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JOURNAL OF AVIAN BIOLOGY

Communication

Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea

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On their migratory journeys, terrestrial birds can come across large inhospitable areas with limited opportunities to rest and refuel. Flight over these areas poses a risk especially when wind conditions en route are adverse, in which case inhospitable areas can act as an ecological barrier for terrestrial migrants. Thus, within the east-Atlantic flyway, the North Sea can function as an ecological barrier. The main aim of this study was to shed light on seasonal patterns of bird migration in the southern North Sea and determine whether departure decisions on nights of intense migration were related to increased wind assistance. We measured migration characteristics with a radar that was located 18 km off the NW Dutch coast and used simulation models to infer potential departure locations of birds on nights with intense nocturnal bird migration. We calculated headings, track directions, airspeeds, groundspeeds on weak and intense migration nights in both seasons and compared speeds between seasons. Moreover, we tested if departure decisions on intense migration nights were associated with supportive winds. Our results reveal that on the intense migration nights in spring, the mean heading was towards E, and birds departed predominantly from the UK. On intense migration nights in autumn, the majority of birds departed from Denmark, Germany and north of the Netherlands with the mean heading towards SW. Prevailing winds from WSW at departure were supportive of a direct crossing of the North Sea in spring. However, in autumn winds were generally not supportive, which is why many birds exploited positive wind assistance which occurred on intense migration nights. This implies that the seasonal wind regimes over the North Sea alter its migratory dynamics which is reflected in headings, timing and intensity of migration.

Keywords: back-trajectory model, departure, nocturnal migration, North Sea, radar, seasonal, wind assistance

Introduction

Large bodies of water, with limited or no opportunities to rest, refuel or find safety, create an inhospitable environment for migratory land birds. Such areas may, therefore, become ecological barriers that are either circumvented or crossed, potentially at high risk if weather conditions en route are unfavourable (Alerstam 2001, Deppe et al.



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2015). The barrier effect becomes even more pronounced if inhospitable areas are combined with anthropogenic structures, such as tall buildings, towers and wind farms, as they are also believed to hinder migratory birds (Drewitt and Langston 2008, Poot et al. 2008, Marques et al. 2014).

The extent to which an inhospitable area can act as a barrier can vary substantially and depends on several factors such as the migration strategy applied, environmental conditions and a bird's physiological condition (Bulte et al. 2014, Gill et al. 2014, Deppe et al. 2015). Multiple studies conducted on songbirds and shorebirds showed that the success of crossing large inhospitable areas is closely tied to an individual's body condition and the occurrence of supporting winds during migration (Bulte et al. 2014, Gill et al. 2014, Duijns et al. 2017, Ward et al. 2018). Body condition also affects how birds navigate a barrier, for example through a higher propensity for crossing when having higher fuel loads and circumnavigating when the fuel loads are low (Schmaljohann and Naef-Daenzer 2011). Simulation models and tracking studies in different migratory systems have shown that without choosing supporting winds, average survival during migration would be quite low for birds crossing the Atlantic Ocean, the Mediterranean sea or the Sahara desert (Erni et al. 2005, Bulte et al. 2014, Loonstra et al. 2019). Weather conditions may also influence the fine-scale timing of migration. For example, songbirds that cross approximately 200 km of Baltic Sea depart early after sunset when they are about to undertake a long flight across the barrier, but have been observed postponing their departure times if the weather conditions were not favourable (Åkesson and Hedenström 2000, Sjöberg et al. 2015, 2017). For oriental honey-buzzards *Pernis ptilorhynchus*, not only the timing but also the routes that they use to navigate 650 km of the East China Sea strongly depend on winds (Yamaguchi et al. 2012). Similarly, Felicísimo et al. (2008) showed that the position of the Intertropical Convergence zone could result in conditions creating a corridor of supporting winds across the Atlantic Ocean influencing where and when seabirds crossed it. Some of the most impressive barrier crossings using wind assistance are those of blackpoll warblers *Setophaga striata* and northern wheatears *Oenanthe oenanthe* that transverse 2500 and 3500 km of the Atlantic ocean (Bairlein et al. 2012, Bulte et al. 2014, DeLuca et al. 2015) and bar-tailed godwits *Limosa lapponica* that perform a flight of 10 400 km over the Pacific Ocean (Gill et al. 2005, 2009).

Ecological barriers of different sizes exist in all the global migratory flyways. With its position between Scandinavia, lowlands of the Netherlands and northern Germany and the British Isles, the North Sea represents a crossroads of migratory routes within one of the world's largest migration systems, the east Atlantic flyway ('Bird Life International' 2010) (Fig. 1). With a maximum length of 960 km between its northernmost and southernmost points, the North Sea can be inhospitable for terrestrial birds which account for the vast majority of migratory birds in the North Sea basin (Lack 1963a, Lensink et al. 1999, Hüppop and Hüppop 2011).

