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Wind energy for all!

The dynamic flight of gulls in human-engineered landscapes

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Summary

Samenvatting

Summary

Looking up into the sky on a cloudless day, it may feel as if there is nothing but emptiness between you and the vastness of space. However, the Earth's atmosphere is in fact a highly dynamic environment, rich with activity and facilitating the movement of organisms from all domains of life. Fungal spores and dandelion seeds are transported by the wind. Insects, birds and bats migrate with global wind patterns, and common swifts can spend up to 10 months in the air without landing. The atmosphere must therefore be treated as a habitat, just as aquatic and terrestrial environments are, and conservation measures must account for the role of the atmosphere in supporting different species. Part of understanding the importance of the atmosphere means studying exactly how it facilitates movement across different scales, from global patterns of movement to fine scale interactions between organisms and the atmosphere that may last only a few minutes or seconds.

The atmospheric habitat does not exist in isolation; the lower atmosphere is under the constant influence of the Earth's surface, which influences atmospheric dynamics on a very fine scale. Structures in the landscape, from mountains to tree lines, deflect wind upward and create pathways of uplift called orographic lift. Heating and cooling of the surface influences atmospheric turbulence, creating vertical uplift called thermals that extend up to hundreds or even thousands of metres into the atmosphere. These sources of uplift provide sources of energy to flying animals, helping them to stay aloft, to gