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### On the radar

*Weather, bird migration and aeroconservation over the North Sea*

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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-Britannië 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 worden gebruikt 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 ontwarren 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 windomstandigheden 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 Bradarić, 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 Bradarić, 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 Bradarić, 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 Bradarić, 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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