UK.

Helcom – Baltic Marine Environment Protection Commission, Helsinki Commission, 2021. Map and Data Service. https://maps.helcom.fi/website/mapservice/. (Accessed 13 December 2021).

Hull, C.L., Muir, S.C., 2013. Behavior and turbine avoidance rates of eagles at two wind farms in Tasmania, Australia. Wind Energy Wild. Cons 37, 49–58.

Hüppop, O., Dierschke, J., Exo, K.-M., Fredrich, E., Hill, R., 2006. Bird migration studies and potential collision risk with offshore wind turbines. Ibis 148, 90–109.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.

Jiguet, F., Bocher, P., Kruckenberg, H., Kämpfer, S., Debenest, E., Lorillière, R., Rousseau, P., Szajda, M., Düttmann, H., 2021. Joint Flight Bouts but Short-Term

Association in Migrating Eurasian Curlews *Numenius Arquata*. Bird Study. https://doi.org/10.1080/00063657.2021.1962805.

Jiguet, F., Schwemmer, P., Rousseau, P., Bocher, P., 2021a. GPS tracking data can document wind turbine interactions: evidence from a GPS-tagged Eurasian curlew. Forens. Sci. Int. Anim. Env. 1, 100036 https://doi.org/10.1016/j.fsiae.2021.100036.

Johnston, D.T., Thaxter, C.B., Boersch-Supan, P.H., Humphreys, E.M., Bouten, W., Clewley, G.D., Scragg, E.S., Masden, E.A., Barber, L., Conway, G.J., Clark, N.A., Burton, N.H.K., Cook, A.S.C.P., 2022. Investigating avoidance and attraction responses in lesser black-backed gulls *Larus fuscus* to offshore wind farms. Mar. Ecol. Prog. Ser. 686, 187–200.

Kays, R., Davidson, S.C., Berger, M., Bohrer, G., Fiedler, W., Flack, A., Hirt, J., Hahn, C., Gauggel, D., Russell, B., et al., 2021. The movebank system for studying global animal movements and demography. Methods Ecol. Evol. 1–13. https://doi.org/10.1111/2041-210X.13767, 2021;00.

Khosravifard, S., Skidmore, A.K., Naimi, B., Venus, V., Muñoz, A.R., Toxopeus, A.G., 2020. Identifying birds' collision risk with wind turbines using a multidimensional utilization distribution method. Wild. Soc. Bull. 44, 191–199.

Kleyheeg-Hartman, J.C., Krijgsveld, K.L., Collier, M.P., Poot, M.J.M., Boon, A.R., Troost, T.A., Dirksen, S., 2018. Predicting bird collisions with wind turbines: comparison of the new empirical Flux Collision Model with the SOSS Band model. Ecol. Model. 387, 144–153.

Kokonendji, C., Demetrio, C., Dossou-Gbete, S., 2004. Overdispersion and Poisson-Tweedie exponential dispersion models. Mon. Sem. Mat. Garcia Galdeano 31, 365–374.

Lato, K.A., Stepanuk, J.E.F., Heywood, E.I., Conners, M.G., Thorne, L.H., 2022. Assessing the accuracy of faltitude estimates in avian biologging devices. PLoS One 17 (10), e0276098. https://doi.org/10.1371/journal.pone.0276098.

Leopold, M.F., Boonman, M., Collier, M.P., Davaasuren, N., Fijn, R.C., Gyimesi, A., de Jong, J., Jungbloed, R.H., Poerink, B.J., Kleyheeg-Hartman, J.C., Krijgsveld, K.L., Lagerveld, S., Lensink, R., Poot, M.J.M., van der Wal, J.T., Scholl, M., 2015. A first approach to deal with cumulative effects on birds and bats of offshore wind farms and other human activities in the southern North Sea. IMARES Wageningen UR Report number C166/14. https://research.wur.nl/en/publications/a-first-approach-to-deal-with-cumulative-effects-on-birds-and-bat. (Accessed 24 October 2022).

Lindén, A., Mäntyniemi, S., 2011. Using the negative binomial distribution to model overdispersion in ecological count data. Ecology 92, 1414.

Mallory, M.L., Gilbert, C.D., 2008. Leg-loop harness design for attaching external transmitters to seabirds. Mar. Ornithol. 36, 183–188.

Masden, E.A., Cook, A., 2016. Avian collision risk models for wind energy impact assessments. Environ. Impact Assess. Rev. 56, 43–49.

