On the radar:
weather, bird migration and aeroconservation
over the North Sea

by
Maja Bradarić

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All data used in this thesis along with scripts used to carry out the analysis will be archived according to the IBED Data Management guidelines prior to the thesis defence.


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Chapter 1

General introduction

1.1 Airspace – a neglected habitat?

The troposphere, the lowest layer of the atmosphere where most of the weather occurs, is occupied by many forms of life that use this space to perform various types of movement, forage and reproduce (Davy et al. 2017). Research on life in the air was limited until a few decades ago due to the lack of suitable observation methods. Consequently, airspace has repeatedly been overlooked in conservation science and plans. In the last few years, there have been multiple calls for aeroconservation (Davy et al. 2017; Lambertucci & Speziale 2021; Zuluaga et al. 2021) and observation methods such as GPS, radiotelemetry and radars allowed to uncover the multifaceted role of the airspace in the life histories of various organisms that extensively utilize it. To emphasize the ecological relevance of this part of the atmosphere, the terms aerosphere and airspace have been coined (Diehl 2013; Davy et al. 2017), and the scientific domain of interactions between organisms and the aerosphere has been termed aeroecology (Kunz et al. 2008).

Passive occupants of airspace include aerial microorganisms and pollen. They get aerosolized from water or land by winds and displaced, their journey through space sometimes covering great distances (Jones & Harrison 2004). Eventually, they return to their terrestrial or aquatic habitats, creating new microbial and plant communities. In contrast, active airspace occupants employ flight to propel themselves through this dynamic medium. Insects ride on selected supportive winds when performing their migratory movements (Reynolds et al. 2017a). Under carefully chosen weather conditions, swarms of insects can cover large areas in airspace with the purpose of mating in the air (Sullivan 1981). Insectivorous birds and bats feed on the wing, catching airborne insects mid-flight (Malmqvist et al. 2018). Multiple bat species perform short and long-distance migrations between their summer roosts and wintering areas, relying on a plethora of weather conditions generated in the airspace to execute their journeys successfully (Pettit & O’Keefe 2017; Haest et al. 2021). Likewise, migratory birds, whose journeys have equally captivated scientists and enthusiasts for centuries now, rely on weather conditions to make departure decisions and choose flight altitudes while balancing energy expenditure and time spent on migration (Richardson 1978; Shamoun-Baranes & van Gasteren 2011; Kemp 2012). Species of birds that employ soaring flight rely on thermals, rising bodies of warm air, to decrease the energetic cost of their movement (Weimerskirch et al. 2016). Common and alpine swifts spend almost all their lives airborne, coming to the ground only to lay their eggs (Liechti et al. 2013; Hedenström et al. 2016). Airspace supports mating displays (Takeuchi 2017; Mikula et al. 2022),
as well as transmission of olfactory (Bossert & Wilson 1963), pheromonal (Law & Regnier 1971; Tuninetti & Megela Simmons 2022) and acoustic (Brown & Handford 2003; Tuninetti & Megela Simmons 2022) signals in many insect, bat and bird species; it supports pollination (Niklas 1985), bacterial and viral transfer (Clark & de Calcina-Goff 2009), food competition (Arlettaz et al. 2000), predator-prey interactions (Malmqvist et al. 2018), movement (Hansson & Åkesson 2014) and reproduction (Sullivan 1981). Although to our current knowledge, no organisms spend their entire lives in airspace, there are plenty of those whose various life stages depend on the airspace as habitat.

Yet, aerial habitat is a relatively new concept in ecology (Diehl 2013). Due to the static nature of habitat definition, which mainly focused on occupancy, airspace was never given the same status as terrestrial and aquatic habitats (Kunz et al. 2008; Diehl et al. 2017). However, revised definitions of what constitutes a habitat started a necessary paradigm shift. In the last decade, an increased number of studies that integrate atmospheric, ecological, physiological and behavioural research of aerosphere and airborne organisms showed that the airspace serves a crucial role in different life stages of various animals, and although animals use it in combination with terrestrial or aquatic habitats, the airspace should have the same status. Still, despite more than decade-long initiatives for giving airspace an official habitat status, it is largely excluded from environmental policies and conservation plans (Davy et al. 2017). Recent pleas of aeroecologists are urging to change this (Davy et al. 2017; Lambertucci & Speziale 2021; Zuluaga et al. 2021) as the quality of aerial habitat deteriorates through pollution and man-made fragmentation (Lambertucci et al. 2015).

1.2 Anthropogenic disturbances in the airspace

Besides climate change, habitat loss and fragmentation are the largest causes of biodiversity decline (Huxel & Hastings 1999; Sih et al. 2000; Hanski 2011). Over the last century, airspace has gradually become crowded with man-made structures such as wind turbines, power lines, aircraft, high-rise buildings and drones (Lambertucci et al. 2015). These technological developments are increasing human-wildlife conflict through increased risk of collision and barrier effect that might result in habitat fragmentation, which can have inconceivable consequences on populations of aerial organisms (Davy et al. 2017). Anthropogenic structures in the airspace create new challenges for aerial organisms that are not used to flying in cluttered environments and can prompt inappropriate or lack of responses that directly and indirectly can lead to decreased survival (Diehl et al. 2017).

Although the effects of man-made structures on insect flight behaviour are greatly unexplored, it is believed that wind turbines may cause the entrapment of insects in streams of air created around them. This has been indirectly supported by observations of insectivorous bats being attracted to wind turbines (Foo et al. 2017;
Bauer et al. 2019). On the other hand, the effects of man-made structures on bats and birds are slightly better understood, even though there is a considerable variation in estimates of adverse effects and their ecological significance (Lambertucci et al. 2015). Birds are attracted to artificial light on high buildings, communication towers and gas platforms. Illuminated high-rise buildings kill millions of birds annually only in the US (Loss et al. 2015; van Doren et al. 2017). Bird collisions with aircraft take both human and bird lives and cost billions of euros per year (Dolbeer & Wright 2015). Especially during low-visibility conditions, migratory bats and birds collide with onshore and offshore wind turbines (Drewitt & Langston 2008; Perold et al. 2020). With the number of wind farms and other man-made structures increasing all over the globe (Gielen et al. 2019), these effects are bound to become more pronounced in the future. Even though aerial organisms can evolve behaviours that will help them deal with altered airscapes (Desholm & Kahlert 2005), the pace of airspace alteration is likely much higher than the one at which evolution of different adaptive behaviours can occur and brings other issues such as increased energetic cost of flight (Masden et al. 2009).

Therefore, it has been suggested that timely executed conservation measures can help drastically reduce the negative effects of man-made structures on wildlife (Bauer et al. 2019). To preserve highly dynamic ecological processes such as animal movement, spatial as well as temporal components must be included in mitigation (Horton et al. 2021). Estimating spatial hotspots for aerial organisms can help the spatial planning of energy infrastructure and guide local mitigation measures (Gauld et al. 2022). It has been shown that partially shutting down lights on high-rise buildings can reduce bird fatalities by 60% (van Doren et al. 2021), planning aviation around bird movements minimizes bird strikes (van Gasteren et al. 2019), and wind turbine curtailment can help bats and birds move safely through the airspace (Singh et al. 2015; Hayes et al. 2019) This is particularly important in the areas where substantial wind energy development and essential movement corridors for different species overlap. Such areas can create movement barriers, especially for migratory species, whose carefully timed migration journeys might get altered due to the need to circumvent these areas, resulting in higher energy expenditure, exhaustion and failure to breed. Alternatively, barrier crossings can lead to increased mortality, as their inhospitality offers no opportunities for refuelling or stopping (Diehl et al. 2014; Klaassen et al. 2014). An example of such an area is the North Sea (Delingat et al. 2008), which is perfect for hosting offshore wind energy infrastructure due to its shallow waters and the abundance of wind.

1.3 The North Sea – a double barrier for aerial movement?

The North Sea occupies the area between the English Channel in the SW, the Scandinavian Straits in the east and 62° latitude in the north. It stretches across 750000 km² and has a mean depth of 90 m (Cohen et al. 2017). This area supports the offshore wind energy infrastructure of all top five European offshore wind energy
producers (the UK, Germany, Denmark, the Netherlands and Belgium) with the current offshore wind capacity of around 25 GW, set to increase 10-fold by 2050 (FPS Economy 2021; Rijksoverheid 2021; Naimoli 2022; Østergaard Nielsen & Hemmer 2022; The UK government 2022).

Considering the magnitude of change that the North Sea airscape will experience in the coming years and following up on the calls for aeroconservation, some countries in the North Sea basin introduced conservation plans for vulnerable groups of airborne animals that use the airspace that is bound to be cluttered with wind turbines. Having in mind that the North Sea accommodates one of the largest migratory bird flyways, the East-Atlantic flyway (BirdLife International 2022), and the fact that migratory birds in Europe are experiencing declines due to various, mainly anthropogenic causes (Bairlein 2016), the Netherlands, for example, will make wind turbine shutdowns mandatory in times of intense bird migration to allow for a safe passage and decrease the pressure on populations of birds migrating over this area. The Netherlands, which by the end of 2022 will produce 4.7 GW of wind energy offshore from wind turbines in 14 offshore wind parks that cover the area of 673 km², will increase its capacity to 64.3 GW produced in 36 offshore wind parks that will cover 6146 km² of the total 57000 km² of the Dutch North Sea by 2050 (Rijkswaterstaat 2022) (Figure 1.1). Introducing wind turbine shutdowns should considerably minimize the collision risk for migratory birds in one of Europe’s largest offshore wind expansion areas. This thesis focuses on migration over the North Sea in the context of wind energy expansion and mitigation in Dutch waters.

![Figure 1.1 Planned offshore wind development in the North Sea by 2050. Operational wind farms are indicated with red polygons, and those that are planned to be built by 2050 are marked with green polygons. The black line indicates the border of the Dutch North Sea. The map is available at Winds of the North Sea in 2050 website (Baas 2022).](image-url)
For migratory landbirds, which represent the majority of migrants within the East-Atlantic flyway (BirdLife International 2020), wind turbines are not necessarily the only risk when flying across the North Sea. Being a relatively large body of water, the North Sea might also pose an ecological barrier for these birds. Ecological barriers are considered landscapes that physically hinder movement or decrease habitat quality, making the occupancy of such a habitat risky for a certain organism. For migratory landbirds, mountain ranges, deserts, and seas represent ecological barriers, as they either physically prevent their movement or have limited or no opportunities to rest and refuel. During migration, this can lead to the evolution of alternative migratory paths and detours, incorporation of new orientational mechanisms or barrier crossings through increased fuel deposition (Alerstam et al. 2003).

When around ecological barriers, birds may make different trade-offs between time, energy and safety, and the currency they will trade depends on their body condition (Deppe et al. 2015). According to optimal migration theory, birds are predicted to balance time spent on migration and energy expenditure (Alerstam 2011). With low fuel loads, birds tend to circumnavigate ecological barriers, taking safer routes but creating detours and running the risk of not completing their migration on time. On the contrary, with high fuel loads, landbirds tend to cross ecological barriers, preventing detours and saving precious time (Schmaljohann & Naef-Daenzer 2011). Barrier crossings bring other perils, such as dehydration and exhaustion. To decrease such risks and increase chances of survival when crossing the seas, birds mainly rely on wind assistance (Gill et al. 2014).

If an ecological barrier is enhanced with a man-made one, as with offshore wind turbines, the chances of successful barrier negotiation drastically decrease (Drewitt & Langston 2008; Poot et al. 2008; Marques et al. 2014). If caught in bad weather such as rain, mist or adverse winds while en route across the sea, birds tend to get disoriented and pushed down (Alerstam 1990), which makes them even more prone to collisions with man-made structures. This is especially dangerous during nocturnal migration, when lights on man-made structures attract birds (McLaren et al. 2018; Horton et al. 2019), putting them in greater danger of collision. Within the East-Atlantic flyway, the vast majority of landbirds migrate at night.

1.4 Nocturnal bird migration

In a world without man-made obstructions, performing migration at night is one way to decrease the dangers of the migratory journey. For birds that migrate in warmer climates, flight at night decreases the risk of dehydration as the temperatures are lower than during the day. Humidity is usually higher at night, which further decreases the dehydration risk. For birds that employ flapping flight, nocturnal migration reduces the total energetic cost of the flight. Cool and dense air at night, lower vertical turbulence and generally lower wind speeds contribute to lower
energy expenditure. Flight at night also leaves more time for feeding during the day and lowers the risk of predation, mainly from diurnal raptors, which migrate during the day (Newton 2008).

Nocturnal migrants generally depart on their journeys around sunset which seems to be influenced by special polarized light conditions that occur at twilight and help birds with orientation (Alerstam 1990; Åkesson et al. 1996; Muheim et al. 2006). By migrating, birds can travel great distances to acquire optimal food supply, decrease competition and predation, or reach sites to breed and raise their young (Alerstam 1990; Newton 2008). Where and when they fly depends on their current life stage and the availability of resources. Before the breeding season, most bird species migrate towards areas with higher latitudes since long days in those areas create conditions with abundant food resources, making them optimal breeding sites (Newton, 2008). In winter, when days become shorter and food scarce, these birds return to areas with relatively warmer climates (Newton 2008).

Following the circannual rhythm, two major migration events over the North Sea happen in spring and autumn every year. In autumn, birds migrate from their breeding areas in Scandinavia and North-western Europe to Southern Europe and Africa, travelling over the North Sea in a south-westerly direction (Lack 1959; Hüppop et al. 2006). Birds from North-eastern Europe migrate to Britain in a west-south-westerly direction (Lack 1959). A third more southerly migration route goes from Norway across the North Sea (Shamoun-Baranes & van Gasteren 2011) (Figure 1.2). While it is assumed that the same migratory axes with reversed migration directions occur in spring, this has never been quantified.

Current studies show that amongst many different groups of birds that migrate nocturnally over the North Sea, songbirds (Passeriformes) are assumed to be predominant. Regardless of the methods used, songbirds accounted for more than 70% of all observed migrating birds in all existing studies. The most numerous songbird migrants in the area are robin (Erithacus rubecula), song thrush (Turdus philomelos), redwing (Turdus iliacus), fieldfare (Turdus pilaris), blackbird (Turdus merula), skylark (Alauda arvensis) and starling (Sturnus vulgaris) (Shamoun-Baranes & van Gasteren 2011). This information mainly comes from visual observations during morning migratory arrivals and sometimes from audio recordings offshore. Even with technological advancements, it remains challenging to discern nocturnal species that migrate offshore.
Figure 1.2 The main bird migration routes across the North Sea in autumn: between Scandinavia and northwest Europe and southern Europe and Africa (green), between North-eastern Europe and the UK (yellow) and from Norway across the North Sea (blue) (Lack 1959; Hüppop et al. 2006; Shamoun-Baranes & van Gasteren 2011).

1.5 Weather – a proximate driver of migration

Many studies tried to explain the main proximate drivers of bird migration. It has been shown that the length of the day, along with birds’ internal clock, mainly influences the timing of migration (Gwinner & Helm 2003; Åkesson et al. 2017). However, these drivers affect the circannual and circadian migration rhythm and not day-to-day variation of migration intensity. Day-to-day bird migration intensity can vary substantially, even during the peak migration season. This is affected by different weather parameters, as birds wait for preferable weather conditions at the site of departure to start their migration (Alerstam 1990; Newton 2008; Kemp 2012; Shamoun-Baranes et al. 2017).

When migrating, birds have to effectively cope with a highly dynamic environment at different spatial and temporal scales. Prioritizing energy expenditure, migration time and safety will affect birds’ behavioural response to atmospheric conditions. As one of the main proximate drivers of bird migration, weather at different temporal and spatial scales strongly influences birds’ decisions about migration and departure times, driving day-to-day migration dynamics (Shamoun-Baranes et al. 2017). Especially in mid-latitudes, the frequent transition between low and high-pressure systems, each related to a specific set of weather conditions, influences
spatiotemporal patterns of bird migration (Richardson 1978; Dokter et al. 2013). Development of different observation techniques over time and, most importantly, increased use of different types of radars in bird migration research allowed us to gain more insight into synoptic, mesoscale and microscale weather conditions that drive mass bird migration patterns. It is hard to quantify individual effects of specific weather parameters on the flight of birds on any scale, as they represent a complex environmental system and are strongly correlated (Lack 1960a; Shamoun-Baranes & van Gasteren 2011; Kemp 2012; Shamoun-Baranes et al. 2017). Nevertheless, we present a short overview of those believed to influence bird migration the most.

1.5.1 Wind

Many studies have shown a clear connection between the mean direction of migration and wind direction and speed (Kemp et al. 2012; Dokter et al. 2013; Shamoun-Baranes et al. 2017; Bruderer et al. 2018). This implies that the wind is one of the key weather factors in determining bird migration. The migration starting time, birds’ arrival success and flight altitude choice depend on preferable wind conditions (Erni et al. 2005; Shamoun-Baranes & van Gasteren 2011; Kemp 2012; Mateos-Rodríguez & Liechti 2012; McLaren et al. 2012; Bulte et al. 2014). When experiencing headwinds, birds are forced to fly at lower altitudes and decrease their flight speed, which increases the risk of predation and collisions with man-made structures (Drewitt & Langston 2008). Studies have shown that birds prefer the tailwinds that help them cross ecological barriers, such as the sea (Stoddard et al. 1983; Deppe et al. 2015). Without wind assistance, the average survival of birds migrating over the Mediterranean sea in autumn would be less than 10% (Erni et al. 2005). In seasons when tailwinds are rare, birds may make detours where possible, resulting in different routes among seasons (Bradley et al. 2014).

1.5.2 Precipitation

Precipitation is considered to have a negative effect on bird migration, as it decreases visibility and birds’ ability to navigate and increases the risk of collisions with obstacles (Kennedy 1970; Schaub et al. 2004; Drewitt & Langston 2008; Shamoun-Baranes et al. 2017). Studies of the bird migration over the southern North Sea show that bird migration density is lower on nights with rain and, if caught by rain during migration, birds will most likely decrease their altitude (Lack 1960b, 1960a; Eastwood & Rider 1965; Eastwood 1967). As these conclusions were mainly derived from radar observations, it is worth mentioning that the radar performance deteriorates during rain events. This is due to rain having similar properties as bird echoes on the radar.
1.5.3 Air pressure

As they advance on their migratory journeys, birds’ flight efficiency and ground speed depend on changes in air pressure in vertical and horizontal space. On the other hand, temporal changes in air pressure, which are related to synoptic weather conditions, affect migration departure times (Alerstam 1990; Richardson 1990a). Air pressure decreases with altitude (approximately one hPa every 10 m) and is believed to be one of the causes of altitude changes during flight (Alerstam 1990; Shamoun-Baranes et al. 2017).

1.5.4 Temperature

Some studies suggest that temperature is the ultimate factor influencing birds’ spring migration (Alerstam 1990; Plonczkier & Simms 2012), while other factors play the most important role during autumn migration. However, passerine inland migration seems to be mainly influenced by temperature in autumn (Shamoun-Baranes et al. 2017). Temperature is also among the factors that strongly influence birds’ migration over the sea (Deppe et al. 2015). Spring migration in mid-latitudes is initiated by increased temperature and warmer winds from lower latitudes. Contrary, autumn migration follows temperature decrease and colder winds from higher latitudes (Alerstam 1990; Kemp 2012). However, having a strong correlation with winds, it is hard to disentangle to what extent temperature, independent of wind conditions, drives seasonal migration patterns.

1.5.5 Differences in weather-driven bird migration

In recent decades, research has identified bird migration’s main general weather drivers. However, differences in how birds exploit certain weather conditions still exist between different regions, topographies and different bird species. Weather-driven departure decisions will be more time-constrained for long-distance migrants, as they cannot afford to sit and wait for long for weather conditions to improve to start their migration, as short-distance migrants often can (Packmor et al. 2020). Most studies on weather’s influence on bird migration have been conducted on land. Atmospheric drivers of bird migration over the sea, even with methodological advancements, remain challenging to explore.

Due to its smooth surface and higher heat capacity at sea, winds tend to be stronger, and temperature changes slower than on land (Stull 1988). This indicates that birds may need to adjust their behaviour when migrating across the sea simply because the weather is different. As seas can be ecological barriers for migratory landbirds, weather-based migratory decisions en route but also at departure become more important when a barrier is present. Thus, birds may be more selective of weather conditions when reaching sea crossings than when travelling over more habitable environments (Alerstam 1990; Newton 2008). This is because any wrong decision
has higher consequences on survival due to landbirds’ inability to land or refuel at seas.

Existing studies of nocturnal bird migration drivers over the sea are limited. They mainly come from the data from individual tracking devices such as GPS and geolocators, which does not allow for an explanation of mass-migration events. On the other hand, sensors such as radars, which allow for tracking of such broad-front mass migration events, are mainly land-based, and portions of their ranges that cover parts above the sea are contaminated with clutter, mainly coming from sea waves. As seas are being exploited for extensive wind energy development to meet CO₂ reduction goals in due time (Leung & Yang 2012), it is becoming increasingly important to understand seasonal patterns of nocturnal migration as the most numerous migratory movement, but also the main drivers behind it to be able to design conservation measures to prevent or minimize adverse effects. To achieve this, radars placed at sea are needed to capture the magnitude and the main dynamics of such a massive movement.

1.6 Radars to track bird movements

Radar was a big step forward in migratory birds’ research as it allows to continuously quantify a number of migrating birds at different altitudes and in different weather conditions (Lack 1959; Eastwood 1967; Alerstam 1990; Bruderer 1997; van Gasteren et al. 2008; Shamoun-Baranes et al. 2008; Dokter et al. 2009; Stepanian et al. 2014; Gürbüz et al. 2015; Stepanian & Horton 2015). Radar sends out electromagnetic energy at a known speed (speed of light) and measures the time that is needed for the energy to reflect (echo), thus calculating the distance of the object (Bruderer 1997; Wolff 1997; Stepanian et al. 2014). Radar antennas can be turned in the desired direction, elevation and azimuth, hence measuring the distance, direction and height of the target (Wolff 1997).

Successful detection of objects by radar is mostly related to their wavelength. If the target has dimensions smaller than one-third of the wavelength, the radar cross-section decreases with the sixth power of the target circumference. This means that if small wavelengths (below 3.75 cm) are used, they will usually be contaminated by echoes of small objects like raindrops and insects. Contrary, if larger (above 3.75) wavelengths are used, they might miss small birds (Bruderer 1997; Gürbüz et al. 2015). Studies showed that birds produce the largest echo in the side view (Edwards & Houghton 1959; Bruderer 1997). Bird echoes make rhythmic fluctuations corresponding to wing-beat patterns, thus allowing bird identification to some extent (Bruderer 1997).

Different radars are used for studying birds (Alerstam 1990; Bruderer 1997; Gürbüz et al. 2015). Pulsed radars measure the time needed for a pulse to find the target and reflect back. Doppler radars are based on Doppler’s effect, which measures
the shift of the target’s speed relative to the radar. Continuous-wave radars are also based on Doppler’s effect, but they continuously transmit the energy while receiving signals simultaneously (Bruderer 1997; Kemp 2012). Different radars and types of radar beams are set up for different purposes, can exploit different features of objects, and their choice can affect the quality of the results (Alerstam 1990; Bruderer 1997; Stepanian et al. 2014; Gürbüz et al. 2015). Those usually used for biological research are military radars (Buurma 1995; Bruderer et al. 2018), weather radars (Dokter et al. 2009; van Doren & Horton 2018; Kranstauber et al. 2022) and specialized radar systems (Fijn et al. 2015; Schmid et al. 2019) calibrated to detect specific animals. Radar systems can provide species-specific information only to a certain extent. Many birds migrating close to the earth’s surface can be missed due to interference from objects on the ground reflecting the radar signal (ground clutter) (Bruderer 1997; Kemp 2012). Due to these limitations, radars require a cautious approach and thorough analysis before using data in ecological research (Schmaljohann et al. 2008). However, they are a useful tool if we want to quantify mass migration events, identify seasons and times of a day with the highest migration density, and if we want to know migrants’ altitude distribution.

Increased usage of radars to study bird migration patterns encouraged the development of specialized bird radar systems. These systems usually transmit S, C or X band frequencies and can use echo or micro-Doppler detection to pick up biological scatter. Beside large-scale movement data, they detect individual bird tracks, distinguish bird sizes and allow to obtain more species-specific results. One of such systems is ROBIN (Radar Observation of Bird Intensity), developed by Robin Radar Systems in the Hague, the Netherlands. Other examples are the MERLIN system developed by DeTect Inc and BirdScan radars developed by Swiss Bird Radar, (Shamoun-Baranes et al. 2008; Gürbüz et al. 2015; Liechti et al. 2019).

This thesis uses data collected offshore by two bird radar systems: ROBIN 3D-fix (Robin Radar Systems, The Hague, The Netherlands) and MERLIN (DeTect Inc, Panama, Florida). Both systems consist of two antennae: one vertically rotating antenna that collects information about birds’ numbers and altitudes and one horizontally rotating antenna that collects information about birds’ numbers, directions and speeds. The overview of the main characteristics of each radar antenna is given in Table 1.1.

### 1.7 Radar tracking algorithms and data quality

Both radar systems work similarly to automatically detect and store targets in the centralized spatial database. If a certain target with similar characteristics such as RCS, speed and direction is detected in consecutive radar scans, a proprietary automated tracking algorithm joins each target’s position in an individual track. In cases when multiple targets with similar properties fly close together in several consecutive scans, the tracking algorithms cannot distinguish individual targets. In
this case, such a group would be tracked as a single object and tagged as a flock in the database. When working with flocks, it is not possible to know the exact number of birds belonging to a flock.

A tracking algorithm can, to a certain extent, distinguish between non-bird and bird tracks based on track properties. Targets with non-bird properties that can originate from boats, aircraft, wind turbines, rain, sea waves and other static and dynamic clutter do not get stored in the database. ROBIN radar employs dynamic clutter filters in each radar scan to remove echoes originating from various types of clutter. The percentage of total radar scans affected by clutter filtering activity automatically gets stored in the database.

Although tracking algorithms work reasonably well, due to similarities in characteristics of different targets, there is a certain number of non-bird tracks erroneously stored as birds in the databases. Based on expert knowledge supported by ground-truthing experiments, we developed a number of automated filtering steps to further remove tracks originating from clutter, and other biological scatter such as insects and improve data quality. Detailed explanations of these steps for ROBIN radar systems can be found in Chapters 4 and 5. Such steps for the MERLIN radar system can be found in Chapters 2 and 3 and Krijgsveld et al. 2011 and Fijn et al. 2015.

Table 1.1. Overview of the main characteristics of the radar systems used in the thesis.

<table>
<thead>
<tr>
<th>Antenna</th>
<th>Merlin</th>
<th>Robin 3D-fix</th>
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<tbody>
<tr>
<td>Band</td>
<td>Horizontal 5</td>
<td>Horizontal 5</td>
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<td>Vertical X</td>
<td>Vertical X</td>
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<td>25</td>
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<td>Rotation speed [rpm]</td>
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<td>45</td>
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<td></td>
<td>24</td>
<td>45</td>
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<tr>
<td>Beam width [degrees]</td>
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<tr>
<td></td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Range (m)*</td>
<td>5560</td>
<td>6000</td>
</tr>
<tr>
<td></td>
<td>1390</td>
<td>1500</td>
</tr>
</tbody>
</table>

*Maximum range for detection of bird targets. Differs from the maximum theoretical range.

1.8 Modelling bird migration

For processes that occur over large spatial and temporal scales, such as bird migration, using models combined with field observations has proven to help better understand such systems’ complexity. Although models strongly depend on the basic assumptions about a particular system, they are a valuable tool in directing research, filling data gaps in space and time and predicting the future (Newton 2008). Models can help with the testing of the alternative hypothesis, analyzing responses to changing parameters, and they help in creating routes for further research (Bauer & Klaassen 2013).
This thesis uses various models and radar data to better understand the nocturnal migration system over the North Sea and predict its dynamics. In different chapters, we apply mechanistic and statistical models to reveal three-dimensional migration patterns and their drivers and to try and predict overseas migratory dynamics for conservation purposes.

1.9 Thesis overview

The overall aim of this thesis is two-fold. Using the North Sea as a study system, we aim to understand how environmental factors such as local and synoptic weather conditions, time of day and year influence spatiotemporal migration patterns of nocturnal bird migration in the airspace over an ecological barrier. We explore if the available radar technologies provide data of good enough quality to develop near-term nocturnal bird migration forecasts that could be used to inform offshore wind turbine shutdowns during intense nocturnal bird migration. With migration predictions, we aim to provide tools for minimizing the number of bird collisions that offshore wind turbines can cause in order to conserve a maximum number of nocturnally migrating birds with minimal impact on the energy market, performing one of the key steps for dynamic aeroconservation of highly-mobile aerial organisms.

Chapter 2 starts by exploring how seasonal wind regimes influence birds’ departure decisions and shape the main migratory axes across the North Sea. We explore whether migratory axes show seasonal reversal or other patterns suggesting that birds employ different strategies to navigate an ecological barrier in different seasons. With this, we aim to get the first overview of seasonal spatio-temporal migration intensity patterns offshore in the region and use this knowledge as a basis for the following chapters.

Besides local weather conditions, synoptic weather conditions can drive bird migration patterns on a regional scale. Chapter 3 examines the synoptic weather conditions related to intense and weak nocturnal bird migration nights over the North Sea. We give an overview of each weather variable in the region on intense and weak migration nights. We present how this knowledge can be used to understand bird migration patterns better and improve aeroconservation in the region, especially in the context of wind energy.

When investigating bird migration in the wind energy context, it is crucial to understand the distribution of nocturnal bird migration in the vertical space. How high do the birds fly when crossing the North Sea? What fraction of migration occurs at low altitudes that correspond to the height of wind turbines? What are the seasonal environmental conditions that drive altitude distributions? By answering these questions in Chapter 4, we aim to better understand the seasons and nights in which the turbine shutdowns would be the most beneficial and cost-effective.
In Chapter 5, we use the knowledge gathered in the previous three chapters to develop algorithms for predicting nocturnal bird migration intensity in two different seasons. We assess the accuracy of these models and discuss their shortcomings. We give insight into the number of nights on which the shutdowns should be performed to save 50% of migratory birds in the area and the amount of energy loss on such nights.

Chapter 6 compiles the main findings of the thesis and discusses them in two main contexts. First, we discuss our findings from the ecological perspective and give space to the theories about ecological barrier navigation and potential adaptive behaviour that arose from interpreting the results. Then, we dive into the aeroconservation perspective, putting the results in the framework of future offshore wind energy development, the scope of environmental changes and the usage of near-term forecasts to preserve highly-dynamic processes when action is needed as soon as possible. We reflect on the importance of the interaction of various stakeholders in conservation processes and our experience with such a setup during this project. We briefly discuss radar data quality and the improvements made during this thesis. Finally, based on our findings, we give an overview of knowledge gaps and starting points for further research in the field.
In the coming days, get ready to move south as soon as we have tailwinds. Note that we fly a different route from the one in spring...

I have to bring my passport and ask Tina where the sunscreen is...
Chapter 2

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

Maja Bradarić, Willem Bouten, Ruben C. Fijn, Karen L. Krijgsveld and Judy Shamoun-Baranes

Abstract

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.
2.1 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. 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 & Langston 2008; Poot et al. 2008; Marques et al. 2014).

The extent to which an inhospitable area can act as a barrier can vary substantively 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 & 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 & 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, Felícíssimo 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 the Atlantic Sea. 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 N 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 2019) (Figure 2.1). 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 & Hüppop 2011). 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 (Krijgsfeld et al. 2005) and counts of birds found on offshore structures (Lensink et al. 1999; Hüppop & Hüppop 2011; Hüppop et al. 2016) or it has been acquired sporadically using radar (Lack 1963a, 1963b; Hüppop et al. 2006; Krijgsfeld et al. 2011; Shamoun-Baranes & van Gasteren 2011; Fijn et al. 2015). Many small-scale migratory routes have been observed over the North Sea (Figure 2.1), but the two biggest ones are between Scandinavia and S Europe and Africa, and between E 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) (Figure 2.1). 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 & van Gasteren 2011). Simulation modelling suggested that these birds were arriving from Scandinavia (Shamoun-Baranes & van Gasteren 2011) when winds were generally supportive (Figure 2.1). 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 & Hedenström 2000). This supports expectations that birds would select winds at departure which reduce the energy or time invested in migration (Alerstam & 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.

2.2 Materials and methods

2.2.1 Radar system and location

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 m/s and > 30 m/s 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.
2.2.2 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, 2018b) We selected tracks that were recorded by the vertical radar within the calculated effective detection range on either side of the radar from sunset up to one hour before sunrise of the following day and calculated the total number of tracks per night within the surveyed area 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 (Figure 2.2). All other nights were considered weak migration nights (WMN). We extracted the track directions and ground speeds of all bird tracks measured by the horizontal radar and calculated headings (flight direction of the bird in still air) andairspeeds (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 (R Core Team 2018). In total, 31 intense migration nights were selected of which 15 nights were in autumn and 16 in spring (Figure 2.2). 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.

![Figure 2.2](image)

**Figure 2.2** 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).

### 2.2.3 Wind data

Gridded wind data from the forecast dataset of the European Centre for Medium-Range Weather Forecasts (ECMWF) HRES model (Owens & Hewson 2018) at 3 h intervals was obtained from 1000 hPa, 925 hPa and 850 hPa which corresponds to altitudes of 101 m, 766 m 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.

### 2.2.4 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 & 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.

2.2.5 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 emdist (Urbanek & 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 Table 2.A.1.

2.2.6 Seasonal patterns of migration

We calculated nightly means of airspeed (AS), groundspeed (GS), heading and track direction and used it to calculate mean ± 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, which estimates the dispersion of directional data around the mean, range between 0 and 1, where 1 represents no dispersion in the data (Jammalamadaka & 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 (R Core Team 2018).
2.2.7 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 \textit{kde2d} function from package MASS (Venables & Ripley 2002) (Figure 2.4).

2.2.8. 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 ± SD for IMN and WMN.

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

$$\text{WA} = y \cos \theta$$  \hspace{1cm} (2.1)

where $y$ is wind speed (m/s) and $\theta$ 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 & Alerstam 2002; 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 ± SD and wind speed ± SD for IMN and WMN were calculated from nightly means and compared between different seasons and IMN and WMN using two-sample t-tests.
2.3 Results

2.3.1. 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 (Figure 2.2). In total, 235815 tracks were recorded during 318 nights in spring, while on 16 IMN 64632 tracks were recorded. In autumn, 489446 tracks were recorded on 300 nights and 143252 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.

Table 2.1. Summary statistics of the 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. For directional data circular means and angular deviation (AD) are provided. A value of mean resultant length r closer to 1 indicates less dispersion in directions (Cabrera-Cruz et al. 2020).

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Track direction (degrees)</th>
<th>Groundspeed (m/s)</th>
<th>Heading (degrees)</th>
<th>Airspeed (m/s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Mean</td>
<td>AD</td>
<td>R</td>
<td>Mean</td>
</tr>
<tr>
<td>Spring (WMN)</td>
<td>271637</td>
<td>96</td>
<td>1.06</td>
<td>0.4</td>
<td>16.9</td>
</tr>
<tr>
<td>Spring (IMN)</td>
<td>141237</td>
<td>94.6</td>
<td>0.6</td>
<td>0.8</td>
<td>18.6</td>
</tr>
<tr>
<td>Autumn (WMN)</td>
<td>503162</td>
<td>228.2</td>
<td>0.9</td>
<td>0.52</td>
<td>17.4</td>
</tr>
<tr>
<td>Autumn (IMN)</td>
<td>133687</td>
<td>233.7</td>
<td>0.6</td>
<td>0.81</td>
<td>19.0</td>
</tr>
</tbody>
</table>

In spring, headings (116°, r=0.4, p<0.001) and track directions (107.6°, r=0.4, p<0.001) on WMN were nonuniformly distributed with the mean direction to the ESE (Table 2.1). 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 (Figure 2.3a; Table 2.1). On WMN, mean airspeed (16.8 m/s±2.4) and groundspeed (18.1 m/s±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 m/s±1.8) and groundspeeds (18.5 m/s±2.4) on IMN (Figure 2.3a; Table 2.1).

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 2.1). Headings (217.9°, r=0.9, p<0.001; Figure 2.3b) 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 2.1). Mean airspeed on WMN (18.4 m/s ± 2.8) was significantly higher (t(9.5)=3.4, p=0.007) from the mean airspeed on IMN (16.5 m/s±1.4; Figure 2.3b), but the mean groundspeed on WMN (18.2 m/s±3) was not significantly different (t(21.8)= -1.6, p=0.53) from the mean groundspeed on IMN (18.7 m/s±0.7; Table 2.1).

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 groundspeed and mean airspeed were not significantly different in spring and autumn on IMN (GS: $t(16.7)=-0.3, p=0.7$; AS: $t(17.9)=-0.9, p=0.3$).

Table 2.2. Summary of the proportion of trajectories tracked back to potential departure locations in spring and autumn on intense migration nights. Also available in Figure 2.A.1.

<table>
<thead>
<tr>
<th>Origin</th>
<th>Trajectories (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
</tr>
<tr>
<td>UK &amp; Ireland</td>
<td>80.83</td>
</tr>
<tr>
<td>Other</td>
<td>14.58</td>
</tr>
<tr>
<td>The Netherlands</td>
<td>2.33</td>
</tr>
<tr>
<td>Germany</td>
<td>1.05</td>
</tr>
<tr>
<td>Belgium</td>
<td>0.56</td>
</tr>
<tr>
<td>France</td>
<td>0.28</td>
</tr>
<tr>
<td>Denmark</td>
<td>0.14</td>
</tr>
<tr>
<td>Norway</td>
<td>0.14</td>
</tr>
<tr>
<td>Sweden</td>
<td>0.05</td>
</tr>
</tbody>
</table>

2.3.2. 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 (Figure 2.3a; Figure 2.4a; Table 2.2). In autumn, almost half of the trajectories (47.51%) were tracked back to the Netherlands and Germany (Figure 2.4b), 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 2.2). 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.
Figure 2.3 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.
2.3.3. 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 Figure 2.5a; Table 2.1). 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) (Figure 2.5b; Table 2.1). In spring, the mean wind speed on WMN (9.6 m/s ± 2.9) was not significantly different (t(14.6)=0.5, p=0.6) from the mean wind speed on IMN (10.1 m/s ± 3.5), but the mean wind speed on WMN in autumn (9.4 m/s ± 2.3) was significantly higher than the mean wind speed on IMN (6 m/s ± 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 2.1).

Mean wind assistance was positive in spring on WMN (0.45 m/s ± 3) and IMN (3 m/s ± 2), whereas in autumn wind assistance was positive only on IMN (1.3 m/s ± 2.7; Figure 2.5b). WMN in autumn had negative wind assistance (-1.84 m/s ± 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 (Figure 2.5b). 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).
Figure 2.5 (a) Distribution of wind directions (degrees) at estimated departure locations on weak (WMN, N spring=739315, N autumn=1049130) 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) values in spring (white) and autumn (cyan) for WMN (N spring=271637, N autumn=503162) and IMN (N spring=141237, N autumn=133687). The red horizontal line marks a threshold between positive and negative wind assistance.
2.4 Discussion

Our study shows that on intense migration nights in spring, the majority of migrants observed off the coast of the Netherlands flying over the southern North Sea predominantly departed from the UK on nights of intense migration. 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 high wind assistance (Figure 2.5b) 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 on nights 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 suggested in previous studies (Alerstam 1979; Schaub et al. 2004).

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 (Figure 2.5; Table 2.1) 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 flying migrants have been recorded in the region over land (Dokter et al. 2013; Kemp et al. 2013), tracks and thus headings 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 & Boldt 2001) 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, observed differences in airspeeds between IMN and WMN in autumn (Table 2.1) and occurrence of IMN in late autumn and early spring imply that different species might be involved in migration on different nights. Therefore, IMN could be represented by mainly short-distance migrants which are more selective of weather conditions at the departure (Marques et al. 2014; Hayes et al. 2019; Perold 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 & 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.
Acknowledgements

We thank Abel Gyimesi, Jonne Kleyheeg Hartman and Maarten Japink from Bureau Waardenburg for help in data acquisition and constructive discussions about migration over the North Sea. We thank Emiel van Loon from the University of Amsterdam for guidance with statistical analysis. We thank Andreas Smith from DeTect, the manufacturer of the Merlin bird radar system, for explaining the details of the Merlin radar technology. This work is part of the Open Technology Programme, project Interactions between birds and offshore wind farms: drivers, consequences and tools for mitigation (project number 17083), which is financed by NWO Domain Applied and Engineering Sciences, in collaboration with the following private and public partners: Rijkswaterstaat and Gemini Windpark and is also a part of a project “Modelling bird migration to mitigate wind turbine collision risk over the North Sea” (project number 31128362), financed by the Dutch Ministry of Infrastructure and Water Management – Rijkswaterstaat.
2.A Appendix for Chapter 2

Table 2.A.1 Results of the sensitivity analysis performed to test if distributions of potential departure locations differed when the back-trajectory model was run with the wind data from different pressure levels (850 hPa, 925 hPa and 1000 hPa). Earth mover’s distance (EMD) is used to compare distributions calculated with the wind data from different pressure levels. Identical distributions have EMD value of 0. The largest differences are generally between simulations at 1000mb and 850mb.

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Figure 2.A.1 The daily proportion of trajectories tracked back to potential departure locations in the spring (a) and autumn (b) migratory seasons

While figure 2.4 shows the potential departure areas aggregated for all nights of intense migration, the spatial distribution of departure locations does differ among nights. Figure 2.A.2 shows daily distributions of potential departure locations of birds for two nights of intense migration in spring (Figure 2.A.2a and 2.A.2b) and autumn (Figure 2.A.2c and 2.A.2d). To demonstrate differences among nights, we intentionally selected two nights in which we observe some deviations from the seasonal pattern (Figure 2.A.2a and 2.A.2c) and two nights that reflect the seasonal distribution of intense migration (Figure 2.A.2b and 2.A.2d).
On 22/04/2008 ~50% of the trajectories were tracked back to Belgium and France (Figure 2.A.2a, bar plot). Trajectories estimated to originate from these two countries had a heading towards north and north-east. The distribution of headings on this night was multi-modal with a mean of 65.08° (r=0.3) (Figure 2.A.2a, rose plot; Table 2.A.2), while the mean wind direction was 285.12° (r=0.81). The resulting departure locations were quite dispersed (Figure 2.A.2a). Figure 2.A.2b shows the individual trajectories in the night of 15/03/2009 which was the most intense spring migration night during this study (N=39821). Approximately 80% of the trajectories on this night were tracked back to the southern UK and Ireland (Figure 2.A.2b, bar plot) with a mean heading of 90.44° (r=0.84), which corresponds with seasonal patterns (Figure 2.A.2b, rose plot; Table 2.A.2). On this night, winds were supporting with a mean wind direction of 107.62° (r=0.89).

On 30/10/2008 we see the arrival of birds that come from Norway and cross the North Sea from north to south (Figure 2.A.2c), which is not something we commonly observed in autumn (Figure 2.4b). Moreover, this night was also the night with the highest number of migrants for the autumn season (N=46729). The mean heading of the trajectories was 225.88° (r=0.84) and the mean wind direction was 209.47 (r=0.89), corresponding with the seasonal patterns. Migration patterns on 13/10/2007 reflect the general pattern observed for intense migration in autumn (Figure 2.A.2c). The mean heading was 219.05° (r=0.85) (Figure 2.A.2c, rose plot; Table 2.A.2) and birds mainly departed from the Netherlands and Germany (Figure 2.A.2c, bar plot). Even though sidewinds prevailed with a mean direction of 349.44°, the mean wind speed (4.25 m/s), was the lowest for all nights (Table 2.A.2). Summary statistics of the individual nights of intense migration is available in Table 2.A.2.
Figure 2.A.2 Simulated trajectories (silver lines) and departure locations (blue-green dots) on 22\textsuperscript{nd} of April 2008 (a), 15\textsuperscript{th} of March 2009 (b), 30\textsuperscript{th} of October 2008 (c) and 13\textsuperscript{th} of October 2007 (d). The red dot on a map represents the radar location. Bar in the upper left corner of each plot shows the proportion of trajectory origins, while the rose plot provides the distribution of headings on each respective night.
Table 2.A.2 Summary statistics of the trajectories at the potential departure locations on individual days. For directional data means are circular means and angular deviation (AD) is presented instead of SD. Value of mean resultant length $R$ closer to 1 indicates higher concentration in directions (Drewitt & Langston 2006; Gaultier et al. 2020). Dates shown in Figure 2.A.2 are highlighted.

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Hey, Bob, time to pack! Stu says the forecast for tonight is no rain and weak winds. I hope he will not screw up again!

Tina, where’s my sunscreen? You borrowed it last year!!!

It seems that we are leaving tonight. Get ready, folks!
Chapter 3

Associations of synoptic weather conditions with nocturnal bird migration over the North Sea

Iris Manola, Maja Bradarić, Rob Groenland, Ruben C. Fijn, Willem Bouten and Judy Shamoun-Baranes

Abstract

The southern North Sea is part of an important flyway for nocturnal bird migration but is also risky as it stretches over a large surface of water. Selecting nights with suitable weather conditions for migration can be critical for a bird’s survival. The aim of this study is to unravel the weather-related bird migration decisions by providing a descriptive analysis of the synoptic weather conditions over the North Sea on nights with very high and low migration intensities and compare these conditions to the prevailing climatology. For this study, bird radar data were utilized from an offshore wind farm off the Dutch coast in the North Sea. The study suggests that atmospheric conditions clear of rain and frontal systems, dominated by high-pressure systems and tailwinds in spring and sidewinds in autumn, are most suitable for nights of intense migration. Differences in temperature, relative humidity and cloud cover appear less significant between intense and low migration nights, suggesting that these variables exert only a secondary role on migration. We discuss how future developments in radar aeroecology and the integration of meteorology can help improve our ability to forecast bird migration.
3.1 Introduction

Twice a year, large flows of terrestrial birds migrate over the North Sea during the night (Lack 1959, 1963b, 1963a; Hüppop et al. 2006; Hüppop & Hüppop 2011; Shamoun-Baranes & van Gasteren 2011). The crossing mainly occurs between the lowlands of Netherlands and Germany and Norway (ca 540 km), Denmark and Netherlands (ca 300 km) and between the United Kingdom and Netherlands (ca 200 km) (Lack 1959; Shamoun-Baranes & van Gasteren 2011; Bradarić et al. 2020). To cross such distances, a bird with an average airspeed of 16 m/s needs between 3.5 and 10 h in still air. Since such large water bodies are not suitable for resting and refuelling for many terrestrial migrants, the trip is considered risky for migration, especially if, at the same time, birds have to cope with unfavourable weather conditions. It is, therefore, important for migrating birds to select nights with atmospheric conditions that support migration (Richardson 1978). An addition to the risk posed by encountering inclement weather en route is the risk of collisions with large man-made structures, such as wind turbines developed within migratory flyways (Brabant et al. 2015; Fijn et al. 2015; Aschwanden et al. 2018; Thaxter et al. 2019). Nowadays, the production of wind energy experiences a rapid expansion, as the necessity to reduce reliance on fossil fuels is large in order to mitigate the risks from human-induced climate change. To reduce the chances of bird collisions, the temporary shutdown of wind turbines is one of the mitigation measures suggested to reduce collision risk when bird migration intensities are high (May et al. 2015). In order to design effective and sustainable early warning systems, a good understanding of migratory behaviour is needed (Bauer et al. 2017).