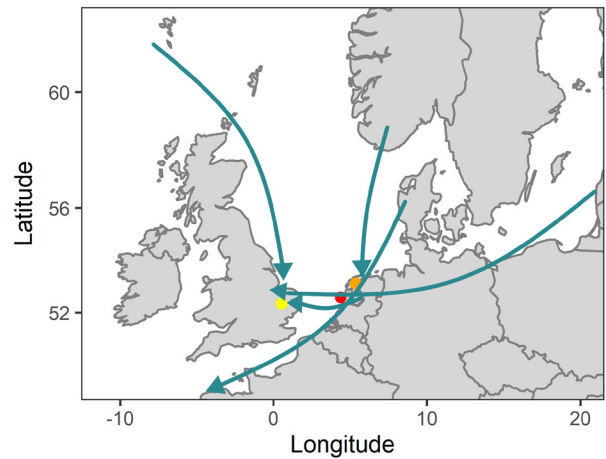


Figure 1. Map of the North Sea with dots indicating radar locations: in the offshore wind farm Egmond aan Zee used in our study (red), in the north of the Netherlands used in the study of Buurma (1995) and Shamoun-Baranes and van Gasteren (2011) (orange) and Norfolk used in studies of David Lack (Lack 1959, 1963a, b) (yellow). Arrows show main small-scale migratory routes over the North Sea (Lack 1963a, b, Buurma 1987, Lensink et al. 1999, Shamoun-Baranes and van Gasteren 2011) as observed in autumn.

Most of the current information available on migration over the North Sea comes from bird ringing (Lensink et al. 2002, Werham et al. 2002), bio-logging (Gyimesi et al. 2017), visual observations (Krijgsveld et al. 2005) and counts of birds found on offshore structures (Lensink et al. 1999, Hüppop and Hüppop 2011, Hüppop et al. 2016) or it has been acquired sporadically using radar (Lack 1963a, b, Hüppop et al. 2006, Krijgsveld et al. 2011, Shamoun-Baranes and van Gasteren 2011, Fijn et al. 2015). Several migratory routes have been observed over the North Sea (Fig. 1), but the two biggest ones are between Scandinavia and southern Europe and Africa, and between eastern Europe and the UK (Lack 1959). Estimates show that several hundred million migratory birds of approximately 250 species migrate over the North Sea every year, many of them being nocturnal migrants (Hüppop et al. 2006). A radar study at the east coast of the UK recorded a prevailing movement from W to E over the North Sea in the first part of the spring season, while the direction shifts towards NW at the end of the season (Lack 1963a) (Fig. 1). Ring recoveries suggest that in spring species such as blackbirds *Turdus merula*, starlings *Sturnus vulgaris*, skylarks *Alauda arvensis* and waders travel between the UK and mainland Europe and cross the North Sea along this general W–E axis (Werham et al. 2002). During autumn, radar observations at the same location in the UK registered track directions mainly towards SSW from Scandinavia and W from the Netherlands (Lack 1963b). Measurements of arrival over the Wadden Islands off the northern coast of Netherlands in autumn registered mainly track directions towards SSW dominated by thrushes (*Turdus philomelos*, *Turdus iliacus*, *Turdus pilaris* and *Turdus merula*) and robins (*Erithacus rubecula*) (Buurma 1995, Shamoun-Baranes

and van Gasteren 2011). Simulation modelling suggested that these birds were arriving from Scandinavia (Shamoun-Baranes and van Gasteren 2011) when winds were generally supportive (Fig. 1). Yet, due to the lack of systematic measurements and a strong bias towards autumn season studies, seasonal patterns of nocturnal bird migration over the North Sea are poorly understood. Moreover, factors that influence them, as well as strategies that terrestrial migrants use to cope with this potentially inhospitable environment are largely unknown.

The primary aim of the current study is to contribute to our understanding of the seasonal patterns of nocturnal migration over the southern North Sea and especially nocturnal mass migration events in the context of seasonal wind regimes. The first objective was to assess how distributions of headings and track directions on weak and intense migration nights differ between spring and autumn in the southern North Sea and whether we observe a seasonal reversal of directions or other patterns which may suggest alternative strategies among seasons. The second objective was to infer potential departure locations of the birds that were recorded by the radar in different seasons. Radar studies of nocturnal migration over land have shown that migration intensity en route is often correlated with local supporting winds (Erni et al. 2005, Van Belle et al. 2007) and tracking studies of passerines have demonstrated that departure directions correlate with wind directions (Åkesson and Hedenström 2000). This supports expectations that birds would select winds at departure which reduce the energy or time invested in migration (Alerstam and Hedenström 1998, Alerstam 2011). Therefore, our third objective was to assess whether birds' departure decisions on intense migration nights were associated with supportive winds at potential departure locations in the North Sea basin.

Material and methods

Radar system and location

From June 2007 until May 2010, radar data was collected by a radar tracking system designed to detect and track birds (Merlin, DeTect Inc., Panama City, Florida, USA). The radar system was located 18 km from the NW Dutch coast and was mounted at a meteorological mast at the SW side of the Egmond aan Zee wind farm (N 52.60, E 4.38). The radar system was operational 90% of the time, except for short breaks due to maintenance, technical failure or weather conditions which could have caused mechanical damage of the radar (wind speed $> 14 \text{ m s}^{-1}$) or affect detection of targets (rain). The system consisted of two marine surveillance radars; one vertically mounted radar, that scanned the air upwards in NW–SE direction and that was set to a range of 1390 m (ca 0.75 NM) (Furuno, 25 kW, X-band, nominal beam angle 20° , rotation speed 24 rpm), and one horizontally mounted radar that scanned the area 360° around the radar and that was set to a range of 5560 m (3 NM) (Furuno,

30 kW, S-band, nominal beam angle 25° , rotation speed 22 rpm) (Krijgsveld et al. 2011, Fijn et al. 2015). The vertical radar recorded the altitude profiles and the number of targets that crossed the vertical beam, while the horizontal radar recorded track direction and groundspeed of targets that were flying parallel through the horizontal beam. Measurements showed that the Merlin system was able to detect even fast-flying species that flew perpendicular to the vertical radar beam (Fijn et al. 2015). Even though the detection probability of a bird decreases with increasing distance from the radar, large and mid-sized birds were successfully detected throughout the whole vertical extent of the radar, while small birds were successfully detected up to 900 m (Fijn et al. 2015). To avoid detection loss, fluxes were only determined in two areas of the beam on either side of the radar, covering an area 500 m horizontally and up to 1370 m vertically. To ensure radar tracks originated from birds rather than erroneous clutter, and to ensure that data used for analysis were free from biases induced by the radar, extensive validation steps were carried out. Data were filtered before analysis based on values of speed (targets with speeds $< 5 \text{ m s}^{-1}$ and $> 30 \text{ m s}^{-1}$ are unlikely to be birds), size and heading of the birds measured in the field. Flux calculations were performed within the limitations that the radar and the study design allowed, such as limitations in beam width, detection range and flight directions in relation to radar orientation. For more information on data filtering procedures, the consequences of radar limitations on resulting flux values, and the measurement campaign see (Krijgsveld et al. 2011, Fijn et al. 2015 and Supplementary information therein).

In this study, data collected by the vertical radar was used to quantify nocturnal migration and select nights on which intense migration occurred. The horizontal radar was used to measure the mean track direction and groundspeed of each recorded track.

Radar data selection

The nights for the analysis were selected between 15 February and 31 May (spring migration season), and between 1 August and 30 November (autumn migration season) from the above-mentioned period of radar activity. Since the majority of land birds migrate at night, we focused on nocturnal migration in our study. Nocturnal migrants generally depart on their migration journey around sunset (Alerstam 1990, Åkesson et al. 1996), but this can vary slightly among nights with different length, different species, birds with different body conditions and between seasons (Sjöberg et al. 2015, Müller et al. 2016, 2018a, b). We selected tracks that were recorded by the vertical radar from sunset up to one hour before sunrise of the following day and calculated the total number of tracks per night within the determined detection range as a measure of migration intensity. We selected the top 5% of nights based on migration intensity and defined them as intense migration nights (IMN) which were used for migration simulations (Fig. 2). All other nights were considered weak migration nights (WMN). We extracted the track

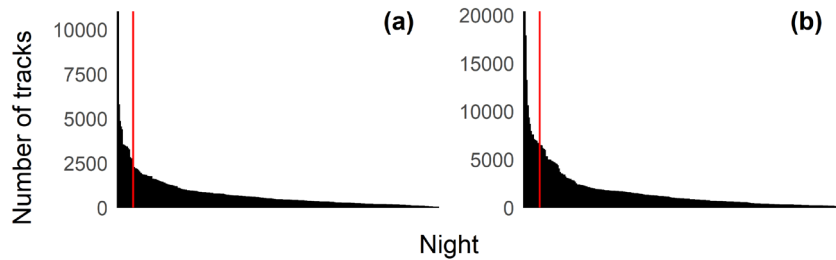


Figure 2. The number of tracks per night (y-axis) detected by the vertical radar during nocturnal migration in spring (a) and autumn (b) during the observation period (see radar data selection section for more details) ranged in descending order. The vertical red lines mark the top 5% threshold which was used to distinguish between IMN (left from the red line) and WMN (right from the red line).

directions and ground speeds of all bird tracks measured by the horizontal radar and calculated headings (flight direction of the bird in still air) and airspeeds (speed of a bird in still air) with the wind data from 925 hPa pressure level for each of the recorded tracks using vector summation (Shamoun-Baranes et al. 2007). The radar used in this study measures up to an altitude of 1500 m, thus the focus of our study is on low altitude flight, which corresponds to a pressure level of 925 hPa and higher. All calculations were done in R (<www.r-project.org>). In total, 31 IMN were selected of which 15 nights were in autumn and 16 in spring (Fig. 2). Of these 31 nights, data on track speed and direction were available from the horizontal radar on 22 nights, resulting in a sample of 14 nights in spring and 8 nights in autumn.

Wind data

Gridded wind data from the forecast dataset of the European Centre for Medium-Range Weather Forecasts (ECMWF) HRES model (Owens and Hewson 2018) at 3 h intervals was obtained from 1000, 925 and 850 hPa which corresponds to altitudes of 101, 766 and 1481 m above mean sea level according to the international standard atmosphere ('U.S. Standard Atmosphere' 1976). These data have a spatial resolution of 0.25° (ca 30 km) and they express wind conditions with two components: the u-component which describes the wind in the west–east direction (wind blowing to the east is positive) and the v-component which describes the wind in the south–north direction (wind blowing to the north is positive). The data were linearly interpolated in space and time to the first location of each track recorded at the radar location.

The back trajectory model

To estimate potential departure locations during nights of intense migration and assess wind selectivity at departure, we applied a back-trajectory model following Shamoun-Baranes and van Gasteren (2011). The model used a 30 min time step and was run for each track detected by the horizontal radar using airspeeds and headings of the birds as determined at the radar location. At each time step, a new latitude and longitude were calculated, and wind data from that location was used to calculate the new groundspeed and track directions. On each IMN, the model was run backwards in

time for a single night for all tracks recorded between sunset and one hour before sunrise. Each radar track was then simulated backwards until sunset. For simplicity we assume that birds set a constant airspeed and heading at departure which is maintained throughout the night, thus employing compass navigation during their flight, without compensating for drift. Similarly, we simulate migration at a constant pressure level. Although some studies show that birds may alter their flight altitude within a night (Bowlin et al. 2015, Liechti et al. 2018), the evidence is still scattered.

The back trajectory model with wind data from different pressure levels

Some studies have shown that altitude distributions of birds may differ among nights in the same region due to differences in the vertical profile of atmospheric conditions (Gauthreaux 1991, Dokter et al. 2013, Kemp et al. 2013). In our model, the choice of a pressure level from which the wind data was obtained could have affected derived groundspeeds and track directions, finally influencing potential departure locations. To test if the potential departure locations would differ when calculated with wind data from different pressure levels, we also ran our model with the wind data obtained from the 1000 and 850 hPa pressure levels. We compared all distributions of birds' potential departure locations for each pressure level using the earth mover's distance method incorporated in R package `emd` (Urbanek and Rubner 2012). The distribution of departure locations on intense migration nights did not differ significantly among different pressure levels (Earth-Mover's distance ≈ 0) and migration could only be detected below ≈ 1000 m (Fijn et al. 2015). Therefore, we focus the description of the results on simulations performed at the 925 hPa. For more information about distributions of departure locations estimated by using the wind data from other pressure levels see Supplementary information.

Seasonal patterns of migration

We calculated nightly means of airspeed (AS), groundspeed (GS), heading and track direction and used it to calculate mean \pm standard deviation (SD) of airspeed and groundspeed, as well as circular mean and mean resultant vector of directional data for both IMN and WMN. Values of r ,

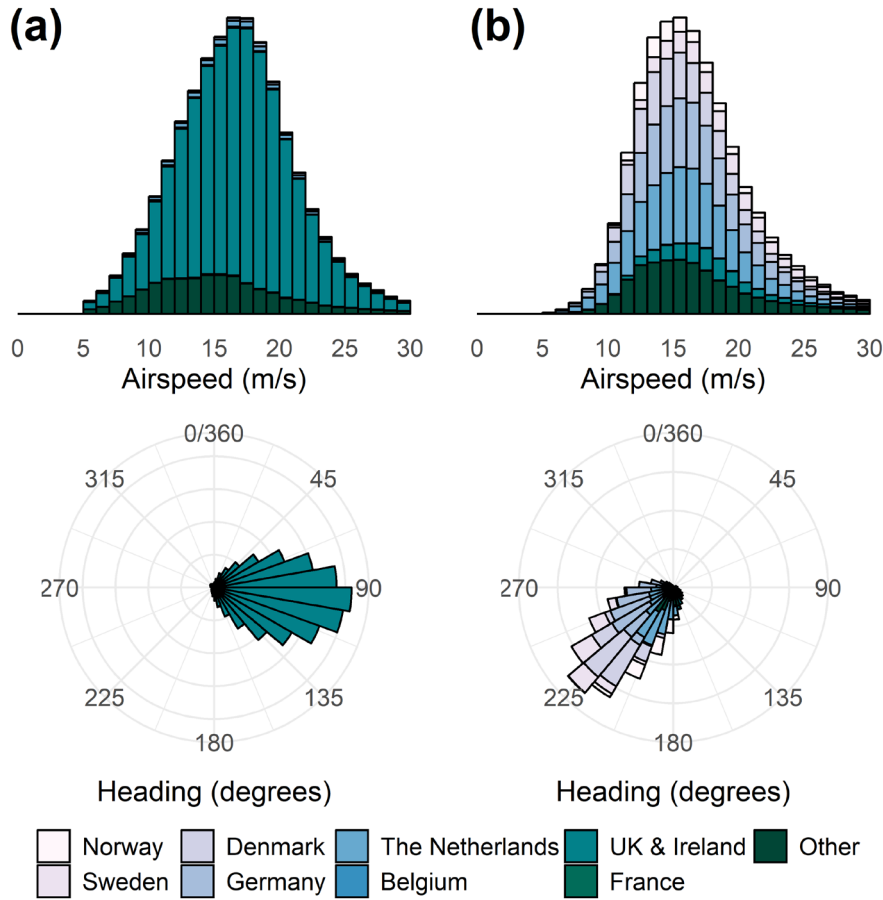


Figure 3. Distributions of airspeeds (top) and headings (bottom) of trajectories in spring (a) and autumn (b) on intense migration nights. Different colours of bars show where the trajectories originate from. Note that trajectories and measured bird tracks have the same values of headings and airspeeds since these two values were kept constant throughout our model.

which estimates the dispersion of directional data around the mean, range between 0 and 1, where 1 represents no dispersion in the data (Jammalamadaka and SenGupta 2001). We performed the Rayleigh test to test for nonuniformity of directional data. Groundspeeds and airspeeds were compared between IMN and WMN of both seasons using a two-sample t-test to test for equal mean and using individual nights as degrees of freedom. All calculations were performed in R (<www.r-project.org>).

Departure locations

The potential departure locations of birds were assessed for each IMN using the endpoints of all simulated trajectories in a night. The main concentration areas of potential departure locations in both seasons were assessed based on geographical boundaries. Categories of potential departure locations in autumn were: ‘Sweden’, ‘Denmark’, ‘Norway’, ‘Germany’, ‘the Netherlands’ and ‘Other’. In spring, categories were: ‘the Netherlands’, ‘Belgium’, ‘France’, ‘The UK’ and ‘Other’. The category ‘Other’ included all tracks on land that were not assigned to one of the other countries and all tracks ending over the sea. For easier interpretation, departure locations

were visually presented as a two-dimensional kernel density using *kde2d* function from package MASS (Venables and Ripley 2002) (Fig. 4).

Winds at departure and wind assistance

The wind speed and direction were extracted at each estimated departure location at estimated departure times on IMN. The same modelled departure locations were used to extract wind speed and direction on WMN at 18:00 UTC. The nightly averages of wind direction and speed were used to calculate the seasonal mean wind direction and mean resultant vector length r and mean wind speed \pm SD for IMN and WMN.

To calculate wind assistance (WA) at departure locations the tailwind equation (Kemp et al. 2012) was used:

$$WA = y \cos \theta \quad (1)$$

where y is wind speed (m s^{-1}) and θ is the difference between wind direction and the preferred migration direction. As the full wind drift was assumed, the preferred migration direction is equal to the heading (Green and Alerstam 2002,

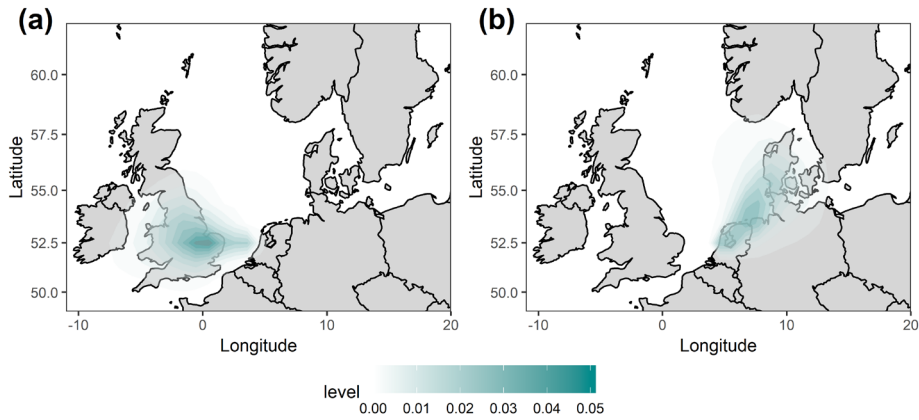


Figure 4. Two-dimensional kernel density of potential departure locations of trajectories on nights of intense migration in spring (a) and autumn (b). Estimated departure areas from which the majority of the trajectories departed are represented with colours of higher intensity.

McLaren et al. 2012). WA on IMN was then calculated using mean nightly wind conditions at the departure at estimated departure times. The same departure locations as on IMN were used for WMN and average nightly wind conditions for all estimated departure locations at sunset on WMN were calculated and assigned by date to all tracks recorded by the radar on WMN. Seasonal mean WA \pm SD and wind speed \pm SD for IMN and WMN were calculated from nightly means and compared between different seasons and IMN and WMN using two-sample t-tests.

Results

Seasonal patterns of migration at the radar location

In general, nights with intense migration in autumn had a higher number of migrants as recorded by vertical radar in comparison to spring (Fig. 2). In total, 235 815 tracks were recorded during 318 nights in spring, while on 16 IMN 64 632 tracks were recorded. In autumn, 489 446 tracks were recorded on 300 nights and 143 252 tracks were recorded on 15 IMN. Thus, 27.4% of total spring migration and 29.3% of total autumn migration occurred on 5% of the total number of nights.

In spring, headings (116° , $r=0.4$, $p < 0.001$) and track directions (107.6° , $r=0.4$, $p < 0.001$) on WMN were

non-uniformly distributed with the mean direction to the ESE (Table 1). During IMN, mean headings (90.8° , $r=0.9$, $p < 0.001$) and track directions (83.8° , $r=0.9$, $p < 0.001$) were to the east and more concentrated than during WMN (Fig. 3a, Table 1). On WMN, mean airspeed ($16.8 \text{ m s}^{-1} \pm 2.4$) and groundspeed ($18.1 \text{ m s}^{-1} \pm 3$) were not significantly different (AS: $t(17)=1.8$, $p=0.08$; GS: $t(16.8)=-0.63$, $p=0.5$) from mean airspeeds ($15.8 \text{ m s}^{-1} \pm 1.8$) and ground-speeds ($18.5 \text{ m s}^{-1} \pm 2.4$) on IMN (Fig. 3a, Table 1).

In autumn on WMN, headings (211.4° , $r=0.7$, $p < 0.001$) and track directions (200.5° , $r=0.5$, $p < 0.001$) were non-uniformly distributed and predominantly towards SW (Table 1). Headings (217.9° , $r=0.9$, $p < 0.001$; Fig. 3b) and track directions (229.4° , $r=0.9$, $p < 0.001$) on IMN were more concentrated than on WMN and on average also towards SW (Table 1). Mean airspeed on WMN ($18.4 \text{ m s}^{-1} \pm 2.8$) was significantly higher ($t(9.5)=3.4$, $p=0.007$) from the mean airspeed on IMN ($16.5 \text{ m s}^{-1} \pm 1.4$; Fig. 3b), but the mean groundspeed on WMN ($18.2 \text{ m s}^{-1} \pm 3$) was not significantly different ($t(21.8)=-1.6$, $p=0.53$) from the mean groundspeed on IMN ($18.7 \text{ m s}^{-1} \pm 0.7$; Table 1).

Headings and track directions did not show a complete seasonal reversal. On WMN, mean airspeed ($t(385.6)=-5.4$, $p < 0.001$) was significantly lower in spring compared to autumn, but the mean groundspeed ($t(332.4)=-0.2$, $p=0.7$) was not significantly different. Both mean ground-speed and mean airspeed were not significantly different in

Table 1. Summary statistics of the bird tracks (N=number of bird tracks) as recorded by horizontal radar beam at the radar location on WMN and IMN in spring and autumn of the full study period, averaged per night (n=number of nights). For directional data, circular means and mean resultant length are provided. A value of mean resultant length r closer to 1 indicates less dispersion in directions (Jammalamadaka and SenGupta 2001, Kutil 2012).

	N	n	Track direction (degrees)		Groundspeed (m s^{-1})		Heading (degrees)		Airspeed (m s^{-1})	
			Mean	r	Mean	SD	Mean	r	Mean	SD
Spring (WMN)	271 637	159	107.6	0.4	18.1	3.0	116.0	0.4	16.8	2.4
Spring (IMN)	141 237	14	83.8	0.9	18.5	2.4	90.8	0.9	15.8	1.8
Autumn (WMN)	503 162	179	200.5	0.5	18.2	3.0	211.4	0.7	18.4	2.4
Autumn (IMN)	133 687	8	229.4	0.9	18.7	0.7	217.9	0.9	16.5	1.4

Table 2. Summary of the proportion of trajectories tracked back to potential departure locations in spring and autumn on intense migration nights.

Origin	Trajectories (%)	
	Spring	Autumn
UK and Ireland	80.83	6.28
Other	14.58	18.37
The Netherlands	2.33	25.18
Germany	1.05	22.33
Belgium	0.56	0.12
France	0.28	0.11
Denmark	0.14	14.40
Norway	0.14	5.17
Sweden	0.05	7.98

spring and autumn on IMN (GS: $t(16.7) = -0.3$, $p = 0.7$; AS: $t(17.9) = -0.9$, $p = 0.3$).

Potential departure areas

In spring, the vast majority of trajectories (80.83%) modelled at 925 hPa were tracked back to departure areas in the UK and Ireland, while only a small proportion was tracked back to locations south or southwest from the radar (Fig. 3a, 4a, Table 2). In autumn, almost half of the trajectories (47.51%) were tracked back to the Netherlands and Germany (Fig. 4b), while a considerable amount originated in different parts of Scandinavia (27.55%), mostly in Denmark and Sweden, and only a small fraction was tracked back to Norway (Table 2). In both seasons, most of the trajectories classified as ‘Other’ were tracked back to different locations in the North Sea and the Atlantic Ocean, but also to some locations on land.

Winds at departure and wind assistance

The mean wind direction at departure locations in spring was towards E on both WMN and IMN although much more concentrated on IMN (WMN: 87.7° , $r = 0.3$, $p < 0.001$; IMN: 75° , $r = 0.7$, $p < 0.001$ Fig. 5a, Table 1). In autumn, the mean wind direction was also towards E on WMN (84.1° , $r = 0.4$, $p < 0.001$), but towards SW on IMN and more dispersed than on IMN in spring (218.9° , $r = 0.3$, $p = 0.4$) (Fig. 5b, Table 1). In spring, the mean wind speed on WMN ($9.6 \text{ m s}^{-1} \pm 2.9$) was not significantly different ($t(14.6) = 0.5$, $p = 0.6$) from the mean wind speed on IMN ($10.1 \text{ m s}^{-1} \pm 3.5$), but the mean wind speed on WMN in autumn ($9.4 \text{ m s}^{-1} \pm 2.3$) was significantly higher than the mean wind speed on IMN ($6 \text{ m s}^{-1} \pm 1.2$). Wind speed was significantly higher in spring than in autumn for IMN ($t(17.7) = 3.9$, $p = 0.001$), but no significant difference between seasons was observed on WMN ($t(301.9) = 0.8$, $p = 0.3$) (Table 1).

Mean wind assistance was positive in spring on WMN ($0.45 \text{ m s}^{-1} \pm 3$) and IMN ($3 \text{ m s}^{-1} \pm 2$), whereas in autumn wind assistance was positive only on IMN ($1.3 \text{ m s}^{-1} \pm 2.7$; Fig. 5b). WMN in autumn had negative wind assistance ($-1.84 \text{ m s}^{-1} \pm 3.5$). For each season wind assistance was significantly higher (S: $t(18.5) = 4.3$, $p < 0.001$; A: $t(8) = 3$,

$p = 0.01$) on IMN than on WMN (Fig. 5b). Wind assistance did not differ significantly between seasons on IMN ($t(11.4) = 1.5$, $p = 0.1$), but it was significantly higher in spring than in autumn on WMN ($t(335.2) = 6.4$, $p < 0.001$).

Discussion

Our study shows that on IMN in spring, the majority of migrants observed off the coast of the Netherlands flying over the southern North Sea predominantly departed from the UK. Considering estimated departure locations and the fact that wind conditions were similar between IMN and WMN and were generally supportive of flight across the southern North Sea from west to east, our study suggests that during spring, departure decisions based on wind selectivity are relaxed due to the prevalence of supporting winds. On IMN in autumn, birds migrated along the west coast of the Netherlands with a mean heading towards SW arriving at the radar location from estimated departure locations in Denmark, Germany and the north of the Netherlands, flying with tailwinds. Supporting winds were not prevalent in autumn, but they did occur on IMN providing higher wind assistance (Fig. 5b) for migratory birds. Even though the majority of autumn migrants departed on WMN, mostly flying with headwinds, we show that almost a third of the migrants on 5% of the nights departed when they could exploit increased wind assistance. It has been shown that some species have very flexible departure decisions that are not bound to specific wind conditions (Grönroos et al. 2012), while survival of others is strongly affected by their departure decisions in relation with supporting winds (Erni et al. 2005, Loonstra et al. 2019). Lower wind speeds and higher wind assistance on IMN in autumn suggest that birds prefer to fly on nights with weak tailwinds at departure, as shown in previous studies (Alerstam 1979, Schaub et al. 2004). However, birds still migrated with negative wind support on several IMN in autumn (Supplementary information) which indicates that the prevalence of headwinds might be the reason why lower wind speeds are preferred on IMN.

Early radar studies in the North Sea basin (Lack 1959, Eastwood 1967) suggest that due to the existing wind regimes birds perform loop migration by crossing directly to the Netherlands from the UK in spring, but flying SW along the eastern coast of the North Sea from Scandinavia to the Netherlands, and then crossing to the UK avoiding wide stretches of water in autumn (Buurma 1987). In our study, mean headings (Fig. 5, Table 1) do not show a seasonal reversal and suggest that on average migrants use different migratory axes in spring and autumn, selecting supporting winds for a direct crossing of the North Sea in spring and coasting in autumn. However, it is possible that due to a limited detection range and its position, our radar did not record the SW–NE migration axes in spring as this might occur more inland and outside of the radar detection range. Moreover, the radar missed all the movements at altitudes higher than 1.5 km. This means that especially in spring, when high

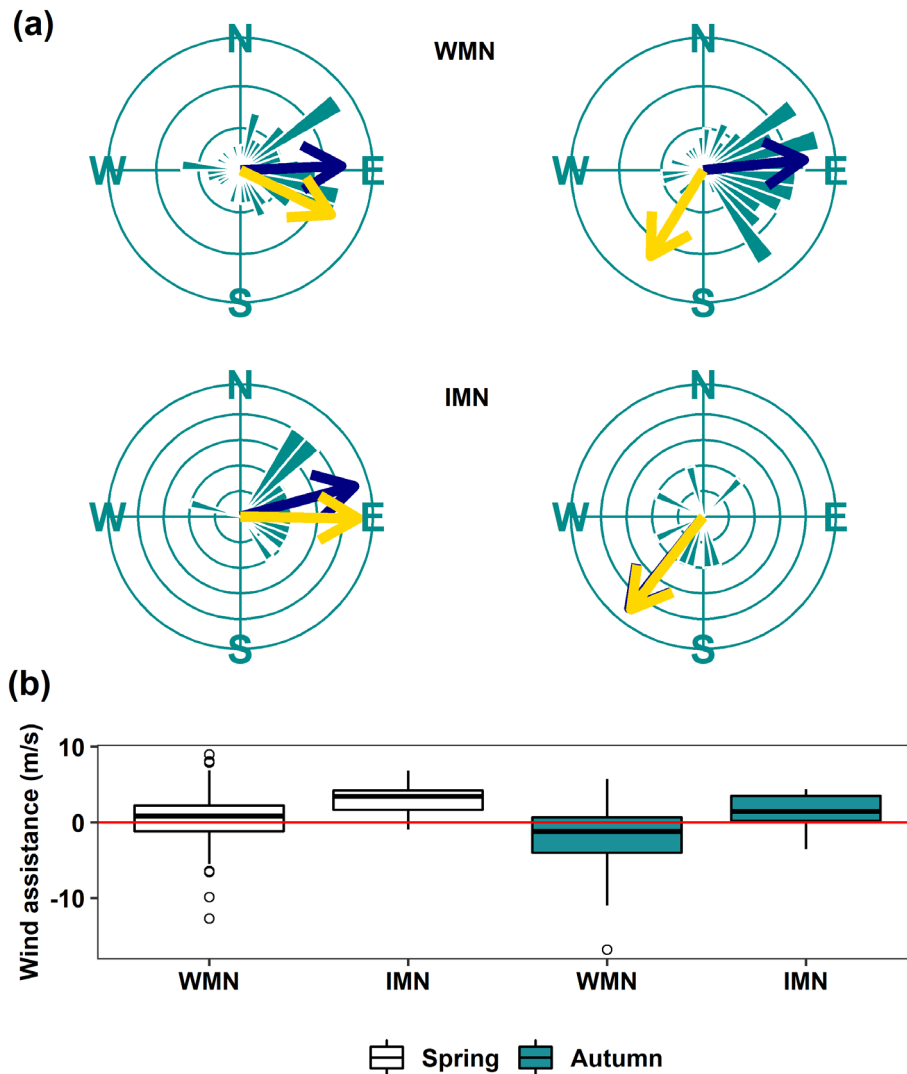


Figure 5. (a) Distribution of wind directions (degrees) at estimated departure locations on weak (WMN, N spring=739 315, N autumn=1 049 130) and intense (IMN, N spring, N autumn) migration nights in spring (left) and autumn (right). The blue arrow represents mean wind direction, while the yellow arrow represents mean heading. (b) Wind assistance (m s^{-1}) values in spring (white) and autumn (cyan) for WMN (N spring=271 637, N autumn=503 162) and IMN (N spring=141 237, N autumn=133 687). The red horizontal line marks a threshold between positive and negative wind assistance.

flying migrants have been recorded in the region over land (Dokter et al. 2013, Kemp et al. 2013), tracks of high flying migrants were missed.

Distributions of airspeeds in this study were similar in spring and autumn and suggest that migrants on IMN in both seasons include a mix of small and slower passerines and faster flying migrants such as waders and waterfowl (Bruderer and Boldt 2001, Alerstam et al. 2007) and the majority of birds observed at the radar location via moon-watching and sound recordings during spring and autumn were songbirds (Krijgsveld et al. 2011). Yet, the occurrence of IMN in late autumn and early spring and the observed differences in airspeeds between IMN and WMN in autumn (Table 1) imply that different species might be involved in migration on different nights. IMN in our study may reflect predominantly

short-distance migrants who have been shown to respond differently to weather conditions at departure than long-distance migrants in a comparative analysis of several songbird species (Packmor et al. 2020). Currently, due to the limitations of the radar system and the similar distributions of airspeeds between seasons we cannot determine whether species composition differs between spring and autumn.

To better understand migration flyways, it is crucial to understand birds' responses to weather conditions (Alerstam 2001). Wind regimes are an important driver of birds' departure decisions and migratory routes on land (Liechti and Bruderer 1998, Van Belle et al. 2007, McLaren et al. 2012), but especially when crossing ecological barriers such as large water bodies (Yamaguchi et al. 2012, Bulte et al. 2014, Ward et al. 2018). We scratched the surface of complex seasonal dynamics

around one of the inhospitable areas of the East-Atlantic Flyway, the North Sea, and revealed that seasonal differences in wind regimes alter its migratory dynamics including routes, timing and intensity of migration. In the coming years, the barrier effect of the North Sea might become even more pronounced, as the North Sea is increasingly being exploited for wind energy and gas extraction (Bailey et al. 2014, Leopold et al. 2014) and the impact of such activities on avian species becomes an even bigger conservation concern. To assess the potential impact of human structures at sea on migratory species and develop mitigation measures, more knowledge is needed about the drivers behind migration patterns and how this influences patterns on a local scale. We have analysed only one site along the west coast of the Netherlands. The increasing deployment of mobile radars offshore for environmental impact assessments, the integration of larger-scale information from weather radar around the North Sea (Dokter et al. 2011, 2013, Kemp et al. 2013) and tracking studies of small migrants facilitated by systems such as Motus (Brust et al. 2019) will greatly benefit future research on the complex dynamics of migration around the North Sea.

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Data deposition

Data will be available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.0rxwdbrbx>> (Bradarić et al. 2020).

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Supplementary information (available online as Appendix jav-02562 at <www.avianbiology.org/appendix/jav-02562>). Appendix 1.