Masden, E.A., Haydon, D.T., Fox, A.D., Furness, R.W., Bullman, R., Desholm, M., 2009. Barriers to movement: impacts of wind farms on migrating birds. ICES J. Mar. Sci. 66, 746–753.

Masden, E.A., Reeve, R., Desholm, M., Fox, A.D., Furness, R.W., Haydon, D.T., 2012. Assessing the impact of marine wind farms on birds through movement modelling. J. R. Sec. Interface 9, 2120–2130.

Masden, E.A., Cook, A., McCluskie, A., Bouten, W., Burton, N., Thaxter, C.B., 2021. When speed matters: the importance of flight speed in an avian collision risk model. Environ. Impact Assess. Rev. 90, 106622 https://doi.org/10.1016/j.eiar.2021.106622.

May, R.F., 2015. A unifying framework for the underlying mechanisms of avian avoidance of wind turbines. Biol. Conserv. 190, 179–187.

Mendel, B., Schwemmer, P., Peschko, P., Müller, S., Schwemmer, H., Mercker, M., Garthe, S., 2019. Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia* spp.). J. Environ. Manag. 231, 429.

Mercker, M., Markones, N., Schwemmer, H., Borkenhagen, K., Wahl, J., Garthe, S., 2021a. An integrated framework to estimate seabird population numbers and trends. J. Wildl. Manag. https://doi.org/10.1002/jwmg.22026.

Mercker, M., Schwemmer, P., Peschko, V., Enners, L., Garthe, S., 2021b. Analysis of local habitat selection and large-scale attraction/avoidance based on animal tracking data: is there a single best method? Move. Ecol. 9, 20.

Muff, S., Signer, J., Fieberg, J., 2018. Accounting for individual-specific variation in habitat-selection studies: efficient estimation of mixed-effects modes using Bayesian or frequentist computation. J. Anim. Ecol. https://doi.org/10.1111/1365-2656.13087.

Pebesma, E., 2018. Simple features for R: standardized support for spatial vector data. The R Journal 10, 439–446. https://doi.org/10.32614/RJ-2018-009. (Accessed 13 December 2021).

Pederson, R., Bocher, P., Garthe, S., Fort, J., Mercker, M., Auernhammer, V., Boschert, M., Delaporte, P., Elts, J., Fiedler, W., Korniluk, M., Krupiński, D., Marja, R., Rousseau, P., Tiess, L., Schwemmer, P., 2022. Bird migration in space and time – chain migration by Eurasian curlew (*Numenius arquata arquata*) along the East Atlantic Flyway. J. Avian Biol. 2022, e02924 https://doi.org/10.1111/jav.02924.

Péron, G., Calabrese, J.M., Duriez, O., Fleming, C.H., García-Jiménez, R., Johnston, A., Lambertucci, S.A., Safi, K., Shepard, E.L.C., 2020. The challenges of estimating the distribution of flight heights from telemetry or altimeter data. Anim. Biotelem 8, 5. https://doi.org/10.1186/s40317-020-00194-z, 2020.

Peschko, V., Mendel, B., Müller, S., Markones, N., Mercker, M., Garthe, S., 2020. Effects of offshore windfarms on seabird abundance: strong effects in spring and in the breeding season. Mar. Environ. Res. 162, 105157.

Phillips, R.A., Xavier, J.C., Croxall, J.P., 2003. Effects of satellite transmitters on albatrosses and petrels. Auk 120, 1082–1090. https://doi.org/10.1093/auk/120.4.1082.

Poessel, S.A., Duerr, A.D., Hall, J.C., Braham, M.A., Katzner, T.E., 2018. Improving estimation of flight altitude in wildlife telemetry studies. J. Appl. Ecol. 55, 2064–2070. https://doi.org/10.1111/1365-2664.13135.

Prater, A.J., Marchant, J.H., Vuorinen, J., 1977. Guide to the Identification & Ageing of Holarctic Waders. British Trust for Ornithology, Norrköping, Sweden.

QGIS Development Team, 2022. The Open Source Geographic Information System (GIS) Software QGIS, version 3.24.0.

R Development Core Team, 2022. R. R, Vienna, Austria, Version 3.5.3.

Ramirez, M.G., Griego, M., DeSimone, J.G., Elowe, C.R., Gerson, A.R., 2022. Depleted lean body mass after crossing an ecological barrier differentially affects stopover duration and refuelling rate among species of long-distance migratory birds. Funct. Ecol. 1–12, 2022;00.

Rue, H., Martino, S., Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. J. Roy. Stat. Soc. B 71, 319. https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1467-9868.2008.00700.x.

Rusu, E., 2020. An evaluation of the wind energy dynamics in the Baltic Sea, past and future projections. Renew. Energy 160, 350–362.

Schaub, T., Klaassen, R.H.G., Bouten, W., Schlaich, A., Koks, B.J., 2020. Collision risk of Montagu's harriers *Circus pygargus* with wind turbines derived from high-resolution GPS tracking. Ibis 162, 520–534.

Schwemmer, P., Mercker, M., Vanselow, K.H., Bocher, P., Garthe, S., 2021. Migrating curlews on schedule: departure and arrival patterns of a long-distance migrant depend on time and breeding location rather than on wind conditions. Move. Ecol. 9, 9. https://doi.org/10.1186/s40462-021-00252-y, 2021.

Schwemmer, P., Pederson, R., Haecker, K., Bocher, P., Fort, J., Mercker, M., Jiguet, F., Elts, J., Marja, R., Piha, M., Rousseau, P., Garthe, S., 2022. Assessing potential conflicts between offshore wind farms and migration patterns of a threatened shorebird specs. Anim. Conserv. https://doi:10.1111/acv.12817.

Sergio, F., Tavecchia, G., Tanferna, A., Blas, J., Blanco, G., Hiraldo, F., 2019. When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. Sci. Rep. 9, 17352. https://doi.org/10.1038/s41598-019-54026-z, 2019.

Signer, J., Fieberg, J., Avgar, T., 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. Ecol. Evol. 9, 880.

Skov, H., Heinänen, S., Norman, T., Ward, R., Méndez-Roldán, R.M., Ellis, S., 2018. ORJIP Bird collision and avoidance study. In: Final Report – Apirl 2018. The Carbon Trust, p. 247. United Kingdom. https://www.dirm.mediterranee.developpement-durable.gouv.fr/IMG/pdf/orjip-bird-collision-avoidance-study_april-2018.pdf. (Accessed 12 December 2022).

Summers, R.W., Pálsson, S., Etheridge, B., Foster, S., Swann, R.L., 2013. Using biometrics to sex adult Eurasian curlews *Numenius a. arquata*. Wader Study Group Bull. 120, 71–74.

Thieurmel, B., Elmarhraoui, A., 2019. Package Suncalc. https://cran.r-project.org/web/packages/suncalc/suncalc.pdf. (Accessed 13 December 2021).

van Roomen, M., van Turnhout, C., Blew, J., Koffijberg, K., Nagy, S., Citegetse, G., Foppen, R., 2019. East Atlantic Flyway. In: Kloepper, S., et al. (Eds.), Wadden Sea Quality Status Report 2017, Common Wadden Sea Secretariat. Wilhelmshaven, Germany. https://qsr.waddensea-worldheritage.org/reports/east-atlantic-flyway. (Accessed 13 December 2021).

Vanermen, N., Courtens, W., Daelemans, R., Lens, L., Müller, W., Van, de Walle, M., Verstraete, H., Stienen, E.W.M., 2020. Attracted to the outside: a meso-scale response pattern of lesser black-backed gulls at an offshore wind farm revealed by GPS telemetry. ICES J. Mar. Sci. 77, 701–710.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, fourth ed. Springer, New York.

Wood, S., 2017. Generalized Additive Models: an Introduction with R. Chapman & Hall/CRC.

Wood, S., 2022. Package Mgcv: Mixed GAM Computation Vehicle with Automatic Smoothness Estimation. https://cran.r-project.org/web/packages/mgcv/mgcv.pdf. (Accessed 12 December 2022).

Wind Europe, 2021. Offshore Wind in Europe. Key Trends and Statistics 2020. https://windeurope.org/intelligence-platform/product/offshore-wind-in-europe-key-trends-and-statistics-2020/. (Accessed 24 October 2022).

Zhang, T., Tian, B., Sengupta, D., Zhang, L., Si, Y., 2021. Global offshore wind turbine dataset. Sci. Data 8, 181.

Zuur, A.F., Leno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effect Models and Extensions in Ecology with R. Springer Science+Business Media, LLC, New York.

Zuur, A.F., Leno, E.N., Saveliev, A.A., 2017. Spatial, Temporal and Spatial-Temporal Ecological Data Analysis with R-INLA, ume vols. I-II. Highland Statistics Ltd, Newburgh.