On the radar
Weather, bird migration and aeroconservation over the North Sea
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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).
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.
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.

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<th>Antenna</th>
<th>Merlin</th>
<th>Robin 3D-fix</th>
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<td>Range (m)*</td>
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*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.