During migration, daily numbers of birds in the air can fluctuate by orders of magnitude, and studies have shown that temporal variation in migration intensity can be explained in part by local weather conditions (Richardson 1978; Erni et al. 2002b; van Belle et al. 2007; Sjöberg et al. 2015). Among diverse atmospheric variables, wind speed and direction are often considered the most influential for nocturnal migrants and especially passerines using flapping flight (Bruderer et al. 1995; Erni et al. 2002b; van Belle et al. 2007; Sjöberg et al. 2015) as with greater wind support travel time and energy expenditure are minimized (Liechti et al. 2000; Schmaljohann et al. 2009). The influence of wind on migratory birds is often discussed in terms of head and tailwinds along a preferred migration direction and sidewinds perpendicular to the preferred migration direction. It has been demonstrated that nocturnal passerine migrants have the ability to partially compensate for the side wind drift during their journey (Alerstam 2011; McLaren et al. 2012; Chapman et al. 2016), but they tend to follow paths where they have to compensate less (Horton et al. 2016b). Studies have shown that the numbers of birds aloft (e.g., Erni et al. 2002b; van Belle et al. 2007), as well as probability of departure of passerines (Åkesson & Hedenström 2000; Schaub et al. 2004; Sjöberg et al. 2015), is higher on nights with supporting winds.
There is evidence that precipitation is another key factor for migrants as it may temporarily suppress migration (Richardson 1978; Schaub et al. 2004). Rain might increase the risk of mortality as it decreases visibility and increases disorientation for birds en route (Newton 2007). However, the impact of precipitation on departure decisions is not always clear, for example, while Schaub et al. (2004) found decreased departure chances of small passerines during precipitation, Andueza et al. (2013) did not find an important effect of precipitation on departure decisions of migrating passerines. Cloud cover and temperature have also been shown to influence departure decisions. For example, a radio telemetry study showed that yellow-rumped warblers *Setophaga coronata* were more likely to depart from stopover sites (i.e., rest and refuelling sites) in autumn in clear skies than overcast (Liu & Swanson 2015) with temperature having less of an impact on departure decisions. The relative importance of weather variables may vary between spring and autumn as the prevailing weather conditions differ. For example, the passage of high-pressure systems can be related to opposing winds in autumn and supporting winds in spring (Dokter et al. 2013). Additionally, species with similar flight modes but contrasting migration strategies, for example, short vs long-distance passerines, may respond differently to weather conditions at departure (Packmor et al. 2020).

As many weather variables are closely intercorrelated, less influential variables such as the relative humidity will tend to vary in predictable ways as a function of the variables of higher importance, such as the pressure systems (Richardson 1990b), or precipitation, especially during relatively unstable atmospheric conditions.

The advancement of radar technology has greatly facilitated studying nocturnal migration even though radar systems cannot distinguish patterns and characteristics of migration at a species level (Bauer et al. 2019). The aim of this study is to increase our understanding of how weather influences mass migration events over the sea. The study compares synoptic scale weather conditions to climatology on nights of very high migration intensities and nights of very low migration intensities over the North Sea. In order to study conditions during migration within the context of seasonal weather conditions, we calculate the climatological anomalies of several key weather variables. The weather conditions associated with the selected high migration intensity nights should indicate conditions that favour migration. Respectively the weather conditions associated with the low migration nights should indicate the conditions that might inhibit migration for the specific latitude and geography over the North Sea. The key variables of interest follow suggestions from previous research (Richardson 1990b) and include winds at 925 hPa, mean sea level pressure (MSLP), 500 hPa geopotential height, precipitation, relative humidity, cloudiness, and temperature. Furthermore, using surface synoptic weather maps, we explore the passage of frontal systems on nights of high and low migration intensity. The research is based on spring and autumn bird radar observations made 18 km from the Dutch coast, in the North Sea, and the concurrent synoptic weather conditions over the sea and in potential departure areas. We expect that intense peaks and lulls in migration observed over the sea will be strongly
influenced by weather conditions at potential departure areas over land during the night of interest. Previous studies of passerine migration have shown that seasonal phenology at stopover sites can be strongly influenced by weather conditions at distant stopover or overwintering areas in spring (Haest et al. 2018) and distant stopover or breeding ranges in autumn (Haest et al. 2019). Thus, we describe the synoptic scale conditions in relation to potential departure areas on nights of high migration intensity. A back-trajectory analysis of migration using the same radar dataset (Bradarić et al. 2020) showed that the most probable departure areas of the birds on nights of high migration intensity observed at the radar site in spring is the southern United Kingdom (area in the blue circle in Figure 3.1) and in autumn is Southern Scandinavia, the north coast of Netherlands and Germany (area in the red circle in Figure 3.1). We discuss similarities and differences between spring and autumn in synoptic scale conditions that support or potentially inhibit migration over the southern North Sea.

3.2 Materials and methods

3.2.1 Radar observations of migration

We utilize data collected for previous projects (Krijgsfeld et al. 2005, 2011; Fijn et al. 2015), recorded by a Merlin radar system (DeTect Inc., Panama City, FL, United States) which was mounted on a meteorological mast of the Egmond aan Zee Offshore Wind Farm (OWEZ) (N 52.60, E 4.38) located 18 km off the Dutch NW coast (location shown in Figure 3.1). The radar system consisted of two marine surveillance radars that allow the detection of individual bird echoes. A vertical X-band Furuno radar scanned the area along a NW-SE direction at a speed of 25 rpm and detected biological objects within a detection range of ~1.4 km from the radar (vertical extent). A horizontal S-band Furuno radar with a detection range of 5.5 km scanned an area of 360° around the radar at a speed of 22 rpm. The detection of targets by the radar system depends on their size, distance from the radar and orientation relative to the radar beam. Measurements showed that effective detection of the Merlin system varied between 900 and 1.4 km for the vertical radar and between 900 m and 4.5 km for the horizontal radar, depending on the previously mentioned factors. Small birds were successfully detected up to an altitude of 900 m.

We utilized radar data collected from June 2007 until May 2010. The radar was operational 90% of the time, except for short breaks caused by technical failure, weather conditions that could have caused mechanical damage to the radar (wind speed >14 m/s) or disrupt detection of targets (rain) and maintenance. The vertical radar recorded numbers of targets that were crossing the radar beam and their altitudes. The horizontal radar collected information about ground speeds and track directions of the targets. Extensive field measurements of the radar performance (Krijgsfeld et al. 2005), which included visual identification of targets and their
flagging in the database, allowed for detailed post-processing of the data. Filters based on echo characteristics of targets such as speed, direction and size were developed (Krijgsfeld et al. 2011). These filters were used to exclude echoes originating from waves, rain, insects and other types of interference (e.g., boats). For more information about data quality, filtering procedures and the quantification of fluxes see Krijgsfeld et al. (2011) and Fijn et al. (2015).

Using track directions and ground speeds recorded by the horizontal radar and hourly \( u \) and \( v \) components of 925 hPa wind from the ERA5 data described below, airspeeds (speed of a bird in still air) and headings (direction of a bird in still air) at the radar location were calculated using vector summation (Shamoun-Baranes et al. 2007). The wind was analysed at 925 hPa since the radar used in this study recorded mainly birds flying below 1000 m of altitude (Fijn et al. 2015) and represents the altitude layer where migration intensity is highest in this region (Kemp et al. 2013). The wind data were linearly interpolated to the start time of tracks as recorded by the radar.

![Figure 3.1](image)

**Figure 3.1** The map of the study area around the North Sea. The star indicates the position of Egmond aan Zee wind farm, where the radar is located. The blue circle indicates the most probable departure area of the migrants on nights of high migration intensity in spring. The red circle indicates the most probable departure area of the migrants on nights of high migration intensity in autumn outside of the Netherlands, according to Bradarić et al. (2020).
3.2.2 Selection of high and low migration intensity nights

In this study, the spring migration season was defined as 15 February–31 May, and the autumn migration season was defined as 1 August–30 November. For each night beginning around sunset and ending at sunrise the next day (18:00–06:00 UTC), we calculated the total number of tracks recorded by the vertical radar as a measure of migration intensity per night. We ranked nocturnal migration intensity in descending order and selected the nights exceeding the 90th percentile separately for spring and autumn, resulting in 24 spring and 22 autumn nights. If successive nights among them exceeded the 90th percentile threshold, then only the maximum night was included in this analysis in order to avoid the analysis of dependent synoptic weather conditions, resulting in the final nine autumns and eight spring nights (called hereafter high migration nights). The 90th percentile was selected for statistical reasons, as with this threshold at least one case per year is selected and thus, all years are represented in the analysis. Nights with very low migration intensity that occurred just before or just after the selected high migration nights were also selected and called thereafter low migration nights. In total, eight nights with low migration were selected in autumn and seven in spring and occurred from 1 to 7 days before or after the high migration nights. The low migration nights, on average, had migration intensities that were 95% lower than the associated high migration nights. Nights in which the radar was not operational were excluded from any selection. The selection of the nights with low migration intensity was made in order to investigate whether inhibiting weather precedes a high migration pulse or pauses it (the nights after the high migration pulse). However, migration intensities might also be low on nights of favouring weather conditions, as the flying migrants also need to feed and rest, or simply because, after nights of high migration intensity, there are not many birds left in the source area (Gauthreaux et al. 2005).

All analysis of directional data was done using the R package circular (Agostinelly & Lund 2017; R Core Team 2018). Circular mean and ± angular deviation (AD) of track direction, heading, and wind direction at the radar location were calculated per night. Furthermore, the mean resultant vector length \( r \) was estimated for each of the parameters to assess the dispersion of directional data around the mean (values closer to 1 indicate less dispersion). Finally, the Rayleigh test was performed to test for non-uniformity of directional data (the alternative hypothesis is unimodal distribution). Density distributions (Figures 3.2, 3.3) of all directional data are kernel densities derived using the density circular function.

3.2.3 Meteorological data and analysis

We used the recently released ERA5 reanalysis product from the European Centre for Medium-Range Weather Forecasts (ECMWF) (Hersbasch & Dee 2016) with hourly temporal and 30 km spatial resolution. The analysed ERA5 variables were 925 hPa wind, MLSP, precipitation, geopotential height at 500 hPa (the height where
the ridges and troughs are usually detected in the middle troposphere), relative humidity, cloudiness and 2 m temperature for three springs and three autumns, for the years 2007–2010. As we are focusing on factors influencing nocturnal migration, we calculated nightly means from 18:00 UTC of the day of interest until the next morning at 06:00 UTC. The nightly precipitation data is the total precipitation from 18:00 to 06:00 UTC. The local Dutch time is UTC+1 in winter and UTC+2 in summer. The weather variables were extracted from the spatial range of 35N–70N and 16W–19E. This entire region is plotted for the MSLP (Figures 3.4, 3.5) to allow a clear overview of the passing synoptic scale pressure systems. The rest of the analysed variables have more local character and are therefore plotted over the North Sea and the continental regions around it (Figures 3.2, 3.3, 3.6, 3.7). Finally, the surface pressure and frontal systems are shown over a broader region as they are extracted from the KNMI data centre (Figures 3.8, 3.9).

The monthly climatology per grid point for spring and autumn migration was calculated as the monthly means from 18:00 to 06:00 UTC for the years 1989–2018. The emphasis of the current work is given on the relation between synoptic weather conditions and bird migration. In order to understand the biological relevance of the synoptic wind directions, though, the local wind directions at the radar site are first assessed and discussed in the context of bird headings and track directions measured by the radar. Afterwards, the synoptic wind conditions are explored in conjunction with the bird headings and track directions on days of high and low migration. The synoptic wind conditions are computed by the intensities of the zonal and meridional wind vectors, and the composites are the averages of the nightly means. In order to calculate the anomalies from climatology for MSLP, precipitation, geopotential height, relative humidity, cloud cover and temperature, the monthly climatology was subtracted from the selected nightly mean for each variable of interest. Then the spatio-temporal composite of the anomalies was calculated as the mean for the selected high and low migration nights, respectively. Additionally, the day-by-day surface pressure and frontal systems maps that are shown and discussed in the following sections are extracted from the Royal Netherlands Meteorological Institute (KNMI) and are taken at 18:00 of each day.

To assess whether the anomalies were statistically different from climatology, we applied Welch’s t-test for unequal variances and unequal sample sizes (Ahad & Yahaya 2014). The test computes the mean and variance of the nightly values of the high (or low) migration nights and compares those to the nightly values of all 30 years of climatology, for the selected migration month, for each grid cell separately in the synoptic maps. If the p-value of each grid cell is below a selected threshold, then the null hypothesis can be rejected, and the value in that grid cell is assumed to be significantly different from climatology. The selected threshold in this work was the 95% confidence level (p-value ≤ 0.05).

For the analysis of the meteorological data in this study, we used CDO, Ferret and
3.2.4 Regional climatic conditions

Here we provide a very brief overview of the climatic conditions in the region to issue the appropriate context for interpreting anomalies in synoptic conditions in relation to bird migration. In Spring, climatologically dry and stable conditions dominate the southern United Kingdom and the southern North Sea as the passage of synoptic systems and frontal activity that is responsible for most of the large-scale precipitation is less frequent, and the sea is still too cold to induce local convection as it approaches the land (Manola et al. 2020b). Most high-pressure systems come from the Azores via the United Kingdom to Iceland or Scandinavia. With calm weather, the levels of relative humidity and low cloudiness depend strongly on the atmospheric temperature. The sea surface temperature is at its lowest point of the year. In periods with south or southwesterly winds, the relatively warm air condenses from the cold sea with fog and low clouds as a result. In autumn and winter, storm tracks with low pressure and frontal systems are most active over the United Kingdom, the North Sea and Scandinavia/Denmark and the Low countries (Woth et al. 2006). The prevailing winds are westerlies and southwesterlies, the atmospheric conditions are very variable, and the frequent passing of the frontal systems often brings a lot of rain.

3.3. Results

3.3.1 Spring

3.3.1.1 Surface winds and bird tracks

On nights of high migration intensity in spring, the average winds are southwesterly (61.47°±53.8°, r=0.55, p=0.08) and the track direction (79.75°±28°, r=0.87, p<0.001) and bird headings (84.47°±22.3°, r=0.92, p <0.001) point toward east and are significantly concentrated around the mean (Figure 3.2A). Considering the suggested departure locations and migratory axes in the North Sea basin, winds on high migration nights support migration from the southern United Kingdom toward the Netherlands as well as from southern Europe toward Scandinavia on nights with intense migration activity. However, on nights with low migration intensity, the winds are on average easterlies but not significant due to high variability in wind direction (267.67°±70°, r=0.25, p=0.7). The track directions (153.43°±68°, r=0.26, p=0.6) and bird headings (173°±68°, r=0.25, p=0.7) are also highly variable and on average point toward south (Figure 3.2B). The high variability of wind on low migration nights can also be seen in the synoptic winds map in Figure 3.2D, as the averaging of the different wind directions results in low-intensity winds of rather unclear directions.
3.3.1.2 Pressure systems and fronts

In spring, the MSLP composite of the high migration nights is characterized by an extended ridge of high pressure from Spain into Central Europe (Figure 3.4A), bringing overall dry conditions over most parts of Western and Central Europe, the North Sea and the southern United Kingdom.

The anomalies do not differ significantly from regional climatology, indicating that the climatic conditions for this region are supportive of migration over the North Sea in the study region. Along the western flank of this ridge, over the North Sea and the southeastern United Kingdom, the winds have a southerly or southwesterly component (Figure 3.2C). It should be noted that at the mid-latitudes, the winds blow approximately parallel to the isobars, having low pressure to their left in the Northern hemisphere. The surface pressure and frontal systems for all high and low migration days are shown in Figure 3.8.

Figure 3.2 Local and synoptic 925 hPa winds in spring. Top panel: Inside each circle, the mean heading of the birds (red arrows), mean 925 hPa wind direction at the radar location (blue arrows), and mean track direction of the birds (green arrows). Around the circle, the circular density distributions of bird heading (solid line), wind direction (dotted line), and track direction (dashed line), in panel (A) for nights of high migration intensity (HM) and in panel (B) for nights of low migration intensity (LM). Bottom panel: synoptic 925 hPa wind conditions in spring, in panel (C) for nights of high migration intensity (HM) and in panel (D) for nights of low migration intensity (LM). The length of the arrows is proportional to the strength of the averaged wind. As a reference, the length of the arrow of 13 m/s wind strength is given under the panels. The circled area designates the most probable area of departure for the detected flying migrants during those nights. The star designates the location of the radar.
**Figure 3.3** Local and synoptic 925 hPa winds in autumn. Top panel: Inside each circle, the mean heading of the birds (red arrows), mean 925 hPa wind direction at the radar location (blue arrows) and mean track direction of the birds (green arrows). Around the circle, the circular density distributions of bird heading (solid line), wind direction (dotted line) and track direction (dashed line), in panel (A) for nights of high migration intensity (HM) and in panel (B) for nights of low migration intensity (LM). Bottom panel: synoptic 925 hPa wind conditions in autumn, in panel (C) for nights of high migration intensity (HM) and in panel (D) for nights of low migration intensity (LM). The length of the arrows is proportional to the strength of the averaged wind. As a reference, the length of the arrow of 13 m/s wind strength is given under the panels. The circled area designates the most probable area of departure for the detected flying migrants during those nights. The star designates the location of the radar.

When the surface pressure, which on average creates the favouring wind conditions seen in Figure 3.2C, is studied individually for each of the high migration nights, we observe several different patterns: (1) high pressure observed over the southern United Kingdom and the Dutch coast on three nights (see pressure isobars in Figures 3.8B,D,F), (2) the study site at sea is positioned between low and high-pressure systems on three nights (see isobars and the location of the core of the high and low-pressure systems indicated with H or L, respectively (Figures 3.8C,E,G,H) and (3) a low-pressure system observed over the North Sea on one night (Figure 3.8A). The individual high migration nights are characterized by the general absence of frontal systems over the coast of the Netherlands, apart from the 14th of March 2010, when a long but weak and dry cold front passed over the North Sea (Figure 3.8E).
On the other hand, the composite of the low migration nights shows a non-significant low surface pressure anomaly over the southern North Sea that leaves the coast of the Netherlands close to the climatological average surface pressure (Figure 3.4B). The anomalies over the sea and potential departure areas do not differ significantly from regional climatology. Among the low migration nights, the Dutch coast is positioned during three nights over low-pressure systems (Figures 3.8I,J,L), during two nights between high and low-pressure systems (Figures 3.8K,O), and during two nights over high-pressure systems (Figures 3.8M,N). During all low migration nights, a front (warm, cold or occluded) or a trough passes over the coast of the Netherlands or the southern United Kingdom.

3.3.1.3 Precipitation, relative humidity, cloudiness and temperature

On high migration nights, potential departure locations in the United Kingdom and arrival locations in continental Europe, as well as the North Sea, are considerably drier compared to the monthly climatological conditions (Figure 3.6A) and considerably wetter on the low migration nights (Figure 3.6B). The dry anomalies during the high migration nights are statistically significant over almost the entire area (hatched areas in Figure 3.6), while the wet anomalies during the low migration nights over the areas of interest are non-significant. When the individual days are examined (not shown), it is observed that during all high migration nights, the conditions are dry, while during low migration nights, rain occurs in at least one of the areas of interest for each night.

Cloud cover is closely related to precipitation but can also occur independently. Neutral to negative non-statistically significant anomalies in cloudiness over the Dutch coast, in Figures 3.6C,D are consistent with the absence of rain during the high migration. Areas of statistically significant increased cloudiness compared to climatology over the southern United Kingdom indicates that the birds might also fly into cloudy but dry skies. The above indicates the partly decoupled behaviour between cloudiness and precipitation (as they don’t necessarily co-occur), while they also indicate a secondary role of cloudiness in the bird’s migration decisions.

As precipitation and relative humidity are closely intercorrelated, especially under unstable atmospheric conditions, we examine whether the birds appear to respond to relative humidity as they might use it as an early indicator for rain. Relative humidity over the southern United Kingdom does not differ significantly from the local climatology on high migration nights but is significantly higher over the coast of the Netherlands (Figure 3.6E). During low migration nights, the pattern is reversed, with somewhat higher (non-significant) relative humidity over the southern United Kingdom and lower over the Netherlands (Figure 3.6F). Surface temperature is also not significantly different over the entire continental region of the map during both high and low migration nights (Figures 3.6G,H).
**Figure 3.4** The composites of the anomalies from climatology for spring migration for the mean sea level pressure (MLS P in hPa, in colours) and for the 500 hPa geopotential height (in decameters, in contours) in panel (A) for nights of high migration intensity (HM) and in panel (B) for nights of low migration intensity (LM). Areas exceeding the 95% confidence level, as concluded by Welch’s t-test, are hatched.

**Figure 3.5** The composites of the anomalies from climatology in autumn for the mean sea level pressure (in hPa, in colours) and for the 500 hPa geopotential height (in decameters, in contours) in panel (A) for nights of high migration intensity (HM) and in panel (B) for nights of low migration intensity (LM). Areas exceeding the 95% confidence level are hatched.
3.3.2 Autumn

3.3.2.1 Surface winds and bird tracks
On nights of high migration intensity the prevailing winds at the radar location were easterlies (277.05°±26.9°, r=0.88, p=0.01), while headings (217.57°±11.4°, r=0.97, p=0.02) and track directions (227°±11.4°, r=0.97, p<0.001) were toward southwest. During nights of low migration intensity the winds blew on average from the west (84.47°±0.39°, r=0.92, p<0.001), while the mean track direction toward southeast (148.48°±0.38°, r=0.92, p=0.01) and the mean heading (185.27°±0.43°, r=0.9, p=0.02) toward south. The local wind directions were more concentrated around the mean on nights of low migration intensity nights. On nights with high migration, the track directions and headings were more concentrated around their mean value compared to nights with low migration activity.

Overall, the synoptic winds in autumn (Figures 3.3C,D) were favourable for crossing between the Netherlands and the United Kingdom on nights of high migration. However, the average track directions and headings suggest that the majority of tracks recorded by the radar were moving more to the SW and indicating birds flying predominantly parallel to the coast rather than crossing directly to the United Kingdom at the radar location.

3.3.2.2 Pressure systems and fronts
Nights of high migration are characterized by an elongated high-pressure anomaly centered over southwest Scandinavia, extending to the British Isles (Figure 3.5A). The 500 hPa geopotential height (the contour lines of Figure 3.5A) shows an upper ridge from the United Kingdom into Scandinavia. This will lead to mostly northeasterly or easterly winds over southern Scandinavia, Denmark and Netherlands, confirmed in Figure 3.3C. The MSLP anomaly is statistically significant over the entire area of interest (over the sea and the potential departure area). The pressure anomaly reaches a maximum of 12 hPa near the potential departure area. High-pressure systems are observed over the Dutch coast on almost all the high migration intensity nights (Figures 3.9A–E,G–I), resulting in the averaged easterly winds seen in Figure 3.3C over the Netherlands. A lack of frontal systems is apparent over the Dutch coast and southwest Scandinavia.
Figure 3.6 and 3.7 Composites of anomalies from climatology in spring and autumn, in the left column for the high migration nights (HM) and in the right column for the low migration nights (LM). In panels (A,B) the total precipitation (in mm) is shown, in panels (C,D) the total cloud cover (units from –1 to +1), in panels (E,F) the relative humidity (in %) and in panels (G,H) the 2 m temperature field (in °K). Areas exceeding the 95% confidence level are hatched.
An exception is the 30th of October 2009, when a front passed over the North Sea between Netherlands and Denmark (Figure 3.9H), though that system was dry and did not render any precipitation. On October 29, 2008, and November 8, 2009 (Figure 3.9F,I, respectively), a trough over the North Sea resulted in some mild precipitation.

On the other hand, the composite of the low migration intensity nights is characterized by a zonal flow with a slight southwest-northeast angle. This spatial pattern also characterizes the Autumn North Europe climatology. The MSLP anomalies are quite low and non-significant, while some positive 500 hPa anomalies are seen west of the Iberian Peninsula and along northwest Europe (Figure 3.5B). A close look into the individual low migration days (Figures 3.9J–Q) shows that frontal systems pass during all low migration nights, either over the Netherlands, North Sea, or potential departure areas (Denmark and Southwestern Scandinavia), indicating that the passing of fronts hinders migration.

3.3.2.3 Precipitation, relative humidity, cloudiness and temperature

In autumn, during nights of high migration, very little to no rain falls over the regions of the potential departure areas of the southern North Sea (Netherlands, Denmark, and south Scandinavia). The composite of the negative precipitation anomalies in these areas is statistically significant (Figure 3.7A). On the contrary, on all low migration nights, precipitation is higher than expected in these areas (Figure 3.7B). During high migration nights, in agreement with the absence of rain over the coast of Denmark and continental Europe, low cloudiness is observed, but over the central North Sea, the cloudiness is somewhat higher than the local monthly climatology (Figure 3.7C). During low migration, cloudiness is generally higher than in climatology, and anomalies are statistically significant (Figure 3.7D), as rainfall occurs during those nights. Over the North Sea, relative humidity is quite low on high migration nights and neutral to high but non-statistically significant during low migration, while it remains low over Denmark and high over the Netherlands both during high and low migration (Figures 3.7E,F). The surface temperature was statistical significantly colder than in climatology during nights of high migration both over sea and land over Denmark and the Netherlands (Figure 3.7G). The colder temperature is related to the upper ridge seen in the 500 hPa geopotential height from the United Kingdom into Scandinavia that drives northeasterly winds, which advect cold air from northeastern Scandinavia. During low migration nights, the temperature was warmer over land and similar to climatology over the sea (Figure 3.7H).
Figure 3.8 Surface pressure and frontal systems for the high migration nights (A–H) and the low migration nights (I–O) for spring at 18:00 UTC. The figures are extracted from the KNMI data centre. The position of the core of a low-pressure system is indicated with an “L” and of a high-pressure system with an “H.” The cold fronts are indicated as lines in blue colour, the warm fronts in red colour and the occluded fronts in purple colour. The side where the symbols are drawn on the front lines indicates the direction of the front’s movement. The thick blue lines indicate troughs.
Autumn - High migration

Figure 3.9 Surface pressure and frontal systems for the high migration nights (A–I) and the low migration nights (J–Q) for autumn at 18:00 UTC. The figures are extracted from the KNMI data centre. The position of the core of a low-pressure system is indicated with an “L” and of a high-pressure system with an “H.” The cold fronts are indicated as lines in blue colour, the warm fronts in red colour and the occluded fronts in purple colour. The side where the symbols are drawn on the front lines indicates the direction of the front’s movement. The thick blue lines indicate troughs.
3.4 Discussion

Using three years of bird migration data measured off the Dutch coast, we revealed differences in the synoptic weather conditions occurring during high and low migration intensity nights in spring and autumn.

Nights of high migration intensities for both spring and autumn were characterized by prevailing high-pressure systems, with a general absence of passing fronts and precipitation over the sea and the probable departure areas over land. Generally, a high-pressure system is associated with dry and stable atmospheres, clear skies and mild winds. On the contrary, nights of low migration were characterized as nights with rain, often with passing fronts and overall low pressure. In spring, a t-test shows that the positive surface pressure anomalies over sea and departure areas were not statistically significant, while in autumn, the positive anomalies were significant. This suggests that the favouring migration conditions in spring are rather close to the average surface pressure climatology for that season, but in autumn, more special conditions are required compared to the average climatology. The MSLP anomalies during low migration nights both in autumn and spring were not statistically significant, suggesting either a weak coupling between synoptic pressure systems and nights of low migration or a combination of nights with unfavourable synoptic conditions for migration and nights of resting and feeding that might be decoupled from the synoptic pressure systems.

Our study shows that conditions free of precipitation support mass migration events. However, when using radar to measure migration, it should be taken into consideration that during rain, the ability of the radar to detect biological targets might be reduced and therefore, the number of birds flying during rain may be underestimated. Nevertheless, even considering a potential underestimate of bird numbers, our findings are similar to previous studies indicating that rain strongly suppresses migration (Alerstam & Bauer 1973; Lyuleeva 1973) and is an important predictor variable for bird migration (Erni et al. 2002a; van Belle et al. 2007).

In spring, prevailing winds at the radar location, as well as in the whole region, generally had a supporting direction for nocturnal migrants, which has previously been shown in this region (Kemp et al. 2013). During autumn nights with high migration, the average winds at the radar location were tailwinds for the birds who could have been migrating between Netherlands and United Kingdom, while the majority of birds on high migration nights were migrating toward the southwest and thus experiencing sideward component stronger than the tailwind on those nights. On nights with low migration intensity, winds at the radar location were predominantly headwinds in both seasons, indicating that tailwind is an important factor supporting migration, as also shown in numerous other studies (Liechti et al. 2000; Erni et al. 2002a; Schmaljohann et al. 2009; Sjöberg et al. 2015). While the majority of migration happens within the lowest 1000 m of altitude in the mid-
latitudes (Kemp et al. 2013; Bruderer et al. 2018), birds have also been observed flying higher to optimize wind support, especially in spring when the beneficial wind at high altitudes are frequent (Dokter et al. 2013; Kemp et al. 2013). In such cases, high-flying migrants would go undetected by the radar.

Since cloudiness is often linked to precipitation, it is observed here that birds prefer clear skies, although occasions of cloudiness during high migration flows also occur in our data. Interestingly warm southsouthwesterly winds, which support migration in spring, may also result in fog and low clouds generated by the condensation of warm air over the sea, creating poor visibility conditions. Studies have shown that birds might attempt to migrate above fog or clouds during overcast or rainy nights (Emlen 1974; Panuccio et al. 2019). However, the occurrence of such behaviour may not be detected by the radar if birds fly above the vertical detection range.

Although the absolute anomalies of the temperature and relative humidity are rather high in the analysis, the anomalies are not consistent for the two seasons. For example, during high migration nights, the anomalies of surface temperature over the areas of interest are positive in spring and negative in autumn. This suggests that the birds rather respond to factors that correlate with these variables and themselves exert only a secondary role, in agreement with Richardson (1978, 1990). The selection for cold temperature has been previously suggested as an indicator of deteriorating conditions and, therefore, as a signal for migration (Alerstam 1990), but this suggestion cannot be verified in the current study.

Our selection of peak nights of migration above the 90th percentile per season resulted in high migration nights occurring in March and October. While we do not have information on the species in our study, the timing of these nights suggests that they may generally be representative of short to medium-distance migrants in the region. Packmor et al. (2020), for example, showed that night-to-night departure decisions of short and medium-distance migratory passerines were influenced by tailwinds and changes in barometric pressure, while these weather factors did not influence departure decisions of long-distance migrants. However, in order to determine whether the differential response to weather among and perhaps even within species results in peak migration over the North Sea occurring predominantly in early spring or late autumn requires further research integrating information on fluxes, species composition and regional synoptic conditions.

Our overall conclusion is that peak nights of bird migration over the North Sea are favoured by the existence of high-pressure systems and the absence of fronts and are hindered by low-pressure systems and precipitation, in agreement with Geil et al. (1974), Richardson (1978) and Shamoun-Baranes et al. (2017). Winds on high migration nights in spring are tailwinds (southwesterlies), while in autumn, they are sidewinds (easterlies). These patterns are similar to those observed in other studies in the region over land (Åkesson & Hedenström 2000; Erni et al.
In order better understand how environmental factors influence the spatio-temporal heterogeneity in migratory systems and improve our capacity to model them, we recommend integrating complementary measurement and modelling techniques and covering longer periods of time where feasible (Shamoun-Baranes et al. 2010; Bauer et al. 2017). Incorporating information on species composition will significantly advance the comprehension of the potentially different responses to weather. Predictive models could integrate the synoptic scale perspective, considering the atmospheric conditions in departure areas of migrants, as well as atmospheric conditions en route in comparison to regional climatology. These advancements will consequently enhance our ability to predict migration flows and will allow us to build effective warning systems to reduce human-wildlife conflicts, such as the risk of collisions with aircraft (van Gasteren et al. 2019) or wind turbines.

**Funding statement**

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Acknowledgements

The authors would like to thank the colleagues of the Department of Theoretical and Computational Ecology (IBED-TCE) in the Institute for Biodiversity and Ecosystem Dynamics of the University of Amsterdam for the fruitful discussions. Radar data on bird movement were collected in a program which was led by Karen Krijgsveld and commissioned by “NoordzeeWind” [as part of the Monitoring and Evaluation Program of OWEZ (MEP-NSW)]]
A great night for flying after all that nasty weather! Just keep cruising, folks! The conditions are AMAZING at this altitude!

Ok, he maybe got the weather right this time, but I still feel like something bad will happen...
Chapter 4

Drivers of flight altitude during spring and autumn nocturnal bird migration and implications for offshore wind energy

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Under review in Conservation Science and Practice

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 below the wind turbine rotor tip (300 m). 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 flight altitudes were higher in spring relative to autumn at Borssele (spring: 390.7 m, autumn: 235.4 m; p<0.001, ES=0.006) and Luchterduinen (spring: 369.7 m, autumn: 225.4 m; p<0.001, ES=0.02). Median flight altitude in spring was above and autumn median below the wind turbine rotor tip. On most nights in both seasons, the majority of migrants flew predominantly at low altitudes, except for intense migration nights in spring when, on 77% of nights in Borssele and 58% of nights in Luchterduinen, migration mainly occurred at high altitudes. The most important predictors of low-altitude migration in both seasons were day of year, wind assistance, and temperature. Birds chose altitudes with wind conditions most favourable of migration in both seasons. The fraction of low-altitude flight increased with lower temperatures in spring, while the relationship was not clear in autumn. The relationship between day of year and low-altitude migration fraction suggests that different species migrate at different altitudes. Our findings suggest that mitigation measures offshore may be more effective during autumn than spring and especially on nights with more supportive wind conditions at altitudes below 300 m.
4.1 Introduction

The North Sea basin has been designated as one of the most important areas for current and future investments in wind energy production due to suitable wind conditions (Kafas et al. 2018). In the Dutch part of the North Sea in 2021, there is approximately 2.5 GW of installed offshore wind power (Rijksoverheid 2021), which is projected to quadruple by 2030 (Rijksoverheid 2019). In the Belgian North Sea, the current capacity of offshore wind is 2.6 GW, with plans to increase it to 4 GW by 2030 (FPS Economy 2021). Moreover, the UK is a global leader in offshore wind energy expansion (up to 40 GW by 2030, mainly in the North Sea area) (Department of Energy & Climate Change 2013).

While offshore wind farms will help achieve targets for reducing carbon emissions, they may negatively influence 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 (Marques et al. 2014; Hayes et al. 2019; Perold et al. 2020) or through barrier effects and habitat change (Drewitt & Langston 2006; Gaultier et al. 2020). With the increase in 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 migrate over the North Sea every year during the night (Dierschke 2003; Hüppop et al. 2006) mainly following two migration axes: between Scandinavia and southern Europe or Africa (NE-SW axis) and between mainland Europe and the UK (E-W axis) (Lack 1959) (Figure 4.1). It is, therefore, important to develop procedures that will minimize the adverse effects of offshore wind farms on birds in this area. Models that predict bird migration intensity rely on environmental factors as input (van Belle et al. 2007; van Doren & Horton 2018) and are used to improve flight safety and decrease the risk of collisions between migratory birds and aircraft (van Gasteren et al. 2019). Similar models can be used for wind turbine stop-start procedures to mitigate collision risk. However, to undertake effective conservation, it is essential to understand not only environmental factors that govern bird migration intensity but also migration altitude distributions, especially those that lead to flight at low altitudes, where birds are more prone to collisions with turbines.

During migration, weather conditions are known to influence departure decisions (Shamoun-Baranes & van Gasteren 2011; Brust et al. 2019; Bradarić et al. 2020), flight directions (Kemp et al. 2012; McLaren et al. 2012; Horton et al. 2016a) and flight altitudes of birds (Bruderer et al. 1995; Bruderer & Liechti 1998; Dokter et al. 2013; Kemp et al. 2013; Galtbalt et al. 2021). Birds may select flight altitudes with weather conditions that will help them maintain the desired migration direction, reduce time or energy invested in migration, or the risk of encountering adverse weather conditions that could negatively impact survival and physiological condition.
The importance of selecting suitable flight conditions may be especially pronounced when birds are about to embark on crossing ecological barriers, where they do not have an opportunity to land or refuel (Sjöberg et al. 2017).

Many land birds migrate during the night (Alerstam 1990), when the troposphere, a layer of atmosphere in which birds’ flight occurs, gets more stratified due to the collapse of the convective boundary layer, thus creating different weather conditions at different altitudes (Stull 1988). By adjusting their altitude, nocturnal migrants should be able to choose between various weather conditions. The extent and manner of altitude selection can vary due to a bird’s physiological condition (Liechti et al. 2000) and type of flight (Shamoun-baranes et al. 2006), but also due to distinct weather regimes (Dokter et al. 2013) and topography (Aschwanden et al. 2019) in different regions.

Studies from the trade-wind zone (between -30 and 30 degrees latitude), where winds can change by 180 degrees with changing altitude (Rohli & Vega 2018), show that birds choose flight altitudes with supporting wind conditions rather than with lower temperatures that would help minimize water loss (Liechti et al. 2000; Schmaljohann et al. 2009). Shorebirds whose migration partly occurs in the trade-wind zone similarly choose altitudes that help them exploit tailwinds while also avoiding high temperatures (Senner et al. 2018).

At mid-latitudes (between 30 and 60 degrees on each side of the equator), wind conditions do not differ with altitude as strikingly as in the trade-wind zone (Rohli & Vega 2018; James & Stull 2019), but wind conditions still show spatial and temporal variability due to the frequent passage of high and low-pressure systems (Richardson 1978). Radar observations over the Netherlands (Kemp et al. 2013), from the North Sea coast (Lack 1960b), and the Bay of Biscay (Weisshaupt et al. 2016) show that birds fly higher in spring than in autumn due to different seasonal weather patterns.

Radar studies over land show that birds search for altitudes with increased tailwind support (Dokter et al. 2013; Kemp et al. 2013) but only climb to altitudes where they first encounter supportive winds (Kemp et al. 2013). Furthermore, Kemp et al. (2013) show that temperature plays a role in altitude choice, as birds avoided altitudes with temperatures below the freezing level 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 (Bellrose & Graber 1963; Eastwood & Rider 1965). Instead, birds have been observed changing their altitude to avoid rain and clouds, usually flying above them (Lack 1963b; Eastwood & Rider 1965).

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 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 up to 115 m (Fijn et al. 2015). Nevertheless, they do not provide insight into the drivers of temporal variation of altitude distributions.

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 (> 300m). 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, 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 (Dokter et al. 2013; Kemp et al. 2013) and lower temperatures above zero (Torre-Bueno 1978; Kemp et al. 2013) to increase migration speed and decrease energy expenditure. Furthermore, we expect they will choose altitudes with low cloud cover (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.

4.2 Materials and methods

4.2.1 The radar system, location and study period

Bird movement data was 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 4.1). 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 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-fix system consists of two antennae: a vertically rotating X-band antenna (beam width 20 degrees) with a power of 25 kW and a horizontally rotating S-band antenna (beam width 25 degrees) 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, while the Luchterduinen radar was positioned on a platform within the wind farm with both antennas at 22 m asl. Both antennae rotate at 45 rpm and collect information about the position of targets in each rotation. The system uses a tracking algorithm to detect moving targets, and those in at least 5 (vertical antenna) or 8 (horizontal antenna) consecutive rotations are joined in tracks based on target characteristics (speed, direction and radar cross-section). Tracks are generated by a proprietary tracking algorithm and automatically stored in a centralized database. The radar system employs automated clutter filters to reduce the number of non-bird targets mistakenly classified as bird tracks. 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.

The vertical radar antenna collected the number of tracks and tracks’ altitude for 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), see Figure 4.1 for the orientation of the vertical antenna at each location. All targets classified as non-birds by proprietary software based on echo characteristics were excluded from the analysis. 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.

4.2.2 Post-processing of radar data

The vertical radar antenna records various bird targets up to 3000 m. However, birds of all sizes are detected up to 1500 m of altitude asl, after which the detection probability significantly decreases, and small birds cannot be detected anymore (Figure 4.A.1). 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 close to the radar and 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 (Figure 4.A.2).

We removed a negligible portion of targets with small average radar cross-sections (<-30 dBm²) from the data, as they mostly correspond to insect targets. Occasionally, the 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.A.1).

In order 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 extremely low (<10 birds/hr). We also removed nights with less than three hours of data remaining.

After post-processing, 109549 tracks, 135 nights and 982 hours were left for the analysis at the Borssele location in spring and 228843 tracks, 175 days and 1501 hours in autumn. At Luchterduinen, 140973 bird tracks, 195 nights and 1398 hours were left in spring and 163035 tracks, 131 days and 1032 hours in autumn. Following post-processing, each track (further referred to as bird) 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 300m as this is currently considered the maximum altitude of rotor blade tips. We calculated the proportion of birds at high or low altitude per hour and per night for analyses described further below. We also calculated the total number of birds per night and selected the top 10% of nights, in spring and autumn, with the highest migration intensity as intense migration nights.

4.2.3 Weather data

European Centre for Medium-Range Weather Forecast ERA5 reanalysis dataset (Hersbach et al. 2020) with a global extent and 0.25-degree 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 hPa and 1012.5 hPa that correspond to altitudes of approximately 1000 and 130 m asl (U.S. Standard Atmosphere 1976).

The altitude above sea level 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 Figure 4.A.3.
4.2.4 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 wind assistance (WA):

$$WA = y \cos \theta$$

(4.1)

where $y$ is wind speed (m/s), and $\theta$ is a 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 (Shamoun-Baranes & van Gasteren 2011; Bradarić et al. 2020). Low-altitude and high-altitude WA were then used to calculate the difference between low and high-altitude WA and average WA.
4.2.5 Migration altitudes

4.2.5.1 Seasonal flight 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).

4.2.5.2 Nights with low and high-altitude migration
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 used Barnard’s unconditional test to statistically compare the percentages of 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.

4.2.6 Birds and the environment
To analyse the relationship between flight altitudes and weather variables under which birds fly at low altitudes, we used Random Forest Regression (RF) 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 4.1). 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. 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 correlated
predictors. 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 on different altitudes than the avg_cc. Furthermore, we expect birds to fly at altitudes with low cloud cover, thus changing their altitude to fly above or below clouds, and such information cannot be extracted from avg_cc. Sunset is when birds embark on their nocturnal journeys and is more common to use as a time determinant in avian literature, which is why suns_h was kept in the model. The correlation matrices can be found in Figure 4.A.4. A complete list of all predictors used for developing the model can be found in Table 4.1.

Table 4.1. Overview of the predictors of migration ratio at low altitudes used in Random Forest. Predictors marked with an asterisk (*) were excluded from the model since they showed a high level of correlation in the correlation matrix (Figure 4.A.4).

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

Random forest regression models require three parameters: num.trees (number of regression trees), mtry (number of variables randomly sampled as candidates in each node split) and node size (the minimal size of terminal nodes of the tree). The default values of num.trees=500, mtry= one-third of the number of variables and min.node.size=5 were selected as the ones with the lowest RMSE after testing 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. The same parameters were used for the spring and autumn season.

4.2.8 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. 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 the root mean squared error (RMSE) between the test dataset and model predictions.

4.2.9 Model evaluation

Each tree in the random forest has its out-of-bag data sample that was not used during the tree construction. These observations were used in the model fitting process to calculate the out-of-bag mean square error (OOB prediction error) and R², 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 (PDP) to assess each predictor’s relationship with the response variable while other predictors remained constant.

4.3 Results

4.3.1 Migration altitudes

4.3.1.1 Seasonal flight altitudes

In spring, the median flight altitude was 390.7 m asl at Borssele and 369.7 m asl at Luchterduinen, both higher than the 300 m turbine threshold (Figure 4.2). In autumn, the median was 235.4 at Borssele and 225.4 m asl at Luchterduinen (Figure 4.2). Altitude distributions differed significantly between spring and autumn in both locations (L:H=5444.3, df=1, p<0.001, ES=-0.006; B:H=12,895, df=1, p<0.001, ES=-0.02). They also significantly differed between Borssele and Luchterduinen in spring (H=74.5, df=1, p<0.001, ES=-0.06) and autumn (H=78.5, df=1, p<0.001, ES=0.05).
Figure 4.2. 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 grey 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).

4.3.1.2 Nights with low and high-altitude migration

On 52% of nights in spring at Borssele, more than 50% of migrants were flying low, which significantly differed (Z=3.74, p=0.0001) from autumn, when on more than 70% of nights, more than 50% of migrants were flying low (Table 4.2, Figure 4.3). On the majority of nights in both spring (54%) and autumn (74%) at Luchterduinen (Table 4.2), more than 50% of migrants were flying low, but the proportion of nights was significantly higher in autumn (Z=3.59, p=0.0001). The proportion of nights when migrants were mainly flying low did not significantly differ between locations in spring (Z=0.31, p=0.38) or autumn (Z=0.17, p=0.47) (Figure 4.3, Table 4.2). Low-altitude migration was more common on nights of intense migration in autumn than in spring at both locations (Table 4.2, Figure 4.3). However, the proportions were not statistically different among sites (spring: Z=1.11, p=0.19; autumn:
Z=0.47, p=0.34) or seasons (Borssele: Z=1.65, p=0.07; Luchterduinen: Z=1.07, p=0.19).

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 4.2). On 14 nights in spring and 35 nights in autumn, migration was concentrated at low altitudes, but seasonal proportions showed no significant difference (Z=2.32, p=0.1). Luchterduinen showed a similar pattern, but here proportions differed significantly between seasons (Z=2.70, p=0.003). Proportions showed no significant differences between locations during both seasons (spring: Z=0.55, p=0.38; autumn: Z=0.15, p=0.50).

During intense migration nights, extremely low migration (> 90% of migrants flying low) occurred on three nights in autumn and not at all in spring. Contrary, extremely high migration occurred on two nights in spring and not at all in autumn. Similar is observed in Luchterduinen, where migrants were flying high on one spring night, and on one autumn night, migrants were flying low.

4.3.2 Influence of environment on low-altitude migration

OOB R² showed that the model explained 60% of the variance for spring and 56% for autumn. OOB RMSE value was 0.18 for spring and 0.17 for autumn, while RMSE between predictions and observed values from the test dataset was 0.25 for spring and 0.23 for autumn.

In spring, day of year (y_day) was the most important variable for explaining the fraction of migrants flying low and is closely followed by the difference in wind assistance (delta_wa) between low and high altitudes, average wind assistance (avg_wa) and average temperature (avg_temp) (Figure 4.4a). In autumn, the most important predictor of the low-altitude migration fraction was average wind assistance (Figure 4.4b), followed by day of year and average temperature (Figure 4.4b), although the effect of average wind assistance was much stronger than all other variables and the effect of average temperature was lower than in spring (Figure 4.4).

Partial dependence plots (Figure 4.5) show how the top four predictor variables affect the low-altitude migration fraction when all other variables are constant.
Figure 4.3 The total number of tracks per night (upper plot) and nightly proportions of low and high-altitude migration (lower plot) in a) spring and b) autumn season of 2020 at Borssele. Triangles in the upper plot represent intense migration nights from Table 4.2. 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 (Figures 4.A.5 - 4.A.8).

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: day of year (y_day) is between 50 and 70 and 130 and 150 (late February – early March, second half of May), delta_wa is -2 m/s or higher (in other words, when the wind was more supportive at lower altitudes) delta_wa is -2 m/s or higher (in other words, when the wind was more supportive at lower altitudes), avg_wa is between -8 m/s and 5 m/s (birds flew low when average wind assistance was lower than 5 m/s) and avg_temp is low. During autumn, the low-altitude migration fraction increases when: avg_wa is between -10 m/s and 2 m/s (meaning that with low wind assistance, birds fly low), y_day is between 240 and 262 (late August, early September), and delta_wa is higher (wind more supportive at lower altitudes). The effect of average temperature (avg_temp) was weak and unclear. Note that the effect of most predictors was unreliable at extremely high and low values due to fewer data points (Figure 4.5, rug plots).
Table 4.2 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.

<table>
<thead>
<tr>
<th></th>
<th>Borssele</th>
<th></th>
<th>Luchterduinen</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>Autumn</td>
<td>Spring</td>
<td>Autumn</td>
</tr>
<tr>
<td></td>
<td>N total</td>
<td>Low (%)</td>
<td>High (%)</td>
<td>N total</td>
</tr>
<tr>
<td>Full season (&gt;50%)</td>
<td>135</td>
<td>52.5</td>
<td>47.5</td>
<td>175</td>
</tr>
<tr>
<td>Intense migration (&gt;50%)</td>
<td>13</td>
<td>23.0</td>
<td>77.0</td>
<td>17</td>
</tr>
<tr>
<td>Full season (&gt;90%)</td>
<td>18</td>
<td>77.7</td>
<td>22.3</td>
<td>36</td>
</tr>
<tr>
<td>Intense migration (&gt;90%)</td>
<td>2</td>
<td>0.0</td>
<td>100.0</td>
<td>3</td>
</tr>
</tbody>
</table>

Figure 4.4 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 RF model. Predictors with the prefix “delta” show a difference in predictor values between low and high altitudes. Abbreviations can be found in Table 4.1.
Figure 4.5 Partial dependence plots show each predictor’s effect on low-altitude migration fraction (y-axis) in a) spring and b) autumn when all the other predictors are kept constant. 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. Delta wind assistance shows the difference in wind assistance between low and high altitudes.

4.4 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 and more frequently above the wind turbines (300 m) than in autumn (Figures 4.2 and 4.3). Nevertheless, the majority of birds flew at low altitudes on most nights in both seasons (Figure 4.3, Table 4.3, Figures 4.A.5 – 4.A.9). An exception was intense migration nights in spring when migrants, on most nights, mainly flew at high altitudes (Table 4.3). These results were consistent between different radar locations, and they corroborate what was previously recorded in this part of the world both over land (Kemp et al. 2013) and sea (Hüppop et al. 2006; Fijn et al. 2015).

Wind assistance was among the top four predictors of low-altitude migration 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 et al. 2020a). 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
wind assistance, which generally increases with altitude (Figure 4.A.3).

The fraction of low-altitude migration increased (Figure 4.5b) when wind assistance 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) when supporting winds can reverse with altitude. Instead, our results imply that birds choose to fly at altitudes with wind conditions that are more supportive for migration than wind conditions birds experience at other altitudes. However, since we assessed wind assistance based on an average migration direction per season, the effect size 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.

The low-altitude migration fraction increased in both seasons when the average wind assistance (avg_wa) was negative or had lower positive values (Figure 4.5a and 4.5b). A higher fraction of low-altitude migration when average wind assistance was negative indicates that birds might fly close to the surface to decrease the effect of overall negative wind assistance (Alerstam 1990), as wind speeds tend to be lower at lower altitudes (Figure 4.A.3). All this allows for flight energy conservation and a decrease of migration 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 (Shamoun-Baranes & van Gasteren 2011; Brust et al. 2019; Bradarić et al. 2020; Brust & Hüppop 2021).

In both seasons, low-altitude migration had a clear temporal pattern, although the effect of day of year in spring was stronger than in autumn. In spring, we observed more birds flying at low altitudes at the beginning and the end of the migration season (Figure 4.5). The low-altitude migration fraction was high throughout autumn but was higher at the beginning of the season. Such temporal 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 wind assistance 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 variability 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 late peaks of low-altitude migration are more challenging to explain but can come from the long-distance flights of waders from Africa, nearly reaching their stopover area in the Wadden Sea (Lensink et al. 2002). In autumn, an early low-altitude migration peak is hard to explain. Although this is when waders depart on migration, they are
expected to fly at higher altitudes (Senner et al. 2018; Loonstra et al. 2019). As late spring and early autumn low-altitude migration peaks show lower bird counts, they more likely reflect disturbance from the local bird movements.

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 (Figure 4.A.3). Our models showed that in addition to wind assistance and day of year, temperature affects altitude distribution in the North Sea basin in both seasons. However, the effect was stronger in spring than in autumn (Figure 4.4). In spring, the fraction of low-altitude migration increased with lower temperatures, especially those below the freezing level. In autumn, we did not observe a strong relationship between low-altitude migration fraction and temperature. The small effect is probably due to the fact that low temperatures, which are expected to prompt birds’ flight at low altitudes, are seldom measured in autumn at our study locations, while they certainly occur in spring, especially at high altitudes (Figure 4.A.3). While other studies found an influence of cloud cover on migration altitude (Eastwood & Rider 1965; Eastwood 1967), 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 (Figure 4.A.3).

The variance explained by our model indicates that the individual 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 (Drewitt & Langston 2008; Desholm 2009; Marques et al. 2014; Hüppop et al. 2016; 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; Marques et al. 2014; May et al. 2020).

One of the strategies to reduce the risk of collision between migratory birds and offshore wind turbines that will be adopted in the coming years 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 will be at greater risk of collision due to the lower flight altitudes on most migration nights, including 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 and temperature. Improving our understanding of variation in altitude distribution can reduce the risk of unnecessary turbine shut down on nights of intense migration when birds are expected to fly above turbine height and improve predictions for nights with low-altitude migration when turbine shutdown would be most effective.
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4.A Appendix for Chapter 4

Figure 4.A.1 Detection probability of a bird the size of 0.125 standard avian target (which corresponds to the radar cross-section of -25 dBm² and a mass of 62.5 g) by an X-band vertical radar beam used in the 3-D fix radar (Robin Radar). A standard avian target is used for evaluating the performance of avian radar systems and corresponds to a carrion crow (Corvus corone) with a radar cross-section of -16 dBm² and a mass of 500 g. Based on this figure, only data that was collected up to 1500 m of altitude was used in the analysis. Figure provided by Robin Radar.

Figure 4.A.2 A side view of targets detected by the X-band vertical radar beam at Luchterduinen (positioned at 22 m ASL). The vertical radar beam is positioned at 0 m in the figure. A range between 500 m and 1500 m on either side of the radar has the highest detection probability for targets of different sizes, which is why only data from this range was included in our analysis. Data is selected from Autumn 2019 in this figure.
Figure 4.A.3 Distributions of seasonal a) wind directions (decimal degrees) b) wind speeds (m/s) c) temperatures (°C), and d) cloud cover (0-1, 0 representing no cloud coverage) at low (left side, shaded area) and high altitudes (right side, white area) in spring (blue) and autumn (orange) in Borssele (upper panel) and Luchterduinen (lower panel) for all hours during our observation period. The yellow arrows and lines represent the mean, while the green ones represent the median of seasonal distributions.
Figure 4.A.4 Correlation matrices based on Spearman’s rank correlation coefficients for predictors in the random forest models for spring (left) and autumn (right). Predictors’ names are shown diagonally in the plots. Larger dots on the right side show a higher positive (blue) or negative (red) correlation between two predictors, which is also numerically reflected on the left side of the plot and corresponds to the colour scale legend on the right side. When highly correlated (Spearman rank correlation coefficients over 0.8), one of the predictors were removed from the model, as described in the main text of the paper. See table 4.1 for abbreviations.

4.A.1 Removal of rain minutes

We performed a two-step filtering to remove rain that mistakenly entered our database recorded as birds. Firstly, KNMI climatological gauge-adjusted radar dataset of 5 min precipitation accumulations at 1 km spatial resolution (grid cell with a centre in 51.58 N 3.44 E for Borssele and 52.36 N 4.49 E for Luchterduinen) was used to remove minutes in which any rainfall occurred. After this step, the edges of rain events which represent periods between the actual start of the rain event and the moment when the rain clutter filter started working, remained in our data. This is why, as a second step, we calculated a 5-minute rolling median of the rain clutter filter in 1-minute increments and excluded all minutes in which the rain clutter filter was equal to or higher than its rolling median (excluding zero values).
Figure 4.A.5 The total number of tracks per night (upper plot) and nightly proportions of low and high-altitude migration (lower plot) in spring 2021 (blue) and autumn 2019 (orange) at Borssele White spaces in proportion plots represent nights which were excluded from the analysis due to filtering steps. Nights marked with a triangle in the upper plot are nights with intense migration that could be considered for wind turbine curtailments.
Figure 4.A.6 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) at Luchterduinen in 2019. White spaces in proportion plots represent nights which were excluded from the analysis due to filtering steps. Nights marked with a triangle in the upper plot are nights with intense migration that could be considered for wind turbine curtailments.
Luchterduinen spring and autumn 2020

![Graphs showing the total number of tracks per night and nightly proportions of low and high-altitude migration in spring and autumn at Luchterduinen in 2020.]

Figure 4.A.7 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) at Luchterduinen in 2020. White spaces in proportion plots represent nights which were excluded from the analysis due to filtering steps. Nights marked with a triangle in the upper plot are nights with intense migration that could be considered for wind turbine curtailments.

Luchterduinen spring 2021

![Graphs showing the total number of tracks per night and nightly proportions of low and high-altitude migration in spring 2019 at Luchterduinen.]

Figure 4.A.8 The total number of tracks per night (upper plot) and nightly proportions of low and high-altitude migration (lower plot) in spring 2019 at Luchterduinen. White spaces in proportion plots represent nights which were excluded from the analysis due to filtering steps. Nights marked with a triangle in the upper plot are nights with intense migration that could be considered for wind turbine curtailments.
Tina, are you for real?! I've asked for that sunscreen a billion times!

I can see them flying! I will turn the wind turbines off! Do you copy? I will turn the turbines off!
Chapter 5

Forecasting nocturnal bird migration to mitigate collisions with offshore wind turbines in the southern North Sea

Maja Bradarić, Bart Kranstauber, Willem Bouten and Judy Shamoun-Baranes
To be submitted

Abstract

To meet climate targets, the world’s energy sector is transitioning to zero-carbon energy production, with a major contribution expected from the expansion of the wind energy sector. This means wind turbines will increasingly clutter airspace and can have negative direct and indirect effects on aerial wildlife. Placement of wind turbines within large migration flyways can contribute to declines of vulnerable migratory bird populations by increasing mortality through collisions and alteration of migratory routes. On-demand curtailment of wind turbines limited to short periods with peak migration can considerably minimize negative impacts on bird populations, and near-term forecasts of bird migration can inform such decisions. Here, we develop a near-term forecast of low-altitude (up to 300 m) nocturnal bird migration over the southern North Sea. We use tracking bird radar data collected off the western Dutch coast and weather and phenological variables to facilitate the curtailment of wind turbines offshore during spring and autumn migration. We demonstrate that the most important predictors of migration intensity in spring are seasonal phenology and wind assistance at an inferred departure region in the UK and at the radar location. In autumn, diurnal phenology and wind assistance were the most important predictors. We show that overall, the model classified migration hours by intensity correctly in more than 90% of cases in spring and more than 80% in autumn. However, the number of correctly predicted intense migration hours was low, likely due to the short-term dataset. We show that to minimize collision risk for 50% of migrants, if predicted correctly, curtailments should be performed during only 18 hours in spring and 26 in autumn (2.5 % of the migration period in spring and 5.5 % in autumn), but this can differ between the years. The amount of energy that would be lost due to curtailments is 0.56% in spring and 1.26% in autumn. Finally, we argue that using near-term ecological forecasts developed with limited datasets in combination with expert knowledge is necessary to speed up conservation efforts in a rapidly changing world.
5.1 Introduction

Airspace, where bird migration journeys occur, is increasingly altered by man-made structures such as wind turbines, power lines, buildings, drones and aircraft (Bauer et al. 2019; Lambertucci & Speziale 2021). These structures pose a risk for migratory birds through collisions (Marques et al. 2014; van Gasteren et al. 2019; van Doren et al. 2021), habitat change and barrier effects (Drewitt & Langston 2006; Gaultier et al. 2020). As the world is transitioning toward sustainable energy production to meet climate targets, the airspace is bound to become riskier (Davy et al. 2017) due to the energy transition relying on increased wind energy production, with many countries concentrating on expansion offshore (Leung & Yang 2012).

To minimize these and other negative impacts of environmental alterations on wildlife, a mitigation hierarchy consisting of four steps (avoid, minimize, remediate and offset) has been developed (Arlidge et al. 2018), and ways to implement these steps have been relatively well-established (Schaub et al. 2020; Serrano et al. 2020; Murgatroyd et al. 2021; Gauld et al. 2022). Institutions, such as wind energy companies, which are developing infrastructure that is cluttering the airspace, are bound by national and international laws to comply with the mitigation hierarchy. When the first step of completely avoiding new energy infrastructure in hotspots for aerial wildlife (Gauld et al. 2022) is not possible, methods such as on-demand wind turbine curtailment have been shown to minimize the adverse effects on bird and bat populations onshore (Singh et al. 2015; Hayes et al. 2019; McClure et al. 2021; Bennett et al. 2022). So far, such curtailments have mainly been performed near real-time and on a small scale, mostly focusing on specific species within individual wind farms. In regions which are experiencing extensive wind energy development and hosting large migratory flyways with broad-front bird migration of various species, turbines in multiple wind farms have to be curtailed simultaneously to allow for a safe passage. An endeavour of that magnitude requires coordination of multiple stakeholders to keep the energy grid stable and cannot be accomplished near real-time. Instead, predicting when birds will arrive in risk areas can help set up cost-effective mechanisms to minimize negative impacts on bird populations (Reynolds et al. 2017b; Shamoun–Baranes et al. 2017).

In recent decades, ecological forecasting has been highlighted as an imperative to improve and speed up conservation efforts while balancing financial and societal costs with nature benefits (Clark et al. 2001; Luo et al. 2011; Dietze et al. 2018; Horton et al. 2021). An increase in data availability and advances in data processing, statistics and computational infrastructure allow for near-term predictive models (Dietze et al. 2018). Such models can help steer environmental management when swift conservation action is needed (Luo et al. 2011; Reynolds et al. 2017b; Dietze et al. 2018), which is particularly important in today’s rapidly changing world (Clark et al. 2001; Dietze et al. 2018). They are, for example, featured as an invaluable tool for the dynamic conservation of migratory birds (Reynolds et al. 2018; Horton et al. 2021).
Near-term forecasts of bird migration with a regional extent are already in use to minimize collisions between birds and aircraft (van Belle et al. 2007; van Gasteren et al. 2019; Kranstauber et al. 2022). Forecast models with a continental extent have been developed (van Doren & Horton 2018) and are used for turning off lights on high buildings (BirdCast 2022) to decrease collisions migratory birds experience in urban areas due to attraction to light (van Doren et al., 2017). Similar types of forecasts could be used to inform wind turbine shutdowns in large wind energy production areas. Several of these models were developed using weather radar data. However, these radars have poor coverage in offshore areas, where a large proportion of new wind energy development will occur, especially at the lower altitudes relevant to wind energy. This is due to the spatial extent of weather radar that generally does not extend above sea and problems with ground clutter sensitivity, making biological information obtained at low altitudes less reliable (Dokter et al. 2009). To inform offshore wind turbine shutdowns, it is necessary to predict migration up to 300 m of altitude offshore.

In the southern North Sea, where Belgium, the UK and the Netherlands are building new wind parks, the currently installed amount of wind power will increase four-fold by 2030 (Department of Energy & Climate Change 2013; FPS Economy 2021; Rijksoverheid 2021). Concurrently, the North Sea is a migratory corridor for several hundred million birds that migrate twice a year between mainland Europe and the UK and between NW Europe and Africa, mainly during the night (Lack 1959; Dierschke 2003; Hüppop et al. 2006). Most migratory birds select nights with specific weather conditions for migration (Richardson 1978; Erni et al. 2002b; Bradarić et al. 2020; Manola et al. 2020a). In the case of the contiguous US, it has been suggested that shutting down turbines on 10% of migration nights would already allow a safe passage for 50% of migratory birds (Horton et al. 2021). Limiting wind turbine curtailment on several intense migration nights is the key to performing aerial conservation actions over large areas with minimal impact on the energy market. Near-term migration forecasts that rely on well-known drivers of migration intensity could be used to achieve that.

Phenology and weather are the two main categories of drivers generally used to predict migration intensity over land (van Belle et al., 2007; van Doren & Horton, 2018; Kranstauber et al., 2022). Many migratory species exhibit a clear circannual rhythm in their migratory activity, often considered to be triggered by seasonal changes in day length (Gwinner & Helm 2003). In addition, many species exhibit a circadian rhythm that can prompt daily migration schedules (Gwinner et al. 1997). For many landbirds migrating at night, migratory activity is often initiated around sunset (Åkesson et al. 1996), with some variation due to environmental factors and body condition (Sjöberg et al. 2017; Müller et al. 2018b). Weather, especially wind, is crucial for departure decisions (Alerstam 1990; Newton 2008). Birds fly with winds that are more supportive of migration (Bradarić et al. 2020), which helps increase their migration speed, thus reducing the time and effort spent on migration
(Liechti 2006). Besides winds, temperature (Kemp 2012; Deppe et al. 2015) and air pressure (Richardson 1990a) can trigger migratory movements. In North-western Europe, migration intensity over land in spring is high when temperatures are above zero, bringing more stable weather conditions (Kemp et al. 2013; Kranstauber et al. 2022). In both seasons, precipitation generally has an inhibiting effect on migration (Richardson 1990a; Erni et al. 2002b). Including weather variables in predictive models allows for capturing finer-scale temporal dynamics of migration, thus increasing the probability of accurately forecasting migration intensity (Kranstauber et al. 2022).

Existing bird migration forecast models currently focus on migration over land. However, the migratory behaviour of landbirds may differ over the sea, as seas may be perceived as ecological barriers. This is because large bodies of water have limited or no opportunities for landbirds to land or refuel, and it has been demonstrated that birds exhibit different departure decisions when embarking on such journeys (Alerstam 2001; Deppe et al. 2015). When crossing ecological barriers, birds become more selective of weather conditions, which influences their departure decisions (Deppe et al. 2015), routes (Diehl et al. 2012; Bruderer et al. 2018) and flight altitudes (Eastwood & Rider 1965; Archibald et al. 2016), consequently influencing migration intensity. It is, therefore, essential to understanding which factors are the main drivers of migration over the sea to provide the most accurate offshore bird migration predictions.

One of the challenges associated with developing predictive models of migration which rely on weather variables as input is having a sufficiently long time series to capture diverse weather conditions and rare peaks in migration. A minimum of two years of radar data has been suggested for the development of predictive models on land (van Belle et al. 2007), although intense migration nights with a rare set of weather conditions can be hard to predict even with 10-year datasets (Kranstauber et al. 2022). Radars that have been collecting data offshore do not yet have such a long time series. However, the pace of the environmental alteration requires swift conservation actions, which include wind turbine curtailment informed by near-term ecological forecasts with less-than-ideal data, and improving models “on the go” (Dietze et al. 2018).

Striving to allow decision-makers to make near-term decisions regarding offshore wind turbine curtailment, we demonstrate the first attempt to make seasonal forecast models of low-altitude nocturnal migration at sea and explore which environmental variables in departure regions and offshore influence migration intensity at low altitudes in the Dutch part of the southern North Sea. We train a random forest model with data collected by a tracking radar positioned offshore of the western Dutch coast. As model input, we use day of year, time of day and weather variables (wind, temperature, precipitation, air pressure) from inferred departure locations and the radar location to predict migration in spring and autumn. We expected that
seasonal and diurnal phenology, the wind and precipitation at sea and potential departure locations would be the most important factors influencing migration, with other factors considered of secondary importance. We test how accurate the forecasts are in each season by creating confusion matrices based on different thresholds and discuss the threshold effect on the curtailment procedure. We demonstrate the model performance in its current form and describe the main drivers of nocturnal bird migration over the North Sea in spring and autumn. We show the percentage of migratory birds that would have a safe passage as a function of the number of curtailment hours and demonstrate the energy loss in relation to the percentage of migratory birds protected. Migration intensity forecasts, created 48 hours ahead, with the models described in this paper and using weather forecast as an input, will be used by an expert committee in the initial stages of the decision-making process created by the Dutch government to determine whether turbine curtailments are necessary during specific periods in spring and autumn. We discuss our findings within the context of these curtailment procedures.

5.2 Materials and methods

5.2.1 The radar system, location and study period

In our study, we used data collected by a tracking radar (Robin Radar 3D fix, Robin Radar Systems BV, the Hague, Netherlands) positioned within the existing offshore wind farm Luchterduinen (52.25 N, 4.10 E), ca 23 km from the western Dutch coast. The radar has been continuously collecting data since 2018. Our study uses data between sunset and sunrise during spring (15th of February – 30th of April) and autumn (1st of October – 30th of November) seasons. This period covers the most intense migration nights between 2019 and 2022 (Figure 5.A.1).

![Figure 5.1 The North Sea area with the radar location (blue dot) and bounding boxes of ERA5 weather data grid cells at departure locations (Bradarić et al. 2020) in spring (green) and autumn (yellow).](image)

The radar system consists of two antennae. An X-band antenna with the power of 25
kW rotates vertically and collects information about bird numbers and altitudes, and an S-band antenna that rotates horizontally and collects information on numbers, flight directions and speeds of birds up to 500m altitude. Both antennae have radar beams 20 degrees wide and rotate at 45 rpm. In this study, we only use the data collected by the horizontal antenna, as this data covers the altitudes of interest and contains more information about individual tracks.

A proprietary tracking algorithm generates tracks of moving targets recorded by the radar based on target characteristics (speed, direction and radar cross-section). The radar system employs automated clutter filters to reduce the number of non-bird targets that can mistakenly be classified as bird tracks. Clutter filters are applied dynamically in each radar scan and expressed as a fraction of the total scan area in which clutter is detected. This is expressed with a value between 0 (no clutter on the radar image) and 1. Dynamic filters reduce reflections coming mostly from landscape features, waves and rain. Tracks lasting for at least eight consecutive rotations are automatically stored in a centralized database. Bird tracks include the following information used in this study: ground speed, track direction, straight-line distance (between the first and the last point of a track), track length, track centroid, and the number of individual points per track.

5.2.2 Radar data post-processing

We apply additional filtering to derive the hourly migratory track count from the radar data. Tracks originating from static clutter entered the database despite the automatic clutter filters. These tracks were characterized by low displacement over time. We calculated displacement over time by dividing the straight-line distance between the first and last track point with track duration and removed 10% of tracks with the lowest values. Due to clutter close to the radar and detection loss of small songbirds further from the radar, only tracks whose central point had a horizontal distance from the radar between 1000 and 2000 m were used in our analysis (excluding the area between 275° and 346° which was blocked by a structure the radar was mounted on). Exploratory analysis of nights of intense migration with highly uniform flight directions has shown that individual tracks have low tortuosity. We, therefore, use only straight tracks in our analysis. The straightness of a track was estimated by dividing the straight-line distance between the first and last track point by a track length. All tracks with straightness lower than 0.7 (based on the visual inspection of the data) were characterized as non-migratory and were removed from the analysis. Tracks with airspeeds ≤ 5 m/s (see section 5.2.5 for airspeed calculation) were removed from the analysis as they most likely come from insects. All hours with no biological data were included as zero measurements. Finally, all minutes in which the clutter filter activity was higher than 0.3 (van Erp et al. 2021) and all hours with ten or fewer minutes of data were excluded from the analysis to avoid including artificially-created low migration intensities due to high clutter
5.2.3 Mean traffic rate (MTR)

To estimate the hourly number of birds passing through an area of interest, we calculated the mean traffic rate of migration (MTR). MTR is expressed as the number of birds (#) per kilometre (km) per hour (h). MTRs (#/km/h) were estimated as follows:

\[ MTR = d \times V_g \]  (5.1)

where \( d \) represents mean bird track density (#/km\(^2\)), and \( V_g \) represents mean ground speed (km/h). Mean bird track density \( d \) was expressed as

\[ d = \frac{P_t}{A} \]  (5.2)

where \( A \) is the surface area of the radar sector (km\(^2\)) from which we sampled our data, and \( P_t \) represents the mean number of all bird track points recorded by the radar per rotation in the area and is calculated as in equation 5.3

\[ P_t = \frac{\sum (P_i)}{rph} \]  (5.3)

where \( P_i \) is the number of points of each track whose central point was recorded within the area in an hour \( t \), and \( rph \) is the number of radar rotations per hour.

All mean ground speeds were expressed as harmonic means of ground speeds (m/s) of each point of a track.

5.2.4 Weather data

Weather data was extracted from the European Centre for Medium-Range Weather Forecast ERA5 reanalysis dataset (Hersbach et al. 2020), which has a global extent, 0.25-degree grid size and 1-hour temporal resolution. Hourly weather variables for the radar location were obtained from the closest grid cell, 52.25 N 4.00 E. Data for potential departure locations in the Eastern UK and Northwestern France in spring and north of Netherlands, Northwestern Germany and central Denmark in autumn (Bradarić et al. 2020) were averaged over multiple grid cells (bounding boxes in Figure 5.1) and over the first two hours after sunset, as that is the time when most birds are expected to depart. We extracted total precipitation (TP, m), mean sea level pressure (MSLP, Pa) and wind components at 100m above the earth’s surface (ASL) that describe wind from west to east (\( u \), m/s) and south to north (\( v \), m/s), from the single level dataset. Air temperature (\( t \), °K) and geopotential height were extracted from several pressure levels. Before doing any calculations, the weather variables units were converted as follows: mean sea level pressure was converted from Pa to hPa, total precipitation from m to mm and air temperature from °K to...
°C. The air temperature was extracted from multiple pressure levels and averaged over those that correspond to the altitudes of interest (100 – 300 m). Altitudes were calculated by dividing the geopotential height of a pressure level by the gravitation acceleration. To capture the change in weather conditions from night to night, we calculated the nightly difference in mean sea level pressure by subtracting the mean sea level pressure of the current night from the mean sea level pressure of the previous night. This variable was calculated for radar and departure locations and included in the model as a predictor.

5.2.5 Wind assistance

Wind assistance (WA, m/s) is an estimate of wind support that birds experience during flight, and it was calculated using the tailwind equation (Kemp et al. 2012)

\[ WA = y \cos \theta \]  

where \( y \) is wind speed (m/s), and \( \theta \) is a difference between the direction the wind is blowing to and the preferred migration direction (PMD). Wind direction and wind speed were calculated using \( u \) and \( v \) components of the ERA5 dataset for different locations (Shamoun-Baranes et al. 2007). At the radar location, PMD was calculated from the data, 91° for spring and 214° for autumn. At the departure locations, the PMD was estimated from the literature. In spring, the PMD for departure location in the UK was 90°. Additionally, wind assistance using 30° as a PMD was calculated to capture movement from NW France towards NE. In autumn, PMD was set to 220° for N Netherlands and Denmark (Shamoun-Baranes & van Gasteren 2011; Bradarić et al. 2020). To represent sea crossings towards the UK in autumn, an additional wind assistance variable was calculated at the radar location for these birds, using 270° as PMD. PMDs and airspeeds at the radar location were calculated from track directions, groundspeed and wind data at 100 m ASL following Shamoun-Baranes et al. (2007).

5.2.6 Accumulations

When weather conditions are not favourable for migration for a few days in a row, birds that would otherwise depart may accumulate in large numbers and depart once weather conditions improve. This effect is particularly evident at the coast before birds embark on crossing ecological barriers, such as large water bodies (Lowery 1945; Biebach et al. 2000). In order to capture accumulation dynamics, we calculated accumulation factors following Erni et al. 2002 and included them as predictors in our models. We first determined a binary variable for migration accumulations based on precipitation at departure locations. We assumed birds would accumulate if hourly precipitation was more than 0.01 mm. We then calculated accumulation due to wind assistance at departure locations, assuming that birds would accumulate if wind assistance is lower than -2 m/s. The thresholds have been
identified by looking into differences in wind assistance and precipitation between the top 10% of intense migration nights and the rest of the data. An accumulation index of $\frac{2}{3}$ has been used following Kranstauber et al. 2022. This means that if wind assistance was lower or precipitation higher than the threshold above, $\frac{3}{4}$ of birds that were supposed to depart on one night would wait until the next night to start their migration. Finally, we calculated nightly differences in accumulations and included them as predictors in our models. Accumulations ranged between zero and one, one representing the highest accumulation due to unfavourable weather conditions explained above.

5.2.7 Seasonal and diurnal phenology

To capture circannual and circadian migration dynamics at the radar location, we created a proxy for seasonal and diurnal phenology by fitting local polynomial regression curves to hourly MTRs grouped by day of year and hour after sunset. Curves were fitted to the full (4-year for spring and 3-year for autumn) dataset using the \textit{loess} function of the ‘base’ R package (R Core Team 2022) and included in the models as predictors. Figures can be found in Appendix (Figure 5.A.2).

5.2.8 Predictive model

We trained random forest models using the R package ‘ranger’ (Wright & Ziegler 2017) to predict migration in spring and autumn separately. Having four years of data for spring and three years of data for autumn, we always used one year of data as a testing dataset, while the rest was used for the model training. The main text shows the model results based on training data from 2019, 2020 and 2021 for spring and 2019 and 2021 for autumn. In spring, 2022 was used as a testing dataset for model evaluation, while 2020 was used in autumn. These combinations showed the best model results, which is why they were presented in the main text. All the other combinations of training and testing years are available in Appendix (Figure 5.A.6). This data division corresponds approximately to a 70:30 ratio of training vs testing datasets usually used in random forest setups. The models were trained with a regression setting, using MTRs as a continuous response variable and accumulations, weather and phenology variables as predictors. The full list of predictors which differed between the two migration seasons can be found in Table 5.A.1.

Before running the models, we generated correlation matrices (Figure 5.A.3) using Spearman’s rank correlation coefficient with the ‘corrplot’ package (Wei & Simko 2021) to remove the correlated predictors, as they do not explain the extra variance and can affect the ability of the model to identify variable importance (Gregorutti et al. 2017). Since the previous research on nocturnal bird migration over the North Sea showed that wind assistance drives departure decisions of migratory birds (Bradarić et al. 2020), wind assistance at the radar and departure locations were kept in the
model. All the other variables with the highest absolute correlation (above 0.7) were removed from the modelling procedure. This means that if the two variables were highly correlated, the correlation of each of those two variables with all the other variables was checked, and the variable with the highest absolute correlation was removed. The full list of the seasonal variables that were highly correlated and removed from the further analysis is given in Appendix (Figure 5.A.3).

The data used for the model training was imbalanced, as the number of hours with high MTRs representing intense bird migration was much lower than the number of hours with low MTRs (Figure 5.3, Figure 5.A.1). Imbalanced data causes imbalanced learning for the random forest algorithm. This means that due to a lack of hours with intense bird migration, the model cannot learn much about the conditions that lead to such high numbers of migrants. Since the aim of this paper was primarily to predict intense bird migration, we applied stratified sampling to balance our data (Brieuc et al. 2018).

Table 5.1 Overview of variables used as model predictors.

<table>
<thead>
<tr>
<th>Description</th>
<th>Unit</th>
<th>Season</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wind assistance toward W</td>
<td>m/s</td>
<td>Autumn</td>
<td>Radar and NW Germany</td>
</tr>
<tr>
<td>Wind assistance toward SW</td>
<td>m/s</td>
<td>Autumn</td>
<td>Radar, N Netherlands and Denmark</td>
</tr>
<tr>
<td>Wind assistance toward E</td>
<td>m/s</td>
<td>Spring</td>
<td>Radar and the UK</td>
</tr>
<tr>
<td>Wind assistance toward NE</td>
<td>m/s</td>
<td>Spring</td>
<td>Radar and NW France</td>
</tr>
<tr>
<td>Total precipitation</td>
<td>mm</td>
<td>Both</td>
<td>Radar and departure locations</td>
</tr>
<tr>
<td>Temperature</td>
<td>°C</td>
<td>Both</td>
<td>Radar and departure locations</td>
</tr>
<tr>
<td>Mean sea level pressure</td>
<td>hPa</td>
<td>Both</td>
<td>Radar and departure locations</td>
</tr>
<tr>
<td>The nightly difference in mean sea level pressure</td>
<td>hPa</td>
<td>Both</td>
<td>Departure locations</td>
</tr>
<tr>
<td>Accumulation due to wind assistance</td>
<td></td>
<td>Both</td>
<td>Departure locations</td>
</tr>
<tr>
<td>The nightly difference in accumulation due to</td>
<td></td>
<td>Both</td>
<td>Departure locations</td>
</tr>
<tr>
<td>wind assistance</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Accumulation due to total precipitation</td>
<td></td>
<td>Both</td>
<td>Departure locations</td>
</tr>
<tr>
<td>The nightly difference in accumulation due to</td>
<td></td>
<td>Both</td>
<td>Departure locations</td>
</tr>
<tr>
<td>precipitation</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diurnal phenology</td>
<td></td>
<td>Both</td>
<td>-</td>
</tr>
<tr>
<td>Seasonal phenology</td>
<td></td>
<td>Both</td>
<td>-</td>
</tr>
</tbody>
</table>

Stratified sampling allows for creating sub-groups of the data and including them equally in the model training procedure, despite the fact that one category is less numerous than the other. The ‘ranger’ function regulates stratified sampling with the ‘inbag’ parameter. The ‘inbag’ parameter is a list whose length corresponds to the number of trees within a random forest. Each list element consists of an array whose length corresponds to the training dataset’s number of observations. Array elements are numbers that specify how often a certain observation will be used when creating
individual trees. With each of these arrays, we specified how many times each of our observations would be used in generating each random forest tree. To determine how to set the inbag parameter to balance our data, we first divided our training dataset into low and high migration intensity observations based on the 95 percentile of the hourly MTRs. All hourly observations that were lower than this threshold were categorized as low-intensity hours, and all observations above the threshold were categorized as high-intensity hours. By dividing data in this way, we determined that the number of low-intensity hours was approximately 20 times higher than the number of high-intensity hours in both seasons. In order to balance this, we set up our random forest algorithm in such a way that all high-intensity hours were used 20 times in the creation of each tree, while low-intensity observations were used only once. Thus, for each tree, we assigned a value of one to 63.2% of random low-intensity observations and a value of 20 to 63.2% of high-intensity observations. This means that all random low-intensity observations used to build each tree will only be used once, while all random high-intensity observations will be used 20 times. The rest of the random data in each category was assigned zeroes and used for out-of-bag (OOB) calculations. 63.2% is a default fraction for randomly sampling the training data in the random forest algorithm of the ranger package.

Before training the models, we performed hyperparameter tuning by running the models with the range of different hyperparameters and chose a combination that led to the lowest out-of-bag RMSE. We varied the node size (node.size) from 5 to 50 with increments of 5 for both seasons, and the number of variables randomly sampled as candidates for each node split (mtry) from 2 to 16 in spring and from 2 to 22 in autumn over the default number of 500 trees. We used 500 trees and the minimum node size of 5 observations in both seasons. In spring we used mtry of 7 and in autumn mtry of 15.

5.2.9. Model evaluation

We report OOB $R^2$ for both seasons to indicate how much variance is explained by each model. However, we focus on other model evaluation methods, as we are mainly interested in how the model predicts hours with high MTRs, as those are the moments relevant for offshore wind turbine curtailments. We create confusion matrices using a threshold of 150 birds/km/h (95th percentile of MTR). All the hours with migration intensity higher or equal to the threshold can be considered hours with high migration intensity and are candidates for offshore turbine curtailments. To show the predictive performance of the model when using different thresholds, we created receiver operating characteristic (ROC) curves based on the 95th percentile (150 birds/km/h) and from there extracted two values which show the best model performance to use as thresholds in two additional confusion matrices. With this, we aimed to demonstrate how the threshold choice in the operational phase of the conservation framework can contribute to the effectiveness of the aeroconservation.
We calculated the cumulative percentage of migration intensity ranked by hourly MTR values in descending order over the course of a season to illustrate the number of hours needed for a certain percentage of migrants to pass, which can be used to estimate the number of hours needed for wind turbine curtailments for the most effective conservation. These calculations were performed for both observed and predicted MTR values, and their comparison can be used to evaluate the accuracy and effectiveness of curtailment based on predictions; if the predictions are ideal, the curves of cumulative percentages would completely overlap.

Finally, we create curves of cumulative energy production ranked by hourly MTR in descending order. The energy production was calculated based on the power curve for wind turbine type V112, the type used within the Luchterduinen wind farm (Bauer & Matysk, 2022). Energy production was calculated using the hourly 100 m wind speed data from the radar location. These curves are created in order to estimate the percentage of energy loss if the curtailments are performed during the intense migration hours.

5.3 Results

5.3.1 MTR, weather variables and phenology

Hourly migration traffic rates could fluctuate between nights over several orders of magnitude and peak nights of migration are much higher in autumn than in spring (Figure 5.A.1, Figure 5.3). In spring, peaks of migration intensity occur in March and the first half of April, while the MTRs are the highest in the second half of October and the first half of November in autumn (Figure 5.3, 5.A.1). Spring peaks are generally fewer than autumn peaks and tend to be of lower magnitude, except for the peak on the 15th of March 2022 (Figure 5.3, Figure 5.A.1).

The most important variables for predicting low-altitude offshore migration in spring are seasonal phenology, followed by nightly difference in accumulation due to wind assistance at the potential departure locations in the UK and wind assistance towards NE at the radar location (Figure 5.2, upper graph). Migration intensity is the highest when the seasonal phenology proxy is above 40, which corresponds to late February and March, when the nightly difference in accumulations due to wind assistance was positive (meaning that the accumulation of birds at the departure of the previous night is higher than on the current night, i.e. conditions improved and birds depart after a period of poor conditions) and when wind assistance towards NE at the radar locations between 0 and 2 m/s (Figure 5.A.4).

In autumn, migration intensity is the highest when wind assistance towards SW at the radar location is positive but not higher than 5 m/s, when wind assistance at the departure location in the North of the Netherlands is between -3 and 0 m/s and when the diurnal phenology proxy is around 40, which corresponds to the first two
hours after sunset, which is indicative of the departure of migrants from the nearby coast around sunset (Figure 5.A.4).

### 5.3.2 Model predictions and evaluation

The OOB $R^2$ showed that the model explains 76% of the variance for spring and 59% for autumn. In spring, confusion matrices (Figure 5.4) were created with 706 (out of a total of 941) hourly data points for which the reference data was available (moments in which the radar was functioning and clutter filtering was not high). The number of available hourly data points in autumn was slightly lower than in spring (467 out of 944). Thresholds used for the creation of the confusion matrices were lower in spring than in autumn (Figure 5.3). The model generally performs well in predicting true negatives with all threshold values in both seasons (Figure 5.4). The true positive fractions, which relate to hours with higher values of MTRs, are low in spring and autumn. The spring model performs slightly better than the autumn one, with overall fractions of true predictions being higher and the fraction of false predictions being lower.

In Figure 5.5, MTRs are plotted as a cumulative seasonal percentage ranked by hourly migration intensity in descending order (hours with highest MTRs values first, plotted from the left side of the x-axis) as observed by the radar and compared with the cumulative seasonal percentage of MTRs as predicted by the model (Figure 5.5 shows spring of 2022 and autumn 2020, while curves for all the other years can be found in Figure 5.A.6). If the model predictions were perfect, these two lines would completely overlap. Reading the x and y coordinates of points belonging to each line, we can determine the percentage of migration (y-axis) that occurs during a certain number of hours (x-axis). For example, in spring, 50% of all recorded migration occurs during only 18 non-consecutive hours (2.5% of the total hours during the period used in this study, 1.9% of the total 2022 spring season), while the spring model predicted that 50% of total spring migration would happen in 36 non-consecutive hours with the highest MTRs (4.5% of hours in the observed period and 3.4% of the entire season). The difference between observed and predicted migration intensity is higher in autumn. In autumn, 50% of all recorded migration occurs within 26 hours with the highest MTRs (5.5% of hours in the observed period and 2.7% of the hours in the entire 2020 autumn season), while the model predicted that 50% of migration would happen within 79 hours (16.9% of hours in the observed period, 8.3% of hours for the entire season). In spring, 50% of migration ranked by MTR in descending order equals to about 10000 birds/km, while in autumn, about 13000 birds/km pass over the radar location.
Figure 5.2 Variable importance in predicting spring (upper plot) and autumn (lower plot) low-altitude migration intensity based on the variance of all other variables when one of the variables was removed from the RF model.
Figure 5.3 Spring 2022 (upper graph) and autumn 2020 (lower graph) time series used to test the performance of the model. Model predictions of MTRs (birds/km/hr) are shown in red (spring) and yellow (autumn), while the observed data is shown in dark blue.
Figure 5.4 Confusion matrices for spring (upper graph) and autumn (lower graph) created with different MTR thresholds (given in the titles of each confusion matrix). Confusion matrix tiles coloured in green (spring) and yellow (autumn) show true positives (upper left tile) and true negatives (lower right tile). Tiles coloured in dark blue show false positives (upper right tile) and false negatives (lower left tile). The numbers in the tiles represent a fraction of predicted hours (0-1) that belong to each category. The total number of hours for which the reference data was available was 706 for spring and 467 for autumn.

Figure 5.6 shows measured MTRs plotted as a cumulative seasonal percentage vs cumulative seasonal percentage of the energy production ranked by hourly migration intensity in descending order (hours with highest MTRs values first, plotted from the left side of the x-axis). Reading the x and y coordinates of points belonging to the line, we can determine the percentage of energy production lost if the curtailment was performed on a certain percentage of hours with high migration intensity. For example, in spring 2022, if the curtailments are performed in order to conserve 50% of the hours with the highest migration intensity, the amount of energy that would be lost is 0.56% of the total energy that is produced in the part of the season we used for the data analysis. In autumn 2020, this amount was 1.26% of the total. Energy production curves for other years are available in Appendix (4.A.7).
Figure 5.5 Cumulative percentage of measured MTRs (birds/km/h) for the testing year of 2022 in spring (left) and the testing year 2020 in autumn (right) for hours ranked by MTRs in descending order based on radar observations (dark blue line) and model predictions (green in spring and yellow in autumn). Hourly MTR decreases going from the left to the right side of the x-axis.

Figure 5.6 Cumulative percentage of measured MTR (y-axis) vs cumulative percentage of energy production (x-axis) for the testing year of 2020 during the measurement period in spring (left) and 2022 in autumn (right). The observations are ranked by hourly MTRs (birds/km/h) in descending order (higher MTR values on the left side of the graphs).

5.4 Discussion

Despite having a limited time series of migration data from the radar location, we demonstrate that, overall, spring and autumn models of low-altitude nocturnal migration can capture migration intensity dynamics quite well, and OOB $R^2$ values indicate that both models explain a large portion of the variance in hourly migration intensity over the southern North Sea, with the spring model performing slightly better. Confusion matrices show that more than 90% of hours in spring and more than 80% in autumn were classified correctly by our models with different MTRs as thresholds. As expected, phenology proxies and wind assistance were the top three predictors of spring and autumn migration, while the expected effect of precipitation was not captured with our models.
Although similar variables were of high importance in both seasons, we show that seasonal phenology has the highest importance in spring (Figure 5.2). In this part of the world, wind generally comes from the west, which supports the dominant migratory movement from the UK towards the Netherlands observed in spring during previous studies (Kemp et al. 2010; Bradarić et al. 2020). Because of this, spring migrants have supportive wind conditions for migration most of the time. Instead, the high importance of seasonal phenology in this season reflects that the circannual rhythm may be more important in influencing migration rates in spring than wind conditions. Nevertheless, wind assistance variables were also among the top predictors of migration intensity (Figure 5.2). Therefore, we conclude that birds still rely on higher wind assistance and choose such moments to cross the North Sea faster, sometimes exploiting higher wind speeds at higher altitudes (Chapter 4; Kemp et al., 2013). In autumn, diurnal and not seasonal phenology was amongst the top predictors. This likely reflects different migration cohorts that can cross the radar in autumn. One cohort consists of birds leaving directly after sunset from the Dutch coast, ca 23 km from the radar, and thus their daily timing would be relatively predictable, while the other cohort is migrants from Scandinavia and NW Germany (Bradarić et al. 2020). The high importance of wind assistance at the radar location and more frequent occurrence of higher migration peaks indicates that birds tend to be more selective of wind conditions in autumn, which are generally not supportive of migration in this season (Bradarić et al. 2020; Manola et al. 2020a), although species differences exist and some groups of birds fly with suboptimal wind conditions (Grönroos et al. 2012).

For over-the-land migration over the contiguous US, it was estimated that 50% of total seasonal migration occurs within 10% of migration nights (Horton et al. 2021). We show that 50% of measured migration offshore occurred within 18 hours (2.5%), with the highest MTRs in spring and 26 (5.5%) in autumn (Figure 5.5). The model predicted that 50% of migration occurred during 36 hours in spring and 79 in autumn. Although such a short period in which the majority of migration occurs is partially due to the fact that we only use part of the migration season with the highest migration intensity, it also most likely illustrates that the ecological barrier affects migratory departure decisions. Studies around large water bodies have shown that birds tend to be more selective of weather conditions when making departure decisions (Newton 2008; Deppe et al. 2015), resulting in fewer occasions when large numbers of migrants make barrier crossings. The results shown in this paragraph are based on the model trained with a combination of years which showed the best model results, and the number of hours in which curtailments should be performed to preserve 50% of migration is higher for all the other combinations (Figure 5.A.6).

Even though the model explained a high percentage of variance in migration intensity in both seasons, the percentage of correctly predicted intense migration hours was low, and the percentage of false negatives was relatively high (Figure
There are several explanations for this. First, the expected issue of having only a few years for model training meant that only a small number of intense migration nights entered our training dataset, as they generally occur only a few times during the migration season (Figure 5.A.1) (Kranstauber et al. 2022). These nights can have complex weather systems passing through the region, especially in autumn and can be very different on different intense migration nights (Manola et al. 2020a). This makes it hard for the model to “learn” to recognize such cases in the training procedure, even with applying methods for balancing the data, such as stratified sampling. A second explanation is the missing data due to radar issues, bad weather conditions (which is probably why our models could not capture the expected effect of the precipitation) under which the radar does not collect reliable information and further “shortening” of the available dataset through a rigorous but necessary filtering procedure. Often, gaps in the observed data occur when the model predicts intense migration, especially in autumn (4.2). The spring model explained more variance and had a higher percentage of correct classifications than autumn. This is most likely due to more consistent weather conditions throughout the spring migration season and the longer time series used for the model training.

Intense migration nights are of the highest priority for wind turbine curtailments, as they provide opportunities to minimize collision risk for the highest number of migrants with minimal energy loss. While we show that to protect 50% of migrants, wind turbine curtailments only have to be performed for a limited number of hours (18 in spring and 26 in autumn), the model predictions showed that the number of hours needed to protect half of the migrants in the season is higher (36 in spring and 79 in autumn). This is because the model was able to correctly predict only a small portion of the intense migration nights. Considering the fact that the model was trained with the reanalysis weather data and that the predictions used for curtailments will be based on weather forecasts, we can expect an additional error in predictions due to weather forecast uncertainty. However, when more radar measurements are available, the model can be recalibrated with the new and longer time series of data, which should improve the model performance. Therefore, the number of curtailment hours needed to protect 50% of seasonal migration will have a smaller discrepancy between the model and the observed values.

In the initial stages of wind turbine curtailments, when model predictions of intense migration are not great due to the limited time series of data, setting the right curtailment thresholds is crucial for achieving the best results. Confusion matrices created with different thresholds indicate that choosing lower MTR values increases the chance of correctly predicting peak migration, but it also increases the percentage of false positives and sometimes even false negatives, which is especially pronounced in spring. For wind turbine curtailments, it is important to strike a balance between all categories. False positives can cause unnecessary shutdowns, resulting in economic loss without conservation effect. On the other hand, false negatives mean that the turbines will not be curtailed in times of intense
migration offshore.

When discussing curtailments, it is important to mention the consequences they would have on the energy grid in terms of energy loss. With our results, we show that if we want to protect 50% of the migrants, the energy loss during the potential curtailment hours is minimal, being below 2% in both seasons (note that this is during the parts of the seasons in which the nights of high migration intensity occur), if the model can correctly predict them. This means that the most intense migration occurs at the times when wind speeds are too low for energy production.

In the current framework created by the Dutch government, wind turbine curtailment decisions will be made by a multi-step process which includes model predictions, evaluation of the expert committee and the assessment of wind conditions and potential energy production/loss. While model predictions for intense migration nights could be improved by training the models with longer time series of radar data, we see that they can already help to initiate curtailments during critical hours, especially in spring (Figure 5.5). When combined with carefully chosen thresholds and expert knowledge in ecology and meteorology, adequate conservation action can be performed, even in these early stages of offshore low-altitude forecast development. With the example from the Netherlands, we want to encourage action-oriented conservation, as the development of extensive research studies followed by carefully planned conservation actions usually cannot keep up with the pace of the environment alteration, and it is necessary to start creating conservation measures with short-term datasets and carefully tailored political decisions (Dietze et al. 2018). We propose that the framework in which prediction models are used with input from expert teams can yield significant results and help minimize the negative effect of various anthropogenic developments on wildlife.
Acknowledgements

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5. A Appendix for Chapter 5

Figure 5.A.1 Time series with migration data from the full observation periods
Figures below show the measured MTRs for February through May (spring 2019 – 2022) and August through November (autumn 2019 – 2021) seasons, of which only the part with the highest migration intensity has been used in our analysis (15 February to 1 May for spring and 1 October to 1 December in autumn). Note that the y-axes are different for each subplot.

Spring (2019-2022)
To capture circadian and circannual migration dynamics at the radar location, a proxy for seasonal and diurnal phenology was created by fitting local polynomial regression curves to hourly MTRs (birds/km/hr) grouped by day of year and hour after sunset. Curves were fitted to the full (4-year for spring and 3-year for autumn) datasets using the `loess` function of the ‘base’ R package (R Core Team 2022) and included in the models as predictors. In the plots below, the blue line represents the values which were used as phenology proxies in our models. If the days and hours of high migration intensity occur at the same time of a year or a day, the phenology proxies will have higher values for those specific moments.
5.A.2.1 Diurnal phenology

Spring

Autumn
5.A.2.2 Seasonal phenology

Spring

Autumn
Figure 5.A.3 Correlation matrices for all predictors in spring and autumn

Spring

Autumn

*glossary available in Table 5.A.2.
Table 5.A.1 Seasonal overview of the variables that were highly correlated, therefore excluded from the model.

<table>
<thead>
<tr>
<th>Spring</th>
<th>Autumn</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean sea level pressure in the UK</td>
<td>Mean sea level pressure in Denmark</td>
</tr>
<tr>
<td>Mean sea level pressure at the radar location</td>
<td>Mean sea level pressure in the N Netherlands</td>
</tr>
<tr>
<td>Accumulation due to wind assistance in France</td>
<td>Nightly difference in mean sea level pressure in Denmark</td>
</tr>
<tr>
<td>Temperature in France</td>
<td>Mean sea level pressure in NW Germany</td>
</tr>
<tr>
<td>Nightly difference in mean sea level pressure in the UK</td>
<td>Total precipitation Danmark</td>
</tr>
<tr>
<td>Temperature in the UK</td>
<td>Temperature in NW Germany</td>
</tr>
</tbody>
</table>

Table 5.A.2 Glossary of abbreviations in correlation matrices

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>acc_diff</td>
<td>(nightly) difference in accumulation</td>
</tr>
<tr>
<td>tp or P</td>
<td>total precipitation</td>
</tr>
<tr>
<td>wa</td>
<td>wind assistance</td>
</tr>
<tr>
<td>t</td>
<td>temperature</td>
</tr>
<tr>
<td>msl</td>
<td>Mean sea level pressure</td>
</tr>
<tr>
<td>UK</td>
<td>United Kingdom</td>
</tr>
<tr>
<td>F</td>
<td>France</td>
</tr>
<tr>
<td>NW</td>
<td>North-west Germany</td>
</tr>
<tr>
<td>NN</td>
<td>North Netherlands</td>
</tr>
<tr>
<td>D</td>
<td>Denmark</td>
</tr>
<tr>
<td>delta</td>
<td>(nightly) difference in weather variable</td>
</tr>
<tr>
<td>Hour_p</td>
<td>Proxy for seasonal phenology</td>
</tr>
<tr>
<td>Year_p</td>
<td>Proxy for yearly phenology</td>
</tr>
</tbody>
</table>
Partial dependence plots (PDPs) below show each of the top three predictor’s relationships with the response variable (MTR) while all the other predictors remained constant. The plots below show these relationships when the model was trained with the data from 2019 – 2022 for spring and the data for 2019 and 2021 for autumn. Grey areas around lines indicate confidence intervals (0.95), and rug plots along the bottom indicate the distribution of the data. A further explanation of these relationships can be found in the main text of the paper’s Results section.

**Spring**

![Spring plots](image)

**Autumn**

![Autumn plots](image)
Figure 5.A.5 ROC curves

The receiver operating curves (ROC) for the spring and autumn models created with a threshold of 150 birds/km/h (95th percentile of MTR values in the data used in this study). These plots show the effectiveness of the model for identifying hours with the high migration intensity while at the same time having the lowest fraction of the false positive predictions. For example, with the threshold of 73.8 birds/km/h in spring, approximately 52% of hours with the migration intensity of 150 birds/km/h can be correctly predicted with the model, with only 0.03% of false positive predictions. ROC plots can be viewed as a continuous version of confusion matrices shown in Figure 5.4.

Spring 2022

Autumn 2020
Cumulative percentage of measured MTRs for spring (left) and autumn (right) for different testing years, which were not shown in the main text of the paper. Hours are ranked by MTRs in descending order based on radar observations (dark blue line) and model predictions (green in spring and yellow in autumn). Hourly migration intensity decreases going from the left to the right side of the x-axis.
Figure 5.A.7 Energy plots

Figures below show cumulative measured MTR (y-axis) vs cumulative energy production (x-axis) for spring (left) and autumn (right) of different years, which were not shown in the main text. The observations are ranked by hourly MTRs in descending order (higher MTR values on the right side of the graphs).
Oh, relax, Kevin! I'm only pulling your leg! Of course, I brought sunscreen!
Chapter 6

Synthesis

Migration is a life history strategy which has evolved in many avian species. For many species, their migration routes cross diverse terrains, some of which may be inhospitable. One such example is the migration of terrestrial avian species over the sea. For landbirds, seas can be ecological barriers, as they do not offer opportunities for migratory stopovers, necessary for rest and refuelling. To bypass the hindrance that ecological barriers create, birds evolved different strategies to navigate these inhospitable areas (Alerstam 2001). By using radars to study nocturnal migration over the North Sea, this thesis sheds light on seasonal patterns of migration of birds over an ecological barrier and their environmental drivers. By revealing how local and synoptic weather conditions and seasonal and daily phenologies influence nocturnal bird migration over the sea, we scratch the surface of a complex system which shows seasonal heterogeneity in timing, migration intensity, departure decisions and altitudes. Throughout this thesis, it has been repeatedly shown that environmental variables such as wind assistance, time of year and temperature influence departure decisions, flight altitudes and migration intensity of nocturnal migrants. The results in this thesis give more insight into migration over one of the regions, a crossroad, within the East Atlantic flyway and inform aeroconservation in the region, necessary due to large wind energy expansion. Furthermore, they contribute to understanding migratory behaviour around the ecological barriers – inhospitable environments that birds navigate differently in different parts of the world.

6.1 Navigating the North Sea – an ecological barrier of the East Atlantic Flyway

Even though ecological barriers pose a considerable risk for migratory birds by increasing their mortality through exhaustion, starvation, predation, collision and harsh environmental conditions, birds have evolved physiological and behavioural strategies to successfully navigate them (Alerstam, 2001; Bairlein et al., 2012; Hawkes et al., 2011). The risk of crossing a barrier can be minimised by having enough fuel loads (Schmaljohann & Naef-Daenzer, 2011) and choosing supportive weather conditions (Bulte et al. 2014; Loonstra et al. 2019; Nourani et al. 2021). When these two criteria are fulfilled, barrier crossing, which considerably reduces the time needed for migration compared to circumnavigating them, can be performed quickly and relatively safely. The speed of migration has higher stakes in spring compared to autumn, as birds return to their breeding grounds and need to compete for the best breeding territories, making earlier arrival preferable (Kokko, 1999).
The North Sea can pose a smaller or larger barrier for migratory birds, depending on the migratory axis they use to cross it. For birds that perform direct crossing from Norway and continue alongside the West coast of the Netherlands, the distance they have to cross in one go is around 700 km. Migrants travelling between Denmark and other parts of Scandinavia and southern Europe and Africa must cross around 500 km. In comparison, those travelling between the southwestern coast of the Netherlands and the UK cross approximately 200 km in one go. In Chapter 2, we show that birds embark on journeys across the sea when they experience higher wind assistance at potential departure locations and in Chapter 3, we demonstrate that intense migration nights occur when high-pressure systems, thus stable weather conditions, dominate the region. This was evident even for migrants performing the shortest crossing between the Netherlands and the UK.

In comparison with larger ecological barriers that birds experience on their migratory journeys, such as the Sahara Desert (ca 2500 km), Atlantic (more than 4000 km), and Pacific ocean (ca 11000 km), the North Sea, especially the distance between the Netherlands and the UK could be considered negligible, as birds can cross within a single night of the flight. However, compared to migration over land in the region (Kemp 2012), we observe a lower number of nights with extremely high migration intensity (Chapters 2, 3 and 5), which can indicate that birds are more selective of weather conditions when embarking on journeys across the sea, even with short distances. Such selective behaviour has been observed in birds that cross the Baltic Sea (Sjöberg et al. 2015) or the Gulf of Mexico (Deppe et al. 2015), which are ecological barriers of similar size to the North Sea. In Chapter 2, we show that, throughout most of the spring season, wind conditions at departure in the UK support migration over the North Sea. However, on nights with calmer weather conditions, migration was more intense, showing that birds still select weather conditions to arrive safely on the other side of the barrier. As indicated in Chapter 3, this does not necessarily have to be only due to more favourable wind assistance but better regional synoptic conditions, which bring more dry and stable weather. In autumn, weather conditions that support migration are a rare occurrence. When they occur, birds fly in great numbers, creating much higher migration peaks than in spring (Chapters 3 and 5). This, however, does not mean that birds do not fly during the rest of the migration season. In Chapter 2, we show that birds with slightly higher airspeeds migrated even with suboptimal weather conditions but chose to fly with lower wind speeds to decrease the magnitude of the negative wind assistance (Chapter 2). A similar effect has been observed in Chapter 4, when birds, once aloft, chose altitudes with lower wind speeds if the wind assistance was negative and climbed up to utilise higher wind speeds if the winds were generally supportive of migration. Higher altitude migration was mainly observed in spring, the season with the abundance of supportive wind conditions and more constrained migration timing.

In regions where weather regimes create conditions that are generally supportive
of migration in one season but not in the other, birds can navigate the same ecological barrier differently, for example, crossing the barrier in one season and circumnavigating in other (Bradley et al., 2014; Tøttrup et al., 2012). Alternate routes among seasons are known as loop migration. By modelling migration across the North Sea in Chapter 2, we demonstrate that the two main migratory axes do not show seasonal reversal: the majority of migratory movement in spring is between west and east at our radar location, while the majority in autumn is between northeast and southwest. A question that naturally arose from this observation is: how did the birds flying to the Netherlands from the UK in spring arrive in the UK in autumn? Could it be that they perform loop migration? In autumn, birds seem to fly following the coast of the Netherlands, flying towards the southwest and presumably crossing the North Sea to the UK at the most narrow site, south of our radar location. In spring, birds then cross the North Sea directly from their departure locations due to favourable wind conditions, performing seasonal loop migration. This has been suggested earlier in the pioneering radar studies of bird migration in the North Sea basin by Lack (1959) and Eastwood (1967), and the topic has been re-opened again by Buurma (1987). However, the lack of radar data from the UK and southern parts close to the Dutch coast made this impossible to test in the current research.

Another interesting observation of migration directions in the North Sea is the limited migration along the NE-SW axis in spring, as this is the dominant axis of migratory movement in autumn. Nocturnal migration patterns observed by weather radars at a more inland location (de Bilt) in the Netherlands indicate that the predominant movement in spring is towards NE. However, the coastal weather radars do not mirror this (Kemp, 2012). There are two explanations for this discrepancy. The first is that in spring, the NE-SW migration axis simply occurs more inland, being entirely missed by offshore radars. Second, considering that the weather radars have a longer detection range, thus covering higher altitudes than the bird radars, this movement may occur at higher altitudes in spring, flying above the detection range of offshore bird radars.

When discussing the North Sea as a barrier to the migratory movement of birds, the ecological aspects and the added barrier factor of anthropogenic alterations must be taken into account. We scratched the surface of understanding the migratory behaviour around the southern North Sea and revealed many intricacies on a seasonal level, which are most likely the product of different weather regimes but could also be a result of other factors such as birds’ physiological condition (Sandberg & Moore 1996). As indicated at the beginning of this section, strategies to navigate a barrier have been developed over many years. The added factor of anthropogenic changes, such as wind farm development within an ecological barrier, could trigger the evolution of alternative migration routes (Alerstam, 2001). Alternative migration routes could lead to an indirect increase in mortality through exhaustion or lower reproductive success due to not arriving on time at the
breeding grounds (Baker et al., 2004). On the contrary, using the same migratory routes could lead to increased direct mortality through collisions (Desholm, 2009). Understanding the navigation of ecological barriers in different seasons can be used to inform conservation measures. It can steer the conservation action, for example, by avoiding expensive wind turbine curtailments in certain parts of the North Sea if the barrier crossing occurs in a different place. This is especially important in the later stages of the offshore wind farm development in the North Sea when the turbine density will be high, and a deeper understanding of fine-scale ecological barrier navigation can facilitate cost-effective conservation.

6.2 Radar data quality

While radar is a great tool for studying mass movements of aerial organisms and increasingly serves as an indispensable tool in biological conservation, there are still limitations reflected in its spatial coverage, varying data quality, and inability to identify organisms to the species level (Bauer et al. 2019; Hüppop et al. 2019). So far, only a few studies before this thesis have been using radars located offshore to study patterns of bird migration (e.g. Hüppop et al. 2006; Fijn et al. 2015; Krijgsveld et al. 2015). Collecting radar data offshore has proven to be challenging due to large amounts of reflections from sea waves and other types of noise that clutter the data. Such reflections, however, can be flagged based on their characteristics and excluded from the analysis. Radars used in this study already had automated clutter filters included as part of their software which discarded tracks belonging to sea wave reflections and other types of clutter such as rain, static clutter or reflections from rotating turbines. However, due to similarities between echo characteristics of birds and different clutter types, there was a certain number of tracks that mistakenly entered the database as bird tracks.

Throughout this thesis, constant effort has been made to produce data of the best quality by developing different types of filtering. This was a collaboration between developers of the radars and a team at the University of Amsterdam, and it required numerous hours of explorative analysis and comparisons in order to come up with the best methods for cleaning the data. These methods can be found in the Materials and Methods section of each chapter in this thesis, but also in Fijn et al. (2015) and supporting information therein, Krijgsveld et al. (2015) and van Erp et al. (2021). While these steps have been developed and are currently in use by the University of Amsterdam team, thanks to the collaboration with Robin Radar, they might subsequently be implemented in the radar software.

Improving radar data quality is a continuous process that evolves with technological advancements and new data insights. However, analysing different biological phenomena, such as bird migration during rain events or harsh winds, remains challenging. Under such weather conditions, radar data quality deteriorates, and observed patterns are unreliable. This is because such weather conditions create
noisy environments in which the radar can pick up more echoes, but also due
to limitations of the current radar technologies. As the number of radars used in
ecological studies increases and new knowledge is gained through exploratory
analysis and ground-truthing, more intricate filtering methods will be developed.
Furthermore, as there are limits to what current radars can record, the development
of new radar technologies will allow researchers to perform studies of good enough
quality under different weather conditions.

6.3 Action plan for aeroconservation

Well-established, adequate conservation measures often take years to implement,
and their execution generally occurs after the adverse effects have already taken a
toll on a specific species or ecosystem. This is why there is general agreement that
success in environmental protection on any scale lies with the ability to anticipate
what kind of effect a certain environmental alteration will have or when a certain
event will occur and act preventively (Clark et al., 2001). Forecast models make
such anticipations possible and can help create conservation plans in advance.
Most of the existing forecast models, however, are scenario-based projections and
are currently not balanced with the conservation needs, which require more near-
term projections which would initiate immediate conservation action (Dietze et al.,
2018).

Unlike in terrestrial and freshwater habitats, where conservation steps have
been relatively well established (Fazey et al. 2005; Orlikowska et al. 2016),
aeroconservation is still in its infancy. As explained in Chapter 1, this is mainly due
to the aerosphere not having the same habitat status as the other two. However,
since airspace is becoming crowded with different types of infrastructure and
aircraft, aeroconservation has been quickly catching up in the recent decade. This
is especially the case in large urban centres where illuminated high-rise buildings
attract birds that collide with them (van Doren et al., 2017). Within the last couple
of years, measures to prevent adverse effects of wind turbine infrastructure on aerial
wildlife are increasingly in place. However, most efforts have focused on individual
wind farms with the aim of protecting specific species (Hayes et al., 2019; McClure
et al., 2021).

Combining the increasing need for near-term ecological forecasts and
aeroconservation due to the rapid development of wind energy infrastructure, the
research conducted in this thesis was a part of a unique framework developed by
the Dutch government that combined input from various stakeholders to achieve a
common goal – to decrease the number of collisions of nocturnally migrating birds
with rotating offshore wind turbines. Studies conducted as part of Chapters 2, 3
and 4 aimed to increase the fundamental knowledge of nocturnal bird migration
patterns over the ecological barrier of the southern North Sea, which was relatively
scarce. Additionally, these studies aimed to identify moments in time in which the
conservation measures would need to be performed to maximise a safe passage for nocturnally-migrating birds with minimal repercussions on the energy market by looking into which environmental factors drive the occurrence of low-altitude intense bird migration and how often. This was the first necessary step of the conservation framework. The second step of the framework is presented in Chapter 5. It considers using the knowledge about environmental drivers of nocturnal bird migration gathered in previous chapters to develop near-term forecasts that would use weather variables from weather forecasts to predict migration intensity at the radar location 48 hours in advance. This brings us to the next step of the framework, which is the expert committee consisting of avian ecologists. At least in the initial stages, the expert committee will evaluate the model output and make a decision on whether to initiate shutdowns or not. As guidelines, they will use migration traffic rate thresholds developed by an external ecological consultant at the same time during which the model was developed. When the forecasts predict migration traffic rates that exceed the threshold, the expert committee will evaluate other parameters, such as confidence of the model prediction, accuracy of the weather forecast and energy production under forecasted weather conditions, and, together with energy grid operators, make a decision whether to curtail the wind turbines. If the decision to curtail has been made, a blanket curtailment of all operational wind turbines in the Zeeuwse and Hollandse Kust zone of the Dutch North Sea will be performed on a nightly basis. The decision to curtail occurs ca 48 hours in advance of the actual curtailment. During that time, the energy grid operators must make necessary adjustments to keep the grid stable and ensure enough energy to prevent blackouts (calamities). At this point, they can still decide to stop the curtailment if a calamity is possible. The schematic overview of the framework can be found in Figure 6.1.

As demonstrated in Figure 6.1 and the framework description above, blanket wind turbine curtailments of this magnitude can only be performed by coordinated action between various stakeholders. This involves researchers, policy-makers, consultants, governmental and non-governmental organisations and private institutions. A vast majority of conservation literature is focused on describing the states of ecosystems and mechanisms that cause change, but only a handful is used to develop strategies and base policies on (Williams et al. 2020). Besides financial reasons, this is, I believe, often due to a lack of communication between stakeholders and unwillingness to initiate the development of complex procedures, especially within limited time frames, as is necessary in a rapidly changing world. Throughout the development of this thesis, I was actively part of a working group to create conservation action. By working on the common goal together, from various perspectives, we were able to understand the needs and limitations of each side and find the best ways to accommodate them while striving to provide the most robust results. Although working together was challenging at times, we managed to develop a conservation action on which we will continue to work in the coming years. An interdisciplinary approach and knowledge exchange between stakeholders are key to a successful future of environmental management.
Figure 6.1 Framework for blanket wind turbine curtailments during intense bird migration events over the North Sea. Each box indicates actions performed by various stakeholders in order to achieve the final goal of cost-effective aeroconservation. Arrows represent a workflow and indicate connections between different stakeholders.

Due to extensive offshore wind energy development in the southern North Sea, studies conducted as part of Chapters 2, 3 and 4 aimed to identify the frequency of necessary wind turbine curtailments by looking into which environmental factors drive the occurrence of low-altitude intense bird migration and how often. In Chapter 4, we demonstrate that the majority of nocturnal bird migration over the North Sea occurs at altitudes that overlap with those of wind turbines and that wind turbine curtailments suggested as part of the aeroconservation plans are necessary to allow for a safer passage of nocturnal migrants. Since, unlike in spring, intense nocturnal migration in autumn mainly occurs at low altitudes, it would be easy to suggest that the curtailments are of special importance in autumn. However, care should be taken with such suggestions since intense migration can, at the same time, also occur at low altitudes in high numbers. We need more research to understand fine-scale changes in migration patterns, and until then, we should focus conservation efforts on all nights with intense bird migration.

6.4 Future outlook

While data collection by already deployed offshore radars continues into the future, additional radars will be positioned at different offshore locations in the North Sea. The growing radar network and respective time series create opportunities not only for expanding our knowledge about bird migration at the crossroad of migratory axes within the East-Atlantic flyway but also for a comparison of patterns and underlying mechanisms that influence these patterns between different radars.
Longer temporal data coverage will allow for the update of the current migration forecast models and improve predictions of migration intensity. This is in line with the advocated type of conservation, which is action-based and does not wait for years of data collection to pass. Instead, it focuses on developing conservation measures when the minimal data requirements are achieved and improving them as new insights are gained (Dietze et al., 2018).

Combining data collected by different systems is challenging. In the future, it would be of great value to develop methods of combining tracking and weather radar data to gain a complete picture of migration systems in the region. These radars complement each other in what they observe, as tracking radars cover lower altitudes that weather radars miss and weather radars have longer ranges allowing to record migration over larger areas. Combining these systems, which cover areas at sea and on land, with spatially explicit simulation models, will give more opportunities to compare migratory behaviour between different topographies. We could, even on a fine scale, study birds’ response to coastlines, whether migration patterns differ above the sea and land and why, and further explore the theory of loop migration.

Data collected by radars at different locations in the North Sea allows us to look for similarities in migration patterns between different locations but also their differences. Potential differences could exist in local environmental factors that drive diverse migration patterns, even though birds respond similarly to them. Alternatively, environmental factors can be similar, but differences in migration patterns might occur due to behavioural differences caused by different migration strategies in different species. While some of these things are hard or impossible to test with just the radar data, a combination of insights gained through the radar observations and tracking technologies, such as the growing network of MOTUS automated radio-telemetry (Brust et al. 2019; Brust & Hüppop 2021), could open new gates for exploration of fine-scale bird behaviour during mass-migration events. However, we can at least infer the origin of potential differences with the data from a wide range of locations. While important and interesting from a fundamental ecological and barrier crossing perspective, filling this knowledge gap also has important implications for wind farm management. Describing migration patterns at different locations and disentangling their underlying mechanisms will show if there is a need for developing separate migration forecast models for different regions in the North Sea.

6.5 Conclusions

The aim of this thesis was to understand how environmental factors influence spatio-temporal migration patterns of nocturnal bird migration in the airspace over an ecological barrier to develop near-term forecasts that would be used to inform offshore wind turbine curtailments during intense nocturnal bird migration. In Chapter 2, we developed trajectory models to explore how birds navigate the
ecological barrier of the North Sea and what influences their departure in high numbers. We reveal that seasonal wind regimes drive intense bird migration across the North Sea and that birds navigate the barrier differently in different seasons, following different migratory axes, which indicates that they might be performing loop migration. In Chapter 3, we learnt that it is not only wind regimes but rather high-pressure systems in the region which bring more stable weather conditions (thus also more supportive winds) that influence the occurrence of migration peaks. Chapter 4 shows that the majority of migratory movement across the North Sea occurs at low altitudes (below 300 m), except for intense bird migration that occurs in spring when generally positive wind assistance prompts birds to make use of higher wind speeds at higher altitudes to speed up their migration and arrive on breeding grounds on time. Finally, in Chapter 5, we show that migration intensity across the sea can successfully be predicted even with datasets of limited temporal coverage. We also show that near-term forecast outputs, in combination with relevant policies, can be used to inform offshore turbine curtailments necessary to reduce collision risk between migratory birds and rotating turbine blades. We demonstrate a detailed curtailment plan based on the results of this thesis and hope to encourage action-based (aero)conservation which is necessary in a rapidly changing world.
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Summary

The air is occupied by many forms of life: from passive occupants, such as pollen and microorganisms that get aerosolised and carried by the wind, to active occupants, namely insects, bats and birds, that perform various types of movement by thrusting through the airspace. Life in the air occurs in the lowest part of the atmosphere, the troposphere. To enhance the ecological relevance of this part of the atmosphere, the term aerosphere has been coined, and the research on life in the air has been termed aeroecology. Coining this terminology has helped increase efforts to give the airspace a habitat status and include it in conservation policies.

The aerosphere is increasingly getting crowded by man-made structures and flying objects such as power lines, aircraft, drones, communication towers, high-rise buildings and wind turbines. These pose various direct and indirect threats to aerial organisms, mainly through collisions, route alteration and habitat fragmentation. For aerial organisms, which are not used to flying in cluttered environments, the existence of such barriers can prompt inadequate responses, which can lead to decreased survival. Therefore, it has been suggested that timely performed conservation measures can help decrease the negative effects of man-made structures on aerial wildlife.

Such conservation measures are of special importance in areas with a high abundance of animals, e.g. where movement corridors of different species overlap with substantial infrastructure development. An area of this kind occurs within the East Atlantic flyway. The North Sea, which represents an important migratory crossroad within this flyway, is experiencing extensive offshore wind energy development. The current wind turbine capacity of around 25 GW in this area is set to increase 10-fold by 2050. Considering that birds that migrate within the East Atlantic flyway are experiencing declines due to various anthropogenic causes, the Netherlands decided to implement wind turbine curtailments in the Dutch North Sea to minimise the negative effects on migratory birds.

Within the East-Atlantic flyway, the majority of landbirds, primarily songbirds, migrate at night. Nocturnal migration occurs during spring and autumn and usually starts shortly after sunset. In autumn, birds from Scandinavia and North-western Europe travel to warmer climates of southern Europe and Africa, flying over the North Sea in a south-westerly direction. Another migration axis over the North Sea is between North-eastern Europe and Britain in a west-south-westerly direction. It is assumed that migrants use the same migratory axes with reversed migration directions in spring to reach their breeding grounds. However, this has never been quantified.

Weather conditions at different temporal and spatial scales are one of the main proximate drivers of variation in day-to-day migration. Out of weather variables,
winds, temperature, precipitation and air pressure are considered the most important. Winds influence birds’ departure decisions, flight altitudes and migration speed. The temperature increase in spring and decrease in autumn is correlated with the onset of migration and can drive flight altitude distributions (e.g. birds will fly higher when the temperature is high). Changes in air pressure affect migration departure time and flight altitudes, while precipitation has an inhibiting effect on migration.

Most studies on the influence of weather on bird migration have been conducted on land, as it is methodologically less challenging to explore. At sea, which can be an ecological barrier (areas that either physically hinder movement or are environments with lower habitat quality for a species, making it risky to cross), birds may be more selective of weather conditions, as wrong departure decisions have greater consequences on survival. As seas are being exploited for extensive wind energy development, it is becoming increasingly important to understand the drivers of nocturnal bird migration offshore to design conservation measures for preventing or minimising adverse effects.

We use the North Sea as a study system to understand how phenology (time of day and year) and environmental factors (local and synoptic weather conditions) influence spatiotemporal patterns of nocturnal bird migration in the airspace above an ecological barrier. We further use this knowledge to develop near-term bird migration forecasts that would be used for wind turbine curtailments during intense nocturnal bird migration. We thus aim to provide tools for minimizing bird collisions offshore with a minimal impact on the energy market production, performing one of the crucial steps for dynamic aeroconservation of highly-mobile aerial organisms.

For this thesis, migration data was collected offshore by two bird radar systems. In addition to the data collected by the above-mentioned radar systems, the research in this thesis relies on mechanistic, statistical and machine learning models. These models were used to better understand the relationship between weather and migration as they can help disentangle complex processes that occur over large spatial and temporal scales.

Sometimes, when crossing ecological barriers, birds can navigate them differently in different seasons, depending on, for example, the availability of tailwinds. In Chapter 2, we investigated the influence of seasonal wind regimes on birds’ departure decisions during migration in the southern North Sea and whether birds used the same migration axes in both seasons. We used migration data collected by a radar located 18 km off the NW Dutch coast to quantify nightly migration intensity, ground speeds and track directions. We developed a mechanistic simulation model to infer potential departure locations of birds on nights with intense bird migration and test if the departure decisions were associated with supportive winds on land. Comparisons of migration headings calculated from the radar and wind data show
during nights of intense migration in spring, the main migration axis is W-E, from the UK to the Netherlands. Prevailing winds from WSW in spring support a direct crossing of the North Sea. In autumn, intense migration nights are characterised by departures from Denmark, Germany and the north of the Netherlands, with migrants following the NE-SW migration axis towards southern Europe. Winds in this season are generally not supportive of migration. However, intense migration is observed on nights when wind assistance is above the seasonal mean. Different migratory axes in spring and autumn seem to be driven by the seasonal wind regimes, suggesting that birds use seasonally different migration routes in the region.

In Chapter 3, we increase the spatial extent of analysis of the influence of weather conditions on departure decisions from local to synoptic. We perform a spatial analysis of anomalies at the synoptic scale and provide a descriptive analysis of the synoptic weather conditions over NW Europe to look at how they influence migratory departure decisions. We compare synoptic weather conditions between the nights with high and low migration intensities, and we also compare them with prevailing climatology to describe the synoptic drivers of high-intensity migration events. As in Chapter 2, we use the data collected by the radar located 18 km off the NW Dutch coast. We show that nights dominated by high-pressure systems with tailwinds in spring and side-winds in autumn create the best conditions for intense nocturnal bird migration. We also demonstrate that intense migration regularly occurs on nights free of rain and frontal systems. At the same time, temperature, relative humidity and cloud cover have only a secondary role in the intensity of bird migration.

Once aloft, weather conditions have been shown to influence the altitude distribution of migrating birds. These influences can be different depending on the region, topography and bird species. In Chapter 4, we use tracking radars at Borssele and Luchterduinen wind farms, located 22 and 23 km off the western Dutch coast, to describe the vertical distribution of nocturnal bird migration over the North Sea and identify its environmental drivers. The special focus is on defining the weather variables that drive a low-altitude flight relevant for wind turbine curtailment procedures to reduce bird fatalities. We show that birds migrate at higher altitudes in spring, flying above the wind turbine rotor tip of 300 m more often and in higher numbers than in autumn. Even though on most nights in both seasons, most migrants predominantly fly at low altitudes, intense migration nights in spring were characterised by high-altitude (above 300 m) flight. Day of year was used as a proxy for seasonal phenology, and its relationship with low-altitude migration suggests that different species migrate at different altitudes. Day of year and wind assistance are identified as the main drivers of low-altitude migration in both seasons, with the addition of temperature in autumn. We show that birds choose altitudes with wind conditions that are less prohibitive of migration in both seasons, and the fraction of low-altitude flight increased with increasing temperature in autumn. We conclude that mitigation measures offshore may be more effective during autumn than spring.
since birds often fly above the turbines. However, this should be taken with care, as the migration intensity can still be high at low altitudes in spring and relevant for the performance of mitigation measures.

In **Chapter 5**, we combine the fundamental knowledge on environmental drivers of spatiotemporal patterns of nocturnal bird migration gathered in the previous chapters and use it to develop near-term forecasts of low-altitude (up to 300 m) nocturnal bird migration over the North Sea. Near-term forecasts are considered important for the future of conservation. They can help anticipate environmental changes and ecological and environmental phenomena on smaller temporal scales and create immediate actions to avoid or minimise the adverse effects on the environment. For the model training, we calculate migration intensity from the tracking radar data collected off the western Dutch coast and use it as a response variable in a random forest regression model, while weather and phenological variables are used as predictors. By developing these models, we aim to understand which environmental drivers influence the dynamics of migration intensity, and we test how well the model can predict hourly migration intensity. We demonstrate that the model classified migration hours by intensity correctly in more than 90% of cases in spring and more than 80% in autumn. We further show that the number of correctly predicted intense migration hours was low, likely due to the short period data has been collected for. By looking into cumulative percentages of measured migration intensity, we show that to minimise collision risk for 50% of migrants, curtailments should be performed during only 18 hours in spring and 26 in autumn (2.5 % of the migration hours in spring and 5.5 % in autumn). However, this can differ between the years. By performing the curtailments during the fraction of the migration season mentioned above, the energy loss would be 0.56% for spring and 1.26% for autumn. We conclude that the overall model performance is good in both seasons and that near-term ecological forecasts developed with limited datasets combined with expert knowledge are necessary to speed up conservation efforts in areas with wind energy development.

Throughout this thesis, we repeatedly show the importance of different environmental factors in shaping the seasonal patterns of nocturnal bird migration over an ecological barrier. Wind assistance and temperature on both local and synoptic scales, as well as the time of year, influence birds’ departure decisions, flight altitudes and migration intensity during nocturnal migration over the North Sea. By revealing relationships in such a complex system, we not only come one step closer to understanding bird behaviour at a migratory crossroad within the East-Atlantic flyway, but we also lay a foundation for aeroconservation in the region. From a personal experience of actively participating in a working group to create conservation action, I argue that the interdisciplinary approach and knowledge exchange between stakeholders is key to a successful future in environmental management.
Samenvatting
Translated by: Marwa Kavelaars and Berend Wijers

De lucht zit vol leven: van stuifmeel en micro-organismen, die door de wind worden verspreid, tot insecten, vleermuizen en vogels, die zich actief door de lucht voortbewegen. Al deze levensvormen bevinden zich vooral in het laagste deel van de atmosfeer, de troposfeer. Om de ecologische relevantie van dit deel van de atmosfeer te benadrukken, is de term *aerosphere* in het leven geroepen. Het daarbij behorende onderzoek naar leven in de lucht wordt *aeroecology* genoemd. Door het gebruik van deze terminologie is er meer aandacht voor het feit dat ook de lucht een habitat is voor leven en dat daar rekening mee moet worden gehouden bij het beleid voor natuurbescherming.

In de *aerosphere* wordt steeds meer ruimte door de mens ingenomen. Zo worden er hoogspanningslijnen, flatgebouwen en windturbines gebouwd, en is er een enorme toename aan vliegende objecten zoals vliegtuigen en drones, met directe en indirecte gevaren voor de organismen in de lucht. Deze obstakels vormen een risico door botsingen, vogels moeten hun vliegroutes wijzigen, en er is sprake van habitatfragmentatie. Voor organismen, die niet gewend zijn om door overvolle lucht te vliegen, kunnen deze obstakels ervoor zorgen dat ze geen optimale keuzes maken, hetgeen zou kunnen leiden tot geringere overlevingskansen. Om de negatieve effecten van deze menselijke bouwwerken en activiteiten in de lucht te verminderen, kan het helpen om hier tijdig rekening mee te houden bij het implementeren van beschermingsmaatregelen.

Zulke beschermingsmaatregelen zijn vooral belangrijk in gebieden waar intensieve vogeltrek overlapt met hoge dichtheid van infrastructuur. De Noordzee is zo’n voorbeeld omdat hij enerzijds deel uitmaakt van de Oost-Atlantische *flyway* maar anderzijds ook een gebied is waar een enorme hoeveelheid windenergie wordt voorzien. In dit gebied ligt de huidige windenergiecapaciteit rond de 25 GW en de verwachting is dat dit in 2050 vertienvoudigd zal zijn. Vogels die gebruik maken van de Oost-Atlantische *flyway* nemen door verschillende menselijke invloeden enorm in aantal af. De Nederlandse overheid heeft daarom besloten om de windturbines in de Noordzee bij intensieve vogeltrek tijdelijk stil te zetten om de negatieve effecten op trekvogels te beperken.

Het merendeel van de vogels die langs de Oost-Atlantische *flyway* trekken, voornamelijk zangvogels, vliegt ’s nachts. Nachtelijke vogeltrek begint vlak na zonsondergang en vindt voornamelijk plaats in de lente en herfst. In de herfst vliegen vogels vanuit Scandinavië en Noordwest-Europa over de Noordzee in zuidwestelijke richting naar warmere gebieden in Zuidwest-Europa en Afrika. Er zijn ook vogels met een trekroute naar westzuidwest, die vanuit Noordoost-Europa over de Noordzee naar Groot-Brittannië vliegen. Tot op heden wordt ervan uitgegaan dat trekvogels in de lente dezelfde route terugnemen om weer op hun broedplek te
komen, maar dit is nooit bewezen.

De belangrijkste oorzaak voor variatie in trekintensiteit tussen dagen zijn de weersomstandigheden op verschillende tijd- en ruimteschalen. Hierbij worden wind, temperatuur, neerslag en luchtdruk als de belangrijkste variabelen beschouwd. De wind beïnvloedt het moment van vertrek, de hoogte waarop vogels vliegen en hun vliegsnelheid. Vogels beginnen hun trektocht wanneer de temperatuur in de lente stijgt en in de herfst wanneer deze daalt. De temperatuur kan ook de vlieghoogte beïnvloeden; zo vliegen vogels vaak hoger als de temperatuur hoog is. Ook veranderingen in de luchtdruk spelen een rol bij de vlieghoogtes en de beslissing wanneer te vertrekken, net zoals neerslag, die er vaak voor zorgt dat vogels hun trek uitstellen.

Het meeste onderzoek naar de invloed van de weersomstandigheden op vogeltrek is boven land uitgevoerd, aangezien dit methodologisch een stuk gemakkelijker is. Een zee kan echter een ecologische barrière vormen. Een ecologische barrière is een gebied dat de vogeltrek fysiek belemmert of een heel lage habitatkwaliteit heeft zodat het riskant is er overheen te vliegen. Bij een barrière, zoals de zee, zou het kunnen dat vogels selectiever zijn in het kiezen van de juiste weersomstandigheden. Een foute vertrek-keuze kan grote gevolgen hebben op hun overlevingskans. Het wordt steeds belangrijker om erachter te komen welke factoren de nachtelijke vogeltrekintensiteit over water bepalen, zodat de juiste beschermingsmaatregelen getroffen kunnen worden om negatieve gevolgen van toenemende windenergie op zee te voorkomen of anders te beperken.

Voor het onderzoek in dit proefschrift gebruiken we de Noordzee als studiesysteem om te begrijpen hoe fenologie (tijd van de dag en jaar) en omgevingsfactoren (lokale en synoptische weersomstandigheden) ruimtelijke en temporele patronen van nachtelijke vogeltrek boven een ecologische barrière (de zee) beïnvloeden. Deze kennis kan gebruikt worden om korte termijn voorspellingen te doen over de intensiteit van de vogeltrek om zo tijdens nachten met veel vogeltrek windturbines stil te kunnen zetten. Op deze manier proberen we om hulpmiddelen te ontwikkelen die niet alleen de kans op vogelbotsingen met windturbines op zee beperken, maar ook de impact van de beschermingsmaatregelen op de energieproductie minimaliseren. Zo leveren we een cruciale bijdrage aan de dynamische bescherming van vliegende organismen.

Voor dit proefschrift zijn gegevens over vogeltrek op zee verzameld met behulp van twee typen (vogel)radarsystemen. Daarnaast worden er mechanistische, statistische en machine learning modellen gebruikt om inzicht te verkrijgen in de relatie tussen weersomstandigheden en vogeltrek. Deze modellen kunnen helpen om complexe processen te ontrafelen die op grote ruimte- en tijdsschalen plaatsvinden.

In verschillende seizoenen steken vogels de barrières soms op een andere manier
over, afhankelijk van bijvoorbeeld of ze de wind in de rug hebben. In *hoofdstuk 2* hebben we onderzocht of seizoensgebonden windrichtingen invloed hebben op de keuzes die vogels maken tijdens de vogeltrek in het zuidelijke deel van de Noordzee en of vogels dezelfde trekroutes gebruiken in de lente en herfst. Om de nachtelijke trekintensiteit, trekrichting en vliegsnelheid te kwantificeren is trekdata verzameld met een radar die zich op 18 km vanaf de noordwestelijke Nederlandse kust op zee bevond. We hebben een mechanistisch simulatiemodel ontwikkeld om de potentiële vertreklocaties van vogels tijdens nachten met intensieve vogeltrek te bepalen en om te testen of de keuze om te vertrekken gerelateerd kan worden aan wind omstandigheden die de vogels zouden kunnen ondersteunen bij hun trek. Vergelijkingen van trekrichtingen tussen herfst en lente berekend met radar- en windgegevens laten zien dat in de lente tijdens nachten met intensieve trek de voornaamste trekrichting van het westen naar het oosten is (van het Verenigd Koninkrijk naar Nederland). Heersende winden uit het westzuidwesten in de lente ondersteunen het oversteken van de Noordzee van oost naar west. In de herfst zijn nachten met intensieve trek gekenmerkt door vertrek vanuit Denemarken, Duitsland en het noorden van Nederland met vogels die vanuit het noordoosten in zuidwestelijke richting naar Zuid-Europa vliegen. In de herfstperiode is er weinig rugwind om vogeltrek te ondersteunen, en intensieve trek zien we tijdens nachten waarin de windondersteuning sterker is dan gemiddeld. Verschillen in trekrichtingen in de lente en herfst lijken samen te hangen met seizoensgebonden windrichtingen. Dit suggereert dat vogels afhankelijk van het seizoen andere trekroutes gebruiken.

In *hoofdstuk 3* verruimen we de ruimtelijke schaal van de analyse van weersomstandigheden op het besluit van de vogels om te vertrekken van lokale naar synoptische schaal. Bij synoptische schaal wordt er rekening gehouden met de samenhang van weersomstandigheden over continentale schaal. In dit hoofdstuk voeren we een ruimtelijke analyse uit waarbij we kijken naar ongewone weersomstandigheden op synoptische schaal. Daarnaast gebruiken we de synoptische weersomstandigheden in Noordwest-Europa voor een beschrijvende analyse om te zien hoe deze de beslissing van vogels om te vertrekken beïnvloeden. Door eerst de synoptische weersomstandigheden tussen nachten met hoge en lage trekintensiteit te vergelijken en deze vervolgens ook met de op dat moment heersende klimatologie te vergelijken, kan op een grotere schaal bepaald worden welke factoren van belang zijn voor nachten met een hoge trekintensiteit. Voor deze analyses wordt data van dezelfde radar gebruikt als in *hoofdstuk 2*. In de lente vond de hoogste trekintensiteit plaats tijdens nachten met hogedrukgebieden en rugwind, in de herfst speelde de zijwind een belangrijke rol. Verder blijkt dat intensieve trek zich vooral voordoet op nachten zonder regen en kou- of warmtefront. De temperatuur, vochtigheid van de lucht en het wolkendek spelen slechts een secundaire rol als het op de intensiteit van de vogeltrek aankomt.

Ook wanneer vogels tijdens de trek eenmaal in de lucht zijn, worden ze door weersomstandigheden beïnvloed. De mate waarin deze omstandigheden van invloed
zijn, kunnen echter verschillen afhankelijk van de regio, topografie en vogelsoort. In hoofdstuk 4 worden de gegevens van de radars in de windparken Borssele en Luchterduinen gebruikt, die respectievelijk 22 en 23 km vanaf de west kust in zee staan. Met deze radars kan de hoogteverdeling van nachtelijke vogeltrek boven de Noordzee worden bestudeerd en kan worden bepaald welke omgevingsfactoren deze verdeling beïnvloeden. In dit hoofdstuk ligt de nadruk op het definiëren van de weersomstandigheden die ervoor zorgen dat vogels op een lagere hoogte vliegen, hetgeen relevant is voor het tijdelijk stilzetten van windturbines om vogelsterfte te verminderen. Wij laten zien dat vogels in de lente vaker dan in de herfst en in grotere aantallen hoger dan 300 m trekken, de hoogte van de windturbines. Hoewel vogels in de meeste nachten van beide seizoenen onder de 300 m vliegen, zien we in de lente tijdens nachten met hoge intensiteit wél meer vogels boven de 300 m. De dag van het jaar werd gebruikt als proxy-variabele voor seizoensgebonden fenologie en de relatie daarvan met trek, die op lagere hoogte plaatsvond, suggereert dat verschillende vogelsoorten op andere hoogtes trekken. De dag van het jaar en de windomstandigheden zijn de belangrijkste verklarende factoren voor lage vlieghoogte tijdens de trek in beide seizoenen en in de herfst blijkt temperatuur ook een belangrijke factor. In beide seizoenen kiezen vogels ervoor om op hoogtes te vliegen met windomstandigheden die hen zo min mogelijk belemmeren. Naar verhouding vliegen meer vogels op lage hoogte naarmate de temperatuur hoger wordt in de herfst. Uit deze bevindingen trekken we de conclusie dat maatregelen, om botsingen met windturbines op zee te voorkomen, belangrijker zijn in de herfst dan in de lente, aangezien vogels in de lente vaak al hoger dan de windturbines vliegen. Hier moet echter wel een kanttekening bij geplaatst worden, want ook in de lente kan het voorkomen dat er tijdens de trek veel vogels op lagere hoogte binnen het bereik van de wieken van de windturbines vliegen.

In hoofdstuk 5 komen de voorgaande hoofdstukken samen en wordt de opgedane fundamentele kennis over relevante omgevingsfactoren en de tijdruimtelijke patronen van nachtelijke vogeltrek gecombineerd om korte termijn voorspellingen te doen omtrent nachtelijke vogeltrek op lage hoogte (tot 300 m) boven de Noordzee. Zulke korte termijn voorspellingen zijn van groot belang voor de bescherming van veel vogelsoorten. Enerzijds kunnen ze helpen om voorbereid te zijn op zowel grote omgevingsveranderingen als op verschijnselen die zich op kleinere tijdsschalen voordoen in de ecologie en omgeving. Anderzijds stelt het ons in staat om onmiddellijk actie te ondernemen om eventuele negatieve effecten op de ecologische omgeving te voorkomen of te minimaliseren. Om deze voorspellingen te doen is eerst de trekintensiteit berekend op basis van de gegevens van de radar die in de zee ten westen van de Nederlandse kust staat. De trekintensiteit werd vervolgens gebruikt als een responsvariabele in een Random Forest regressiemodel, waarbij fenologische en weersvariabelen gebruikt zijn als voorspellende variabelen. Deze modellen helpen bij het begrijpen welke omgevingsfactoren een rol spelen bij de dynamiek van de trekintensiteit. Daarnaast testten we in dit hoofdstuk hoe goed het model de trekintensiteit per uur kan voorspellen. Het model blijkt uren met hoge
of lage vogeltrek intensiteit correct te classificeren in 90% van de gevallen in de lente en 80% van de gevallen in de herfst. Het model was echter niet goed in staat om correct te voorspellen op welke uren de trekintensiteit hoog was, waarschijnlijk doordat de periode waarover data beschikbaar is te kort was. Als gekeken wordt naar de cumulatieve percentages van de gemeten vogeltrek, blijkt dat in de lente en de herfst respectievelijk slechts 18 en 26 uur de windturbines stilgezet moeten worden om het botsingsgevaar voor trekvogels met 50% te reduceren. Dat komt neer op 2.5% van de trekuren in de lente en 5.5% in de herfst, hetgeen echter kan verschillen tussen jaren. Dit stilzetten van de windturbines zou een energieverlies van 0.56% in de lente en 1.26% in de herfst betekenen. We concluderen dat het model over het algemeen in beide seizoenen goed presteert en dat korte termijn voorspellingen gebaseerd op een beperkte datasets gecombineerd met expertkennis nodig zijn, om sneller beschermingsmaatregelen te ontwikkelen in gebieden met veel windturbines.

In dit proefschrift wordt herhaaldelijk aangetoond dat verschillende omgevingsfactoren van belang zijn voor de seizoensgebonden patronen van nachtelijke vogeltrek boven een ecologische barrière zoals de zee. De tijd van het jaar, wind en temperatuur (op zowel lokale als bredere synoptische schaal) kunnen van invloed zijn op het moment waarop vogels hun trek starten, de hoogte waarop ze vliegen en de trekintensiteit gedurende de nacht boven de Noordzee. Door deze verbanden in een dermate complex systeem te ontrafelen, zijn we een stap dichterbij gekomen bij het begrijpen van vogelgedrag bij een belangrijk knooppunt van de Oost-Atlantische flyway gekomen. Daarnaast leggen we hiermee ook de basis voor aeroconservation in de regio. Ik heb actief deelgenomen in een werkgroep, die zich bezighoudt met het opstellen van beschermingsmaatregelen. Vanuit die persoonlijke ervaring kan ik stellen dat een interdisciplinaire aanpak en kennisuitwisseling tussen de verschillende belanghebbende partijen de sleutel is tot een succesvol toekomstig milieubeheer.
Author contributions

Chapter 2. Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea
Maja Bradaric, Willem Bouten, Ruben C. Fijn, Karen L. Krijgsveld & Judy Shamoun-Baranes

MB, JSB and WB conceived the study. WB developed the initial trajectory model, and MB adapted the model for this specific study. KLK and RCF facilitated data collection and filtering. MB made all the figures and undertook all data analysis. MB led the writing of the manuscript, with all authors commenting on the manuscript drafts. JSB was responsible for acquisition of funding for the project leading to this publication.

Chapter 3. Associations of synoptic weather conditions with nocturnal bird migration over the North Sea
Iris Manola, Maja Bradaric, Rob Groenland, Ruben C. Fijn, Willem Bouten & Judy Shamoun-Baranes

IM, JSB, and MB conceived the study. IM and MB analysed the data and made the figures. All the authors have contributed to writing the text of this work. JSB was responsible for acquisition of funding for the project leading to this publication.

Chapter 4. Drivers of flight altitude during spring and autumn nocturnal bird migration and implications for offshore wind energy
Maja Bradaric, Bart Kranstauber, Willem Bouten, Hans van Gasteren & Judy Shamoun-Baranes

MB, WB and JSB conceived the study. MB undertook all the data filtering, supported by HvG. Analysis and model development were led by MB and supported by BK with contributions from WB, HvG and JSB. MB led the manuscript writing, with all authors providing feedback and the final approval of the manuscript. JSB was responsible for acquisition of funding for the project leading to this manuscript.

Chapter 5. Forecasting nocturnal bird migration to mitigate collisions with offshore wind turbines in the southern North Sea
Maja Bradaric, Bart Kranstauber, Willem Bouten & Judy Shamoun-Baranes

All authors conceived the study. MB led the data filtering, analysis and model development, supported by BK and input from WB and JBS. MB led the manuscript writing, and all authors provided feedback on manuscript versions. JSB was responsible for acquisition of funding for the project leading to this manuscript.
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