Conservation Science and Practice
A journal of the Society for Conservation Biology   WILEY

CONTRIBUTED PAPER

Drivers of flight altitude during nocturnal bird migration over the North Sea and implications for offshore wind energy

Maja Bradarić[1] ⓘ | Bart Kranstauber[1] | Willem Bouten[1] |
Hans van Gasteren[1,2] | Judy Shamoun Baranes[1]

[1]University of Amsterdam, Amsterdam, The Netherlands

[2]Royal Netherlands Air Force, Breda, The Netherlands

Correspondence
Maja Bradarić, University of Amsterdam, Amsterdam, The Netherlands.
Email: m.bradaric@uva.nl

Abstract

Each year, millions of birds migrate nocturnally over the North Sea basin, an area designated for significant offshore wind energy development. Wind turbines can harm aerial wildlife through collisions and barrier effects, especially when birds fly at low altitudes below the wind turbine rotor tip. We aim to quantify seasonal and nightly differences in flight altitudes of nocturnal bird migration over the North Sea and identify how weather influences low-altitude flight to inform wind turbine curtailment procedures for reducing bird fatalities. We used bird tracking radars at Borssele and Luchterduinen offshore wind parks, 22 and 23 km from the western Dutch coast, to monitor altitude distributions during migration. We show that median flight altitude was higher in spring compared to autumn at Borssele (spring: 285.5 m, autumn: 169.2 m; $p < .001$, effect size [ES] = 0.0001) and Luchterduinen (spring: 133.8 m, autumn: 126.0 m; $p < .001$, ES = 0.002) and below wind turbine rotor tip in both seasons. On most nights in both seasons, the majority of migrants flew predominantly at low altitudes, except for intense migration nights in spring in Borssele where, on 87% of these nights, migration mainly occurred at high altitudes. The most important predictors of low-altitude migration in both seasons were day of year and wind assistance. Birds chose altitudes with the most favorable wind conditions for migration in both seasons. The relationship between day of year and low-altitude migration fraction suggests that different species migrate at different altitudes. In spring, birds were flying lower at the beginning and the end of the night, reflecting departures and arrivals of birds, while radar location in autumn was a good predictor of low-altitude flights, indicating that different local migratory axes have distinct altitude distributions. Our findings suggest that mitigation measures offshore may be more effective during autumn than spring, especially on nights with more supportive wind conditions at altitudes below 300 m.

1 | INTRODUCTION

The North Sea basin is an important area for current and future investments in European wind energy production due to suitable wind conditions (Kafas et al., 2018). While offshore wind farms will help achieve targets for reducing carbon emissions, they may negatively impact marine (Bergström et al., 2014; Wright et al., 2020) and aerial wildlife (Cabrera-Cruz et al., 2020). A growing body of literature shows that wind farms pose a threat to bats and birds through mortality due to collisions (Hayes et al., 2019; Marques et al., 2014; Perold et al., 2020) or through barrier effects and habitat change (Drewitt & Langston, 2006; Gaultier et al., 2020). With the increase of wind turbine density and size over the years (McKenna et al., 2016), these adverse effects are expected to be more pronounced in the future (Lambertucci & Speziale, 2021).

Millions of birds, mainly thrushes (*Turdus* sp.), migrate over the North Sea every year during the night (Hüppop et al., 2006; Hüppop et al., 2016; Lensink et al., 1999). Governed by weather, primarily wind (Bradarić et al., 2020; Manola et al., 2020; Shamoun-Baranes & van Gasteren, 2011), they follow two primary migration axes: between Scandinavia and southern Europe or Africa (NE–SW axis) and between mainland Europe and the United Kingdom (E-W axis) (Lack, 1959) (Figure 1). When performing nocturnal migration, birds experience the stratification of the troposphere due to the collapse of the convective boundary layer, which creates different weather conditions at different altitudes (Stull, 1988). Because of this, birds can select altitudes with
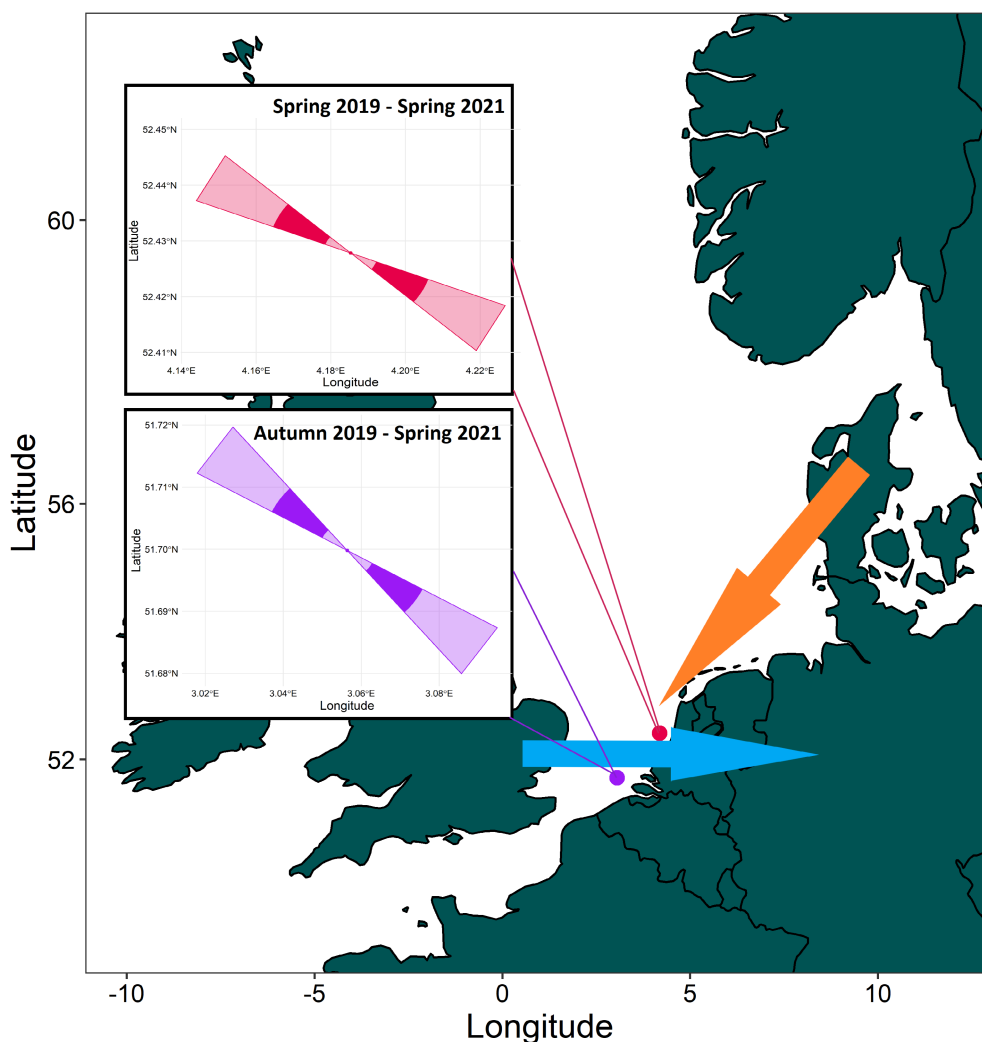
FIGURE 1 Map of the Dutch Northern Sea, showing radar locations in Luchterduinen (red dot) and Borssele (purple dot). Inlays show the orientation of vertical radar beams in the horizontal plane, color-coded according to the radar locations. The darker areas represent the areas with the highest detection probability within the vertical beam from which the data for the analysis was extracted (between 500 and 1500 m from the radar location). The migration periods used for the study are indicated in the upper right corner of the inlays. Arrows show the main migration directions in the area in spring (90° blue) and autumn (220° orange) (Bradarić et al., 2020; Shamoun-Baranes & van Gasteren, 2011). These migration directions were used to calculate wind assistance.

weather conditions that will help them maintain the desired migration direction and reduce time or energy invested in migration (Alerstam, 1990, 2011; Liechti, 2006; Newton, 2008).

At mid-latitudes (between 30 and 60° on each side of the equator), wind conditions do not differ with altitude as strikingly as in the trade-wind zone (James & Stull, 2019; Rohli & Vega, 2018), but they still show spatial and temporal variability due to the frequent passage of high and low-pressure systems (Richardson, 1978). Radar studies over the Netherlands (Kemp et al., 2013), from the North Sea coast (Lack, 1960), and the Bay of Biscay (Weisshaupt et al., 2016) showed that birds flew higher in spring than in autumn due to different seasonal weather patterns. Radar studies over land showed that birds selected altitudes with increased tailwind support (Dokter et al., 2013; Kemp et al., 2013) but only climbed to altitudes where they first encounter supportive winds (Kemp et al., 2013). Furthermore, Kemp et al. (2013) showed that birds avoided altitudes with temperatures below freezing when migrating over land. Contrary to what was observed over land in mid-latitudes, early radar studies of migration over the North Sea did not find a correlation between wind speed and direction and altitude choice (Eastwood & Rider, 1965). Instead, birds have been observed changing their altitude to avoid rain and clouds, usually flying above them (Eastwood & Rider, 1965; Lack, 1963).

Apart from the early radar studies, knowledge about the effect of weather on flight altitudes of nocturnal migrants over the North Sea is limited. Studies in the German North Sea recorded nocturnal migration mainly at the lowest 200 m above sea level (asl) (Hüppop et al., 2006), and measurements in the Dutch North Sea showed that about 40% of total nocturnal bird activity per year occurred at altitudes below 115 m (Fijn et al., 2015). Nevertheless, they do not provide insight into the drivers of temporal variation of altitude distributions.

To implement effective conservation, it is essential to understand not only environmental factors that govern bird migration intensity but also the altitude distributions, especially those conditions that result in flight at low altitudes, where birds are at risk of colliding with turbines. Adverse effects of offshore wind farms on birds flying at low altitudes can be minimized by developing procedures that include forecast models relying on environmental factors as input to predict bird migration intensity (Doren & Horton, 2018; van Belle et al., 2007). Such models have already been in place to improve flight safety and decrease the risk of collisions between migratory birds and aircraft (van Gasteren et al., 2019). In the case of the North Sea, similar models can be used for wind turbine stop–start procedures to mitigate collision risk when intense migration occurs at rotor height.

We investigate mid-latitude nocturnal migration over the sea by quantifying seasonal differences in flight altitudes over the North Sea and identify the main drivers of hourly altitude distributions to inform wind turbine curtailment procedures to reduce bird fatalities. In the context of wind energy, we distinguish between low-altitude migration (occurs up to 300 m, which is the maximum turbine rotor tip height) and high-altitude migration (>300 m). This study addresses the following questions: (i) What is the seasonal altitude distribution of migration, and how does it compare to the wind turbine rotor tip height? (ii) Since the wind turbine curtailment will be performed on a nightly basis, what is the percentage of nights in which the majority of the nocturnal migrants fly at low altitudes and how does this differ between spring and autumn and different radar locations? (iii) How does the hourly fraction of low-altitude migration vary with wind, temperature, cloud cover, location, day of the year, and hour of night in two migration seasons? We use data collected by offshore bird tracking radars at two wind farms off the Dutch western coast to answer these questions. We hypothesize that birds will choose flight altitudes with higher wind assistance (WA; Dokter et al., 2013; Kemp et al., 2013) and temperatures above zero (Kemp et al., 2013) to increase migration speed and decrease energy expenditure. Furthermore, we expect birds will generally fly at altitudes where cloud cover is relatively low (Eastwood & Rider, 1965) to improve visibility. Due to differences in migration direction and weather regimes, flight altitude distributions are expected to differ between spring and autumn, with migration occurring at higher altitudes in spring (Dokter et al., 2013; Kemp et al., 2013). We explain how our results can better inform conservation measures, especially in light of the curtailment of wind turbines when flight altitudes are critical.

2 | MATERIALS AND METHODS

2.1 | The radar system, location, and study period

Bird movement data were collected by bird radars (Robin Radar 3D fix, Robin Radar Systems BV, the Hague, Netherlands) at two offshore locations in the Dutch North Sea (Figure 1). One radar, located in Luchterduinen wind farm (52.25 N, 4.10 E), has been operational since August 2018, ca 23 km from the western coast of

4 of 15 | WILEY— _Conservation Science and Practice_
A journal of the Society for Conservation Biology
BRADARIĆ ET AL.

the Netherlands. The radar in Borssele wind farm (51.35 N, 3.00 E), ca 22 km from the SW Dutch coast, has collected data since August 2019.

Robin radar's 3D-fixed system consists of two antennae: a vertically rotating X-band antenna (beam width 20°) with a power of 25 kW and a horizontally rotating S-band antenna (beam width 25°) with a power of 60 kW. The Borssele radar was mounted on a platform with the vertical antenna at 47.6 m asl and the horizontal antenna at 39.5 m asl (Appendix 1) while the Luchterduinen radar was positioned on a platform within the wind farm with both antennas at 22 m asl. The vertical antenna was oriented perpendicular to the main migratory direction observed in the region (Bradarić et al., 2020; Shamoun-Baranes & van Gasteren, 2011) to maximize the number of detected birds (Figure 1). Both antennae rotate at 45 rpm and collect information about the position of targets in each rotation. The system uses a proprietary tracking algorithm to detect moving targets and distinguish between birds and non-birds based on target characteristics (e.g., speed, direction, and radar cross-section in the horizontal antenna and radar cross-section in the vertical antenna). Targets in at least five (vertical antenna) or eight (horizontal antenna) consecutive rotations are joined in tracks and automatically stored in a centralized database. In this system, flight altitude is measured by the vertical antenna. As part of its software, the radar system employs automated clutter filters to reduce the number of non-bird targets. Clutter filters are applied dynamically in each radar scan and expressed as a fraction of the total scan in which clutter is detected with a value between 0 (no clutter on the radar image) and 1. Dynamic filters mainly reduce clutter from landscape features, waves, and rain.

We extracted the number of tracks and track altitude measured by the vertical radar antenna from spring (February 15–May 31) and autumn (August 15– November 30) migratory seasons of 2019 (only autumn for Borssele radar), 2020 and 2021 (only spring). Targets with a radar cross-section below -40 dBm^2 and greater than 10 dBm^2 were classified as non-birds (e.g., insects, boats) by the proprietary software and excluded from the analysis. The subsequent post-processing steps, detailed in the following text, effectively reduce the number of targets that could be potentially misclassified as insects due to overlapping RCS values with small birds. Visual inspections of RCS distributions across different months confirm the negligible impact on analysis outcomes. Since most migratory land birds in this area are nocturnal migrants, in this study, we used only tracks recorded between civil sunset and sunrise for the periods mentioned above.

2.2 | Post-processing of radar data

To improve the dataset quality, we implemented several post-processing steps in addition to the filters that are part of the proprietary radar software. The vertical radar antenna records various bird targets up to 3000 m. However, the probability of detecting small birds decreases significantly after 1500 m asl (Appendix 2). Therefore, we only included the tracks recorded up to 1500 m asl in our analysis. Furthermore, due to the narrow beamwidth close to the radar resulting in insufficient detections, clutter and a higher probability of insect detection close to the radar, as well as detection loss of small songbirds further from the radar, only tracks with a horizontal distance from the radar between 500 and 1500 m were used in our analysis (Appendix 3).

Occasionally, rain was mistakenly recorded as bird targets despite the dynamic clutter filter. We performed a two-step filtering procedure to exclude such targets from our dataset, which included filtering out the rain minutes from the data (Appendix 4).

To identify environmental drivers influencing altitude distributions during migration, we focus on nights with substantial migration and sufficient hourly coverage within a night. Therefore, after the performance of the previous filtering steps, we removed all hours in which bird counts were low (<10 birds/h). We also removed nights with less than 3 h of data remaining.

We report percentages of tracks removed with each filtering step in Appendix 5. After post-processing, 289,358 tracks, distributed across 167 nights and 1658 h, were left for analysis at the Borssele location in spring and 631,711 tracks, 186 days, and 2199 h in autumn. At Luchterduinen, 511,794 tracks, within 255 nights and 2649 h, were left in spring and 561,932 tracks, 186 nights and 2079 h in autumn. Following post-processing, each track was classified as either low (<=300 m) or high (>300 m) altitude based on the altitude measured by the radar. We selected a threshold of 300 m as this is the altitude of the rotor blade tips for the largest turbines currently developed. We calculated the percentage of tracks at high or low altitudes per hour and per night for analyses described further below. We also calculated the total number of tracks per night and selected the top 10% of nights, in spring and autumn, with the highest migration intensity as intense migration nights.

2.3 | Weather data

European Centre for Medium-Range Weather Forecast ERA5 reanalysis dataset (Hersbach et al., 2020) with a

global extent and 0.25° grid size was used to assess weather variables closest to the radar locations. Weather variables were obtained from the closest grid cells to the radar, 52.25 N 4.00 E for Luchterduinen and 51.25 N 3.00 E for Borssele. We extracted air temperature (t, °C) and the fraction of cloud cover (cc, 0–1, 0 representing no cc) at each location from pressure levels of 912.5 and 1012.5 hPa that correspond to altitudes of approximately 1000 and 130 m asl (U.S. Standard Atmosphere, 1976). The altitude asl of these variables can vary depending on changes in pressure systems. Wind components that describe wind from west to east (u) and south to north (v) were retrieved from 912.5 hPa pressure level and a single level of 100 m of altitude above the surface of the Earth. In contrast to the pressure level variables, the single-level variables always contain values from the exact altitude. Low-altitude winds were calculated from the single-level dataset to ensure the most representative measurements were used. Other variables were not available at a single level. When applicable, all weather variables from 912.5 hPa will be referred to as "high-altitude weather variables," while the temperature and cloud cover from 1012.5 hPa and wind from 100 m asl will be referred to as "low-altitude weather variables." As we are interested in understanding the influence of weather variables on the fraction of birds flying at low altitudes, the difference in conditions between altitudes is likely more relevant than the specific conditions at a given altitude. Therefore, to capture the difference in conditions between altitudes and to limit the number of predictors, we calculated the differences between low- and high-altitude weather variables and the average between low and high altitudes. An overview of the seasonal weather variables at low and high altitudes for our study period is available in Appendix 6.

2.4 | Wind assistance

To estimate the support of wind that birds experience, hourly low and high-altitude wind direction and wind speed were calculated and used in the tailwind equation (Kemp et al., 2012) to calculate low and high-altitude WA:

$$WA = y\cos\theta$$

where y is wind speed (m/s), and θ is the difference between the wind direction the wind is blowing to and the preferred migration direction. We rely on the average direction per season as no directional information is available for migration within the vertical radar. The seasonal primary migration direction of birds in the area

was calculated in previous studies as follows: 90° in spring and 220° in autumn (Bradarić et al., 2020; Shamoun-Baranes & van Gasteren, 2011). Low-altitude and high-altitude WA were then used to calculate the difference between low and high-altitude WA and average WA.

2.5 | Migration altitudes

We used kernel density estimation to estimate altitude probability density functions for each season and location based on all tracks included in the data analysis. The median and 90% percentile of flight altitude in spring and autumn were calculated for both radars and compared with the 300 m threshold. We performed a Kruskal–Wallis test to assess whether altitude distributions differed between seasons and locations. We used eta squared based on the H statistics to estimate the effect size (ES).

Since wind turbine curtailment will be performed on a nightly basis, we wanted to show what percentage of nights would be a candidate for curtailment based on the proportion of birds flying at low or high altitudes. Therefore, we assessed the percentage of nights in which the majority (>50%) of birds flew at low or high altitudes per season and radar location. Similarly, we calculated the percentage of nights when flight altitude was concentrated (>90% of tracks per night) at either low or high altitudes (we refer to these nights as nights with extremely low or high altitude migration). We used Barnard's unconditional test to statistically compare the percentages of extremely low and high-altitude migration nights between different seasons and locations. In addition, to consider nights in which conservation implications for curtailment would be higher, we qualitatively compared the number of intense migration nights when 50 and 90% of the tracks were either low or high, as sample sizes were very small.

To analyze the relationship between flight altitudes and weather variables under which birds fly at low altitudes, we used random forest (RF) regression models implemented in the "ranger" package (Wright & Ziegler, 2017) within the R software (R Core Team, 2020). We developed separate models per season (spring and autumn) and used data from both locations in the same model. The hourly fraction of birds at low altitudes was used as a continuous response variable. Radar location and weather variables described above were used as predictors in our model (Table 1). We included day of year (year_day) as a predictor in our model to account for potential phenological differences in response to weather and flight altitude selection due to different timings of migration between short and long-distance migrants (Lensink et al., 2002; Werham

6 of 15 | **WILEY** Conservation Science and Practice
A journal of the Society for Conservation Biology
Open Access

BRADARIĆ ET AL.

TABLE 1 Overview of variables considered as predictors of migration ratio at low altitudes. Variables marked with an asterisk (*) were excluded from the model since they showed a high level of correlation in the correlation matrix (Appendix 5).

Predictor	Abbreviation	Unit	Explanation
Average cloud cover	avg_cc*	0–1	The average value of low and high altitude cloud cover.
Delta cloud cover	delta_cc	0–1	The difference in cloud cover between low and high altitudes.
Average temperature	avg_temp	°C	The average value of low and high altitude air temperature.
Delta temperature	delta_temp	°C	The difference in air temperature between low and high altitude.
Average wind assistance	avg_wa	m/s	The average value of low and high altitude wind assistance.
Delta wind assistance	delta_wa	m/s	The difference in wind assistance between low and high altitudes.
Hour before sunrise	sunr_h*	hours	The number of hours before sunrise.
Hour after sunset	suns_h	hours	The number of hours after sunset.
Day of year	y_day	days	Day number since the start of a year.
Radar location	radar		A category that indicates which radar recorded the measurements.

et al., 2002). Finally, the number of hours after sunset (suns_h) and before sunrise (sunr_h) were also used as predictors to determine if low-altitude migration is more likely to occur at a specific time during the night.

Highly correlated predictors do not explain additional variance in the model and can affect its ability to identify the importance of predictors (Gregorutti et al., 2017). Therefore, we generated correlation matrices using Spearman's rank correlation coefficient with the "corrplot" package (Wei & Simko, 2021), removing the highly correlated predictors with a correlation coefficient of 0.8 and higher (Dormann et al., 2013; Mukaka, 2012). Correlation matrices identified average cloud cover (avg_cc) and difference in cloud cover between low and high altitudes (delta_cc) and suns_h and sunr_h as highly correlated predictors. In both seasons, delta_cc and suns_h were kept in the model. Delta_cc was retained as it contains more information about cloud cover at different altitudes than the avg_cc. Furthermore, we expect birds to fly at altitudes at which cloud cover is low, thus changing their altitude to fly above or below clouds, and such information cannot be extracted from avg_cc. Birds generally embark on their nocturnal journeys around sunset, creating a peak of migration intensity (Åkesson et al., 1996; Alerstam, 1990; Doren & Horton, 2018), which is why suns_h was kept in the model. The correlation matrices can be found in Appendix 7. A complete list of all predictors used for developing the model can be found in Table 1.

2.6 | Model calibration

RF regression models require three parameters: *num.trees* (number of regression trees), *mtry* (number of variables randomly sampled as candidates in each node split) and *min.node.size* (the minimal number of observations included in terminal nodes of the tree). We tested *num.trees* values from 100 to 5000 with 100 increments, *mtry* from 2 to 7 with increments of 1 and *min.node.size* from 2 to 9 with increments of 1 to select model parameters with the lowest root mean squared error (RMSE). In spring, the lowest error was reached with *num.trees* = 1300, *mtry* = 4 and *min.node.size* = 2. In autumn *num.trees* = 500, *mtry* = 5 and *min.node.size* = 2 were selected.

2.7 | Cross-validation

Before developing RF regression models, we randomly split the datasets for both seasons into training and testing datasets based on the 70:30 rule (Nguyen et al., 2021). We assigned data to a training dataset by choosing all the tracks recorded by the radar on 70% of randomly chosen nights. The rest (30%) was assigned to a test dataset. Random nights were used to split the data to decrease the effect of temporal autocorrelation in biological and environmental processes. We used the test dataset to assess the performance of model predictions by calculating RMSE between the test dataset and model predictions.

2.8 | Model evaluation

Each tree in the RF has its out-of-bag (OOB) data sample that was not used during the tree construction. These observations were used in the model fitting process to calculate the OOB mean square error (prediction error) and R^2, which showed how much variance the model explained. The RF algorithm evaluated each predictor's importance based on the variance explained when the predictor was removed from the model. Furthermore, we created partial dependence plots to assess each predictor's relationship with the response variable while other predictors remained constant.

3 | RESULTS

3.1 | Migration altitudes

In spring, the median flight altitude was 285.5 m asl at Borssele and 133.8 m asl at Luchterduinen, both lower than the 300 m turbine threshold (Figure 2). In autumn, the median was 169.2 at Borssele and 126.0 m asl at Luchterduinen (Figure 2). Altitude distributions differed significantly between spring and autumn in both locations (B: H = 176.9, df = 1, $p < .001$, ES = 0.0001; L: H = 3330.1, df = 1, $p < .001$, ES = 0.003). They also significantly differed between Borssele and Luchterduinen in spring (H = 1665.3, df = 1, $p < .001$, ES = 0.002) and autumn (H = 4277.1, df = 1, $p < .001$, ES = 0.003).

On 68.9% of nights in spring at Borssele, more than 50% of migrants were flying low, which did not differ significantly ($Z = 0.54$, $p = .338$) from autumn when on 66.1% of nights, more than 50% of migrants were flying low (Table 2, Figure 3). On the majority of nights in both spring (85.5%) and autumn (88.2%) at Luchterduinen (Table 2), more than 50% of migrants were flying low, and the percentage was not significantly different ($Z = 0.81$, $p = .310$). The percentage of nights when migrants were mainly flying low differed significantly between locations in spring ($Z = 4.09$, $p < .001$) and autumn ($Z = 5.06$, $p < .001$) (Figure 3, Table 2).

Low-altitude migration was more common on nights of intense migration in autumn (66.7%) in Borssele, which differed significantly ($Z = 2.81$, $p = .003$) from spring, where high-altitude migration was predominant (87.5%) on these nights (Table 2, Figure 3). At Luchterduinen, proportions were not different between seasons ($Z = 0.21$, $p = .461$), nor did they differ between the two locations in autumn ($Z = 0.19$, $p = .461$). However, the proportions were statistically different among sites in spring ($Z = 2.81$, $p = .003$).

(a) Altitude Borssele

(b) Altitude Luchterduinen

Season — Spring — Autumn
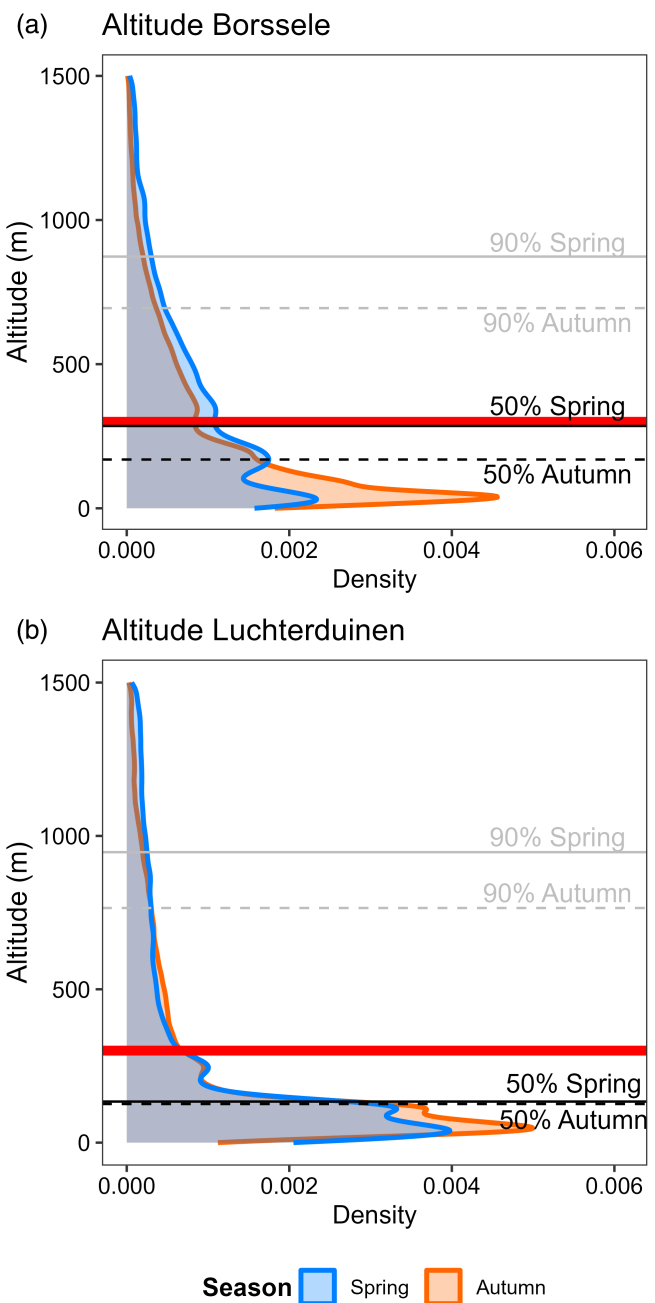
FIGURE 2 Probability density functions of altitude distributions of bird tracks at (a) Borssele and (b) Luchterduinen location in spring (blue) and autumn (orange). Black lines indicate median altitudes and gray lines are the 90% quantiles of migration altitudes in spring (solid line) and autumn (dashed line). The red line represents the threshold of 300 m (the estimated maximum height of the wind turbines in the coming years).

On most extremely low or high-altitude migration nights (>90% of migrants at low or high altitudes), migration occurred at low altitudes at Borssele (Table 2). On 35 nights in spring and 44 nights in autumn, migration was concentrated at low altitudes, and seasonal proportions

8 of 15 | **WILEY**— *Conservation Science and Practice*
A journal of the Society for Conservation Biology — Open Access

BRADARIĆ ET AL.

TABLE 2 Proportions of nights in which >50 and >90% of migrants were flying at low or high altitudes during the entire migration season and on intense migration nights (10% of nights with the highest number of migrants) per radar per season.

|	Borssele						Luchterduinen					
	Spring			Autumn			Spring			Autumn		
	N total	Low (%)	High (%)	*N* total	Low (%)	High (%)	*N* total	Low (%)	High (%)	*N* total	Low (%)	High (%)
Full season (>50%)	167	68.9	31.1	186	66.1	33.9	255	85.5	14.5	186	88.2	11.8
Intense migration (>50%)	8	12.5	87.5	27	66.7	33.3	18	72.2	27.8	26	69.2	30.8
Full season (>90%)	35	100.0	0.0	45	97.8	2.2	62	100.0	0.0	75	100.0	0.0
Intense migration (>90%)	0	0.0	0.0	12	91.7	8.3	2	100.0	0.0	3	0.0	0.0
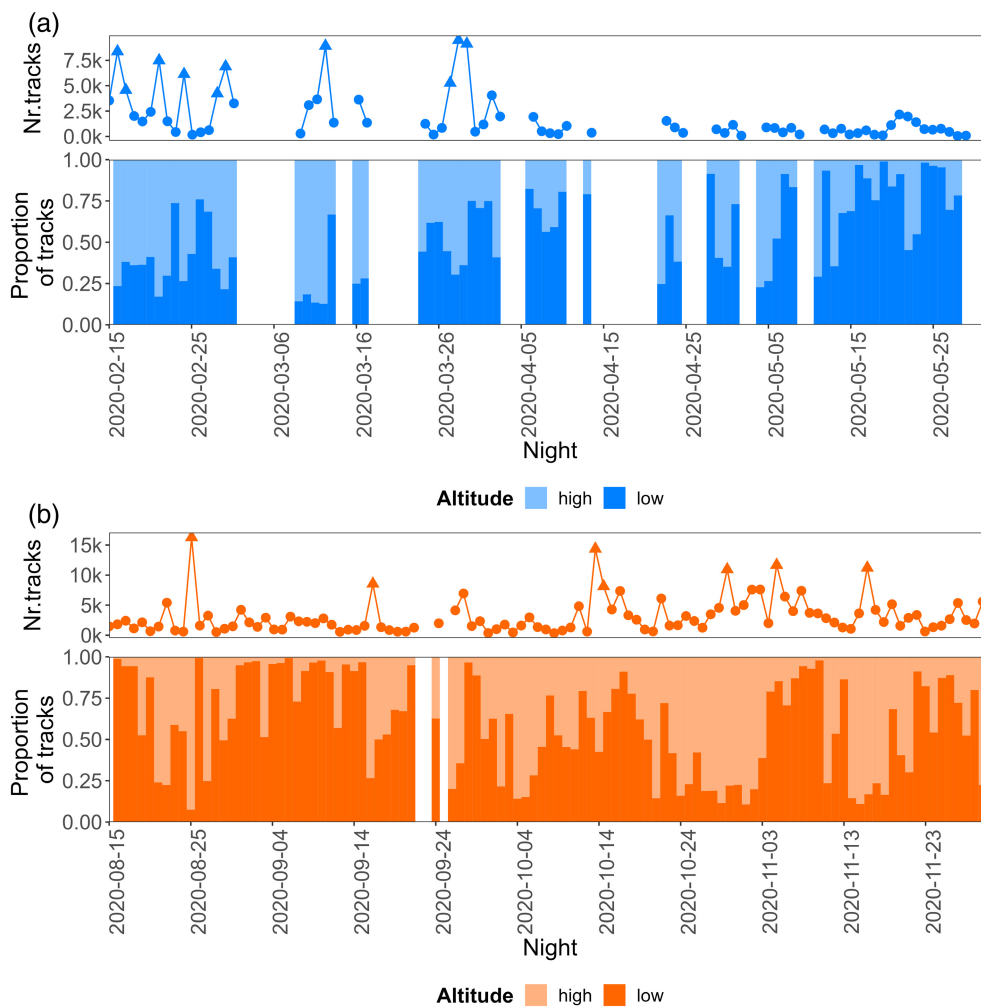
FIGURE 3 The total number of tracks per night (upper plot) and nightly proportions of low and high-altitude migration (lower plot) in spring (blue) and autumn (orange) of 2020 at Borssele. Triangles at the upper plot represent intense migration nights from Table 2. White spaces in proportion plots represent nights excluded from the analysis due to filtering steps. The same graphs for other years and locations can be found in Appendix 8.

showed no significant difference ($Z = 0.88$, $p = .299$). Luchterduinen showed the same pattern. Proportions showed no significant differences between locations during both seasons (spring: $p = 1.00$; autumn: $Z = 1.29$, $p = .17$).

During intense migration nights in Borssele, extremely low or high migration (>90% of migrants flying low) did not at all occur in spring. In autumn, extremely low migration occurred on 11 nights and extremely high

FIGURE 4 Importance of predictors of low-altitude migration fraction in (a) spring and (b) autumn based on the variance of their responses when the predictor variable was removed from the random forest (RF) model. Predictors with the prefix "delta" show a difference in predictor values between low and high altitudes.
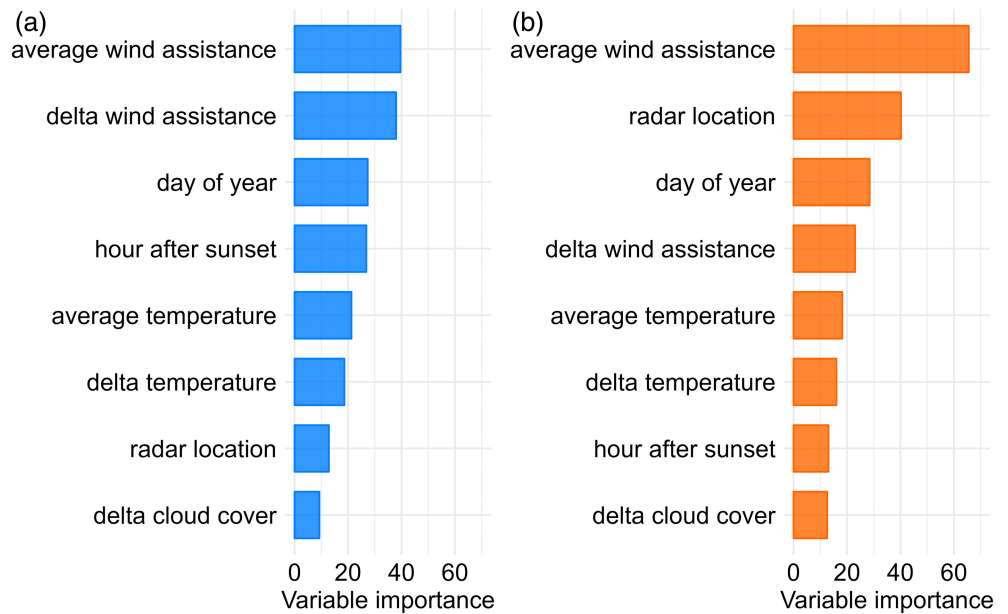
migration on one night. At Luchterduinen, migrants were flying extremely low on two nights in spring and three in autumn, while the extremely high migration did not occur in any of the seasons.

OOB R^2 showed that the model explained 65% of the variance in low-altitude migration fraction for spring and 69% for autumn. OOB RMSE value was 0.15 for spring and 0.14 for autumn, while RMSE between predictions and observed values from the test dataset was 0.19 for spring and 0.21 for autumn.

In spring, average WA (avg_wa) was the most important variable for explaining the fraction of migrants flying low and was closely followed by the difference in WA (delta_wa) between low and high altitudes, day of year (y_day) and hour after sunset (suns_h) (Figure 4a). Similarly, in autumn, the most important predictor of the low-altitude migration fraction was average WA (Figure 4b). It was followed by radar location and day of year (Figure 4b), although the effect of average WA was much stronger than all other variables and stronger than in spring (Figure 4).
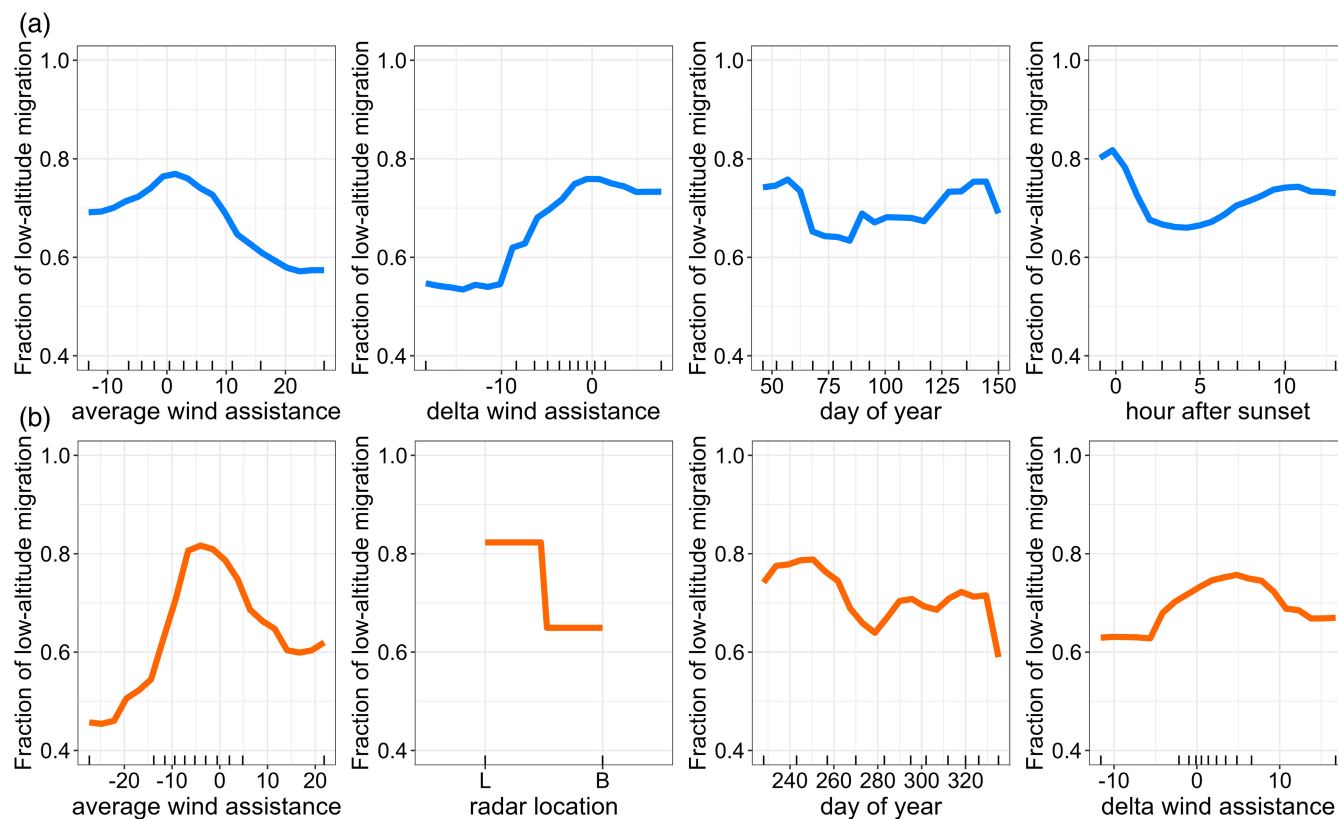
Partial dependence plots (Figure 5) show how the four predictor variables that explain most variation affect the low-altitude migration fraction on average when all other variables are marginalized. The higher value on the y-axis indicates a larger fraction of migrants flying at low altitudes. The hourly fraction of birds migrating at low altitudes in spring is higher when: avg_wa is between −5 and 5 m/s, delta_wa is −2 m/s or higher (in other words, when the wind was more supportive at lower altitudes), day of year (y_day) is between 50 and 70 and 130 and 150 (late February–early March, second half of May) and suns_h is between 0 and 1 and 7 and 10. During autumn, the low-

altitude migration fraction increases when: avg_wa is between −10 and 2 m/s (meaning that with low WA, birds fly low), when birds are flying over the Luchterduinen radar location, y_day is between 240 and 262 (late August, early September), and delta_wa is higher (wind more supportive at lower altitudes). Note that the effect of most predictors was unreliable at extremely high and low values due to fewer data points (Figure 5, rug plots).

4 | DISCUSSION

In line with our hypothesis, we demonstrate that altitude distributions of nocturnal bird migration in the North Sea basin differ between spring and autumn. In spring, birds flew higher than in autumn (Figures 2 and 3). Nevertheless, the majority of birds flew at low altitudes on most nights in both seasons (Figure 3, Table 2, Appendix 8). An exception was intense migration nights in spring in Borssele, when migrants, on most of these nights, mainly flew at high altitudes (Table 2). The results were consistent between different radar locations, and they corroborate what was previously recorded at midlatitudes both over land (Kemp et al., 2013; La Sorte et al., 2015) and large water bodies (Archibald et al., 2017; Cohen et al., 2022; Fijn et al., 2015; Hüppop et al., 2006).

WA was among the top predictors of the low-altitude migration fraction in both seasons. Over the study area, winds mainly come from the west in both seasons (Kemp et al., 2010). Such conditions tend to support migration from the UK to the Netherlands, the largest migration cohort in this region during spring (Bradarić et al., 2020; Manola

10 of 15 | **WILEY**— Conservation Science and Practice
A journal of the Society for Conservation Biology | Open Access
BRADARIĆ ET AL.

FIGURE 5 Partial dependence plots show each predictor's average effect on low-altitude migration fraction (y-axis) in (a) spring and (b) autumn when all the other predictors are marginalized. The order of plots follows the variable importance. In each plot, the x-axis indicates the range of the predictor variable, and rug plots along the bottom indicate the minimum, maximum and deciles of the predictor's distribution. For variable radar location, abbreviations stand for Luchterduinen (L) and Borssele (B).

et al., 2020). On the contrary, wind conditions do not support the migration coming from the NE in autumn (Bradarić et al., 2020). These seasonal wind patterns were reflected in the observed altitude distributions. In spring, migration occurred at altitudes higher than in autumn due to the vast availability of positive WA, which generally increases with altitude (Appendix 6).

The low-altitude migration fraction increased in both seasons when the average WA (avg_wa) was negative or had lower positive values (Figure 5a,b). A higher fraction of low-altitude migration when average WA was negative indicates that birds might fly close to the surface to decrease the effect of overall negative WA (Alerstam, 1990), as wind speeds tend to be lower at lower altitudes (Appendix 6). Such behavioral responses to wind conditions can reduce energy expenditure or flight time, which is especially important when crossing ecological barriers, where birds perform their flights in one go (Ward et al., 2018), as observed in our study area (Brust et al., 2019; Brust & Hüppop, 2021).

The fraction of low-altitude migration increased (Figure 5b) when WA at low altitudes was higher than at high altitudes. This does not necessarily show that birds

choose the altitudes with supporting winds (tailwinds) as has been shown in studies over land from the trade wind zone (Bruderer & Liechti, 1995; Liechti et al., 2000; Schmaljohann et al., 2009) and mid-latitudes (Dokter et al., 2013; Gauthreaux, 1991). Instead, our results imply that similar to what was observed in this region over land (Kemp et al., 2013), birds choose to fly at altitudes with wind conditions that are more supportive of migration than wind conditions experienced at other altitudes. However, since we assessed WA based on an average migration direction per season, the effect of choosing altitudes with tailwinds was potentially reduced in our results. Furthermore, local movements at low altitudes can also disturb our hourly measurements, especially for hours with low migration intensity.

In both seasons, low-altitude migration had a clear seasonal pattern, although the effect of day of year in autumn was stronger than in spring. In spring, we observed more birds flying at low altitudes at the beginning and the end of the migration season (Figure 5). The low-altitude migration fraction was high throughout autumn but was higher at the beginning of the season. Such seasonal variation in low-altitude migration can

reflect differences in weather-governed migration phenology between short and long-distance migrants in the area. For example, short-distance migrants strongly rely on WA in both spring and autumn, while long-distance migration is more governed by the temperature and precipitation in autumn (Haest et al., 2018, 2019). Different choices of weather conditions at departure might cause potential differences in altitude selection due to variations in weather conditions available during the flight. In spring, early-season low-altitude migration might reflect movements of mainly short-distance migrants such as starlings (*Sturnus vulgaris*), skylarks (*Alauda arvensis*) and redwings (*Turdus iliacus*). The peaks of low-altitude migration later in the season could come from the long-distance flights of waders from Africa, nearly reaching their stopover area in the Wadden Sea (Lensink et al., 2002; Shamoun-Baranes et al., 2010). Based on the seasonal phenology of migration in the region, the low-altitude migration peak early in autumn might also come from waders, for example, bar-tailed godwits (*Limosa lapponica*), redshanks (*Tringa totanus*), and greenshanks (*Tringa nebularia*) (Lensink et al., 2002). We may also be measuring predominantly local movements of birds like gulls this time of year (McLaren et al., 2016). Besides yearly phenology, nightly phenology in spring drives altitude distributions in the region, with birds flying at low altitudes at the beginning and at the end of the night, which reflects their departures at sunset and arrivals in the second part of the night before sunrise (Doren & Horton, 2018; Sjöberg et al., 2017).

Luchterduinen location generally had a higher fraction of low-altitude migrants than Borssele (Figure 5), and birds were flying at lower altitudes when crossing this location in both seasons (Figure 2). These local differences in flight altitudes could reflect distinct migration axes that short and long-distance migrants use in the region (Lensink et al., 2002), and the availability of supportive wind conditions for the migration direction in which they want to go (Bradarić et al., 2020; Buurma, 1995; Lack, 1959). For example, short-distance migrants that cross the North Sea from the Netherlands to the United Kingdom at Luchterduinen might fly lower to minimize the effect of negative WA and reduce the flight costs when navigating an ecological barrier (Grönroos et al., 2012). On the contrary, long-distance migrants, which might not be picked up at Luchterduinen location as much due to flying more inland, might cross Borssele when migrating toward SW, making use of increased WA at slightly higher altitudes (Kemp et al., 2013).

When flying over land in mid-latitudes, birds avoid altitudes with low temperatures (Kemp et al., 2013), and early radar studies indicate the so-called "ceiling effect" of the temperature on flight altitudes over the North Sea, where birds were climbing to altitudes with temperatures just below the freezing level (Eastwood, 1967). With this in mind, we expected that birds would fly lower with lower average temperature as temperature generally decreases with altitude (Appendix 6). Our models showed that in addition to WA and day of year, temperature affects altitude distribution in the North Sea basin in both seasons. However, the effect is much lower in comparison to the above-mentioned predictors and, therefore, probably of low biological relevance. While other studies found an influence of cloud cover on migration altitude (Eastwood, 1967; Eastwood & Rider, 1965), our results do not identify this as a driving factor relative to the other environmental variables. However, it is worth noting that high cloud cover was rarely observed during our study period (Appendix 6).

The variance explained by our model (65% in spring and 69% in autumn) indicates that the effects of the included predictors cannot fully explain the low-altitude migration ratio over the North Sea and that other factors might be involved. Flight altitude distributions can result from complex, interlinked factors that include birds' species and type of flight (Shamoun-Baranes et al., 2006), birds' physiological condition (Liechti et al., 2000), and as of recently, man-made obstacles (Desholm, 2009). Our models did not account for all these factors or their interdependence; due to their complex nature, more data with broader temporal coverage might be needed to capture such relationships. While combinations of radar observations and our models could not capture the full extent of such an intricate system, RMSE values of our model predictions indicate that these predictors add a valuable contribution to our understanding of the occurrence of low-altitude flights and their drivers in the North Sea basin, especially in spring.

As mentioned earlier, the North Sea basin is targeted for wind energy expansion. Studies at sea and on land show that the effect of the turbines on birds' mortality through collisions and barrier effect can be substantial (Desholm, 2009; Drewitt & Langston, 2008; Hüppop et al., 2016; Marques et al., 2014; Therkildsen et al., 2021). Turbine height is expected to increase, with new turbines reaching 300 m at the rotor tip. These tall structures substantially influence the aerial environment, which is increasingly recognized as an environment that requires conservation (Bauer et al., 2019; Lambertucci & Speziale, 2021). The call for aerial conservation action is partly due to vertical human structures such as wind turbines. Different measures are being developed to combat the adverse effects of wind turbines, especially for migratory birds (Desholm, 2009; May et al., 2020).

One of the strategies to reduce the risk of collision between migratory birds and offshore wind turbines that

are currently being adopted in the Netherlands is wind turbine curtailment during nights of intense migration. In order to reduce the impact on the energy market while optimizing the conservation effect, wind turbine curtailment will be triggered by bird migration forecasts, a strategy already deployed by military aviation to reduce collisions between birds and aircraft (van Belle et al., 2007; van Gasteren et al., 2019). Our study shows that existing and new turbines will largely overlap with the altitudes at which migrants fly over the North Sea in both spring and autumn. However, migratory birds in autumn seem to be at greater risk of collision due to the lower flight altitudes on more migration nights, especially nights of intense migration. While our study shows that, on average, migration occurs at low altitudes, we observed hourly variation in altitude distributions, which is in part influenced by wind conditions, day of year, hour after sunset and radar location. Improving our understanding of variation in altitude distribution can reduce the risk of unnecessary turbine curtailment on nights of intense migration when birds are expected to fly above turbine height while maximizing the conservation impact.

ORCID

Maja Bradarić https://orcid.org/0000-0003-2987-4855

REFERENCES

Åkesson, S., Alerstam, T., & Hedenstroim, A. (1996). Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. *Journal of Avian Biology*, *27*, 95–102. doi:10.2307/3677138

Alerstam, T. (1990). *Bird migration* (1st ed.). Cambridge University Press.

Alerstam, T. (2011). Optimal bird migration revisited. *Journal of Ornithology*, *152*, 5–23. https://doi.org/10.1007/s10336-011-0694-1

Archibald, K. M., Buler, J. J., Smolinsky, J. A., & Smith, R. J. (2017). Migrating birds reorient toward land at dawn over the Great Lakes, USA. *Auk*, *134*, 193–201. https://doi.org/10.1642/AUK-16-123.1

Bauer, S., Shamoun-Baranes, J., Nilsson, C., Farnsworth, A., Kelly, J., Reynolds, D. R., Dokter, A. M., Krauel, J., Petterson, L. B., Horton, K. G., & Chapman, J. W. (2019). The grand challenges of migration ecology that radar aeroecology can help answer. *Ecography*, *42*, 861–875. https://doi.org/10.1111/ecog.04083

Bergström, L., Kautsky, L., Malm, T., Rosenberg, R., Wahlberg, M., Åstrand Capetillo, N., & Wilhelmsson, D. (2014). Effects of offshore wind farms on marine wildlife—A generalized impact assessment. *Environmental Research Letters*, *9*, 034012. https://doi.org/10.1088/1748-9326/9/3/034012

Bradarić, M., Bouten, W., Fijn, R. C., Krijgsveld, K. L., & Shamoun–Baranes, J. (2020). Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea. *Journal of Avian Biology*, *51*, e02562. https://doi.org/10.1111/jav.02562

Bruderer, B., & Liechti, F. (1995). Variation in density and height distribution of nocturnal migration in the south of Israel. *Israel Journal of Zoology*, *41*, 477–487. https://doi.org/10.1080/00212210.1995.10688815

Brust, V., & Hüppop, O. (2021). Underestimated scale of songbird offshore migration across the south-eastern North Sea during autumn. *Journal of Ornithology*, *163*, 51–60. https://doi.org/10.1007/s10336-021-01934-5

Brust, V., Michalik, B., & Hüppop, O. (2019). To cross or not to cross—Thrushes at the German North Sea coast adapt flight and routing to wind conditions in autumn. *Movement Ecology*, *7*, 1–10. doi:10.1186/s40462-019-0173-5

Buurma, L. S. (1995). Long-range surveillance radars as indicators of bird numbers aloft. *Israel Journal of Zoology*, *41*, 221–236. https://doi.org/10.1080/00212210.1995.10688795

Cabrera-Cruz, S. A., Cervantes-Pasqualli, J., Franquesa-Soler, M., Muñoz-Jiménez, Ó., Rodríguez-Aguilar, G., & Villegas-Patraca, R. (2020). Estimates of aerial vertebrate mortality at wind farms in a bird migration corridor and bat diversity

hotspot. *Global Ecology and Conservation*, *22*, e00966. https://doi.org/10.1016/j.gecco.2020.e00966

Cohen, E. B., Buler, J. J., Horton, K. G., Loss, S. R., Marra, P. P., Smolinsky, J. A., & Cabrera-cruz, S. A. (2022). Using weather radar to help minimize wind energy impacts on nocturnally migrating birds. *Conservation Letters*, *15*(4), e12887. https://doi.org/10.1111/conl.12887

Desholm, M. (2009). Avian sensitivity to mortality: Prioritising migratory bird species for assessment at proposed wind farms. *Journal of Environmental Management*, *90*, 2672–2679. https://doi.org/10.1016/j.jenvman.2009.02.005

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*, 1–8. https://doi.org/10.1371/journal.pone.0052300

Doren, B. M. V., & Horton, K. G. (2018). A continental system for forecasting bird migration. *Science*, *361*, 1115–1118. https://doi.org/10.1126/science.aat7526

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Drewitt, A. L., & Langston, R. H. W. (2006). Assessing the impacts of wind farms on birds. *Ibis*, *148*, 29–42. https://doi.org/10.1111/j.1474-919X.2006.00516.x

Drewitt, A. L., & Langston, R. H. W. (2008). Collision effects of wind-power generators and other obstacles on birds. *Annals of the New York Academy of Sciences*, *1134*, 233–266. https://doi.org/10.1196/annals.1439.015

Eastwood, E. (1967). *Radar ornithology*. Methuen & Co Ltd.

Eastwood, E., & Rider, G. (1965). Some radar measurements of the altitude of bird flight. *British Birds*, *58*, 393–430.

Fijn, R. C., 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. https://doi.org/10.1111/ibi.12259

Gaultier, S. P., Blomberg, A. S., Ijäs, A., Vasko, V., Vesterinen, E. J., Brommer, J. E., & Lilley, T. M. (2020). Bats and wind farms: The role and importance of the Baltic Sea countries in the European context of power transition and biodiversity conservation. *Environmental Science and Technology*, *54*, 10385–10398. https://doi.org/10.1021/acs.est.0c00070

Gauthreaux, S. A. (1991). The flight behavior of migrating birds in changing wind fields. *American Zoologist*, *31*, 187–204. https://doi.org/10.1093/icb/31.1.187

Gregorutti, B., Michel, B., & Saint-Pierre, P. (2017). Correlation and variable importance in random forests. *Statistics and Computing*, *27*, 659–678. https://doi.org/10.1007/s11222-016-9646-1

Grönroos, J., Green, M., & Alerstam, T. (2012). To fly or not to fly depending on winds: Shorebird migration in different seasonal wind regimes. *Animal Behaviour*, *83*, 1449–1457. https://doi.org/10.1016/j.anbehav.2012.03.017

Haest, B., Hüppop, O., & Bairlein, F. (2018). The influence of weather on avian spring migration phenology: What, where

and when? *Global Change Biology*, *24*, 5769–5788. https://doi.org/10.1111/gcb.14450

Haest, B., Hüppop, O., van de Pol, M., & Bairlein, F. (2019). Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects. *Global Change Biology*, *25*, 4064–4080. https://doi.org/10.1111/gcb.14746

Hayes, M. A., Hooton, L. A., Gilland, K. L., Grandgent, C., Smith, R. L., Lindsay, S. R., Collins, J. D., Schumacher, S. M., Rabie, P. A., Gruver, J. C., & Goodrich-Mahoney, J. (2019). A smart curtailment approach for reducing bat fatalities and curtailment time at wind energy facilities. *Ecological Applications*, *29*, 1–18. https://doi.org/10.1002/eap.1881

Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., … Thépaut, J. N. (2020). The ERA5 global reanalysis. *Quarterly Journal of the Royal Meteorological Society*, *146*, 1999–2049. https://doi.org/10.1002/qj.3803

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. https://doi.org/10.1111/j.1474-919X.2006.00536.x

Hüppop, O., Hüppop, K., Dierschke, J., & Hill, R. (2016). Bird collisions at an offshore platform in the North Sea. *Bird Study*, *63*, 73–82. https://doi.org/10.1080/00063657.2015.1134440

James, S., & Stull, R. B. (2019). Global wind circulations. Retrieved from https://www.eoas.ubc.ca/courses/atsc113/sailing/met_concepts/09-met-winds/9a-global-wind-circulations/

Kafas, A., Ripken, M., Wright, K., Billet, M., Sangiuliano, S., Ooms, E., & Scheffler, U. (2018). Status quo report on offshore energy planning provisions in the North Sea Region. Retrieved from http://www.northsearegion.eu/media/4930/northsee-offshore-energy-status-quo-main-report-final-version-120418.pdf

Kemp, M. U., Shamoun-Baranes, J., Dokter, A. M., van Loon, E., & Bouten, W. (2013). The influence of weather on the flight altitude of nocturnal migrants in mid-latitudes. *Ibis*, *155*, 734–749. https://doi.org/10.1111/ibi.12064

Kemp, M. U., Shamoun-baranes, J., Gasteren, H. V., Bouten, W., & Van, E. E. (2010). Can wind help explain seasonal differences in avian migration speed? *Journal of Avian Biology*, *41*, 672–677. https://doi.org/10.1111/j.1600-048X.2010.05053.x

Kemp, M. U., Shamoun-Baranes, J., van Loon, E. E., McLaren, J. D., Dokter, A. M., & Bouten, W. (2012). Quantifying flow-assistance and implications for movement research. *Journal of Theoretical Biology*, *308*, 56–67. https://doi.org/10.1016/j.jtbi.2012.05.026

La Sorte, F. A., Hochachka, W. M., Farnsworth, A., Sheldon, D., van Doren, B. M., Fink, D., & Kelling, S. (2015). Seasonal changes in the altitudinal distribution of nocturnally migrating birds during autumn migration. *Royal Society Open Science*, *2*(12), 150347. https://doi.org/10.1098/rsos.150347

Lack, D. (1959). Migration across the sea. *Ibis*, *101*, 374–399. https://doi.org/10.1111/j.1474-919X.1959.tb02395.x

Lack, D. (1960). The height of bird migration. *British Birds*, *53*, 5–10.

Lack, D. (1963). Migration across the southern North Sea studied by radar part 4. Autumn. _Ibis_, _105_, 1–54. https://doi.org/10.1111/j.1474-919X.1963.tb02473.x

Lambertucci, S. A., & Speziale, K. L. (2021). Need for global conservation assessments and frameworks to include airspace habitat. _Conservation Biology_, _35_, 1341–1343. https://doi.org/10.1111/cobi.13641

Lensink, R., Camphuysen, C. J., Jonkers, D. A., Leopold, M. F., Schekkerman, H., & Dirksen, S. (1999). _Falls of migrant birds, an analysis of current knowledge_. Bureau Waardenburg BV. Retrieved from https://puc.overheid.nl/rijkswaterstaat/doc/PUC_56325_31

Lensink, R., van Gasteren, H., Hustings, F., Buurma, L., van Duin, G., Linnartz, L., Vogelzang, F., & Witkamp, C. (2002). _Vogeltrek over Nederland 1976-1993_. Schuyt & Co.

Liechti, F. (2006). Birds: Blowin' by the wind? _Journal of Ornithology_, _147_, 202–211. https://doi.org/10.1007/s10336-006-0061-9

Liechti, F., Klaassen, M., & Bruderer, B. (2000). Predicting migratory flight altitudes by physiological migration models. _The auk_, _117_, 205–214. https://doi.org/10.1093/auk/117.1.205

Manola, I., Bradaric, M., Groenland, R., Fijn, R. C., Bouten, W., & Shamoun-Baranes, J. (2020). Associations of synoptic weather conditions with nocturnal bird migration over the North Sea. _Frontiers in Ecology and Evolution_, _8_, 542438. https://doi.org/10.3389/fevo.2020.542438

Marques, A. T., Batalha, H., Rodrigues, S., Costa, H., Pereira, M. J. R., Fonseca, C., Mascarenhas, M., & Bernardino, J. (2014). Understanding bird collisions at wind farms: An updated review on the causes and possible mitigation strategies. _Biological Conservation_, _179_, 40–52. https://doi.org/10.1016/j.biocon.2014.08.017

May, R., Nygård, T., Falkdalen, U., Åström, J., Hamre, Ø., & Stokke, B. G. (2020). Paint it black: Efficacy of increased wind turbine rotor blade visibility to reduce avian fatalities. _Ecology and Evolution_, _10_, 8927–8935. https://doi.org/10.1002/ece3.6592

McKenna, R., Ostman, P., & Fichtner, W. (2016). Key challenges and prospects for large wind turbines. _Renewable and Sustainable Energy Reviews_, _53_, 1212–1221. https://doi.org/10.1016/j.rser.2015.09.080

McLaren, J. D., Shamoun-Baranes, J., Camphuysen, C. J., & Bouten, W. (2016). Directed flight and optimal airspeeds: Homeward-bound gulls react flexibly to wind yet fly slower than predicted. _Journal of Avian Biology_, _47_, 476–490. https://doi.org/10.1111/jav.00828

Mukaka, M. M. (2012). Statistics corner: A guide to appropriate use of correlation coefficient in medical research. _Malawi Medical Journal_, _24_(3), 69–71.

Newton, I. (2008). _The migration ecology of birds_. Academic Press.

Nguyen, Q. H., Ly, H. B., Ho, L. S., Al-Ansari, N., van Le, H., Tran, V. Q., Prakash, I., & Pham, B. T. (2021). Influence of data splitting on performance of machine learning models in prediction of shear strength of soil. _Mathematical Problems in Engineering_, _2021_, 4832864. https://doi.org/10.1155/2021/4832864

Perold, V., Ralston-Paton, S., & Ryan, P. (2020). On a collision course? The large diversity of birds killed by wind turbines in South Africa. _Ostrich_, _91_, 228–239. doi:10.2989/00306525.2020.1770889

R Core Team. (2020). _R: A language and environment for statistical computing_. R Core Team. Retrieved from https://www.r-project.org/

Richardson, W. J. (1978). Timing and amount of bird migration in relation to weather: A review. _Oikos_, _30_, 224–272. https://doi.org/10.2307/3543482

Rohli, R. V., & Vega, A. J. (2018). _Climatology_ (4th ed.). Jones & Bartlett Learning.

Schmaljohann, H., Liechti, F., & Bruderer, B. (2009). Trans-Sahara migrants select flight altitudes to minimize energy costs rather than water loss. _Behavioral Ecology and Sociobiology_, _63_, 1609–1619. https://doi.org/10.1007/s00265-009-0758-x

Shamoun-Baranes, J., Leyrer, J., van Loon, E., Bocher, P., Robin, F., Meunier, F., & Piersma, T. (2010). Stochastic atmospheric assistance and the use of emergency staging sites by migrants. _Proceedings of the Royal Society B: Biological Sciences_, _277_, 1505–1511. https://doi.org/10.1098/rspb.2009.2112

Shamoun-Baranes, J., & van Gasteren, H. (2011). Atmospheric conditions facilitate mass migration events across the North Sea. _Animal Behaviour_, _81_, 691–704. https://doi.org/10.1016/j.anbehav.2011.01.003

Shamoun-Baranes, J., van Gasteren, H., van Belle, J., Bouten, W., & Buurma, L. (2006). A comparative analysis of the influence of weather on the flight altitudes of birds. _American Meteorological Society_, _87_, 47–61. https://doi.org/10.1175/BAMS-87-1-47

Sjöberg, S., Alerstam, T., Åkesson, S., & Muheim, R. (2017). Ecological factors influence timing of departures in nocturnally migrating songbirds at Falsterbo, Sweden. _Animal Behaviour_, _127_, 253–269. https://doi.org/10.1016/j.anbehav.2017.03.007

Stull, R. B. (1988). _An Introduction to boundary layer meteorology_. Kluwer Academic Publishers.

Therkildsen, O. R., Balsby, T. J. S., Kjeldsen, J. P., Nielsen, R. D., Bladt, J., & Fox, A. D. (2021). Changes in flight paths of large-bodied birds after construction of large terrestrial wind turbines. _Journal of Environmental Management_, _290_, 112647. https://doi.org/10.1016/j.jenvman.2021.112647

U.S. Standard Atmosphere. (1976). NTRS—NASA Technical Reports Server.

van Belle, J., Shamoun-Baranes, J., Van Loon, E., & Bouten, W. (2007). An operational model predicting autumn bird migration intensities for flight safety. _Journal of Applied Ecology_, _44_, 864–874. https://doi.org/10.1111/j.1365-2664.2007.01322.x

van Gasteren, H., Krijgsveld, K. L., Klauke, N., Leshem, Y., Metz, I. C., Skakuj, M., Sorbi, S., Schekler, I., & Shamoun-Baranes, J. (2019). Aeroecology meets aviation safety: Early warning systems in Europe and the Middle East prevent collisions between birds and aircraft. _Ecography_, _42_, 899–911. https://doi.org/10.1111/ecog.04125

Ward, M. P., Benson, T. J., Deppe, J., Zenzal, T. J., Diehl, R. H., Celis-Murillo, A., Bolus, R., & Moore, F. R. (2018). Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration. _Proceedings of the Royal Society B: Biological Sciences_, _285_, 20181747. https://doi.org/10.1098/rspb.2018.1747

Wei, T., & Simko, V. (2021). R package "corrplot": Visualization of a correlation matrix (version 0.90). Retrieved from https://github.com/taiyun/corrplot

Weisshaupt, N., Maruri, M., & Arizaga, J. (2016). Nocturnal bird migration in the Bay of Biscay as observed by a thermal-imaging camera. *Bird Study*, *63*, 533–542. doi:10.1080/00063657.2016.1239693

Werham, C., Toms, M., Marchant, J. H., Clark, J., Siriwardena, G., & Baillie, S. R. (2002). *The migration atlas: Movements of the birds of Britain and Ireland* (1st ed.). Gardners Books.

Wright, A. J., Araújo-Wang, C., Wang, J. Y., Ross, P. S., Tougaard, J., Winkler, R., Márquez, M. C., Robertson, F. C., Williams, K. F., & Reeves, R. R. (2020). How 'blue' is 'green' energy? *Trends in Ecology and Evolution*, *35*, 235–244. https://doi.org/10.1016/j.tree.2019.11.002

Wright, M. N., & Ziegler, A. (2017). A fast implementation of random forests for high dimensional data in C++ and R. *Journal of Statistical Software*, *77*, 1–17. https://doi.org/10.18637/jss.v077.i01

SUPPORTING INFORMATION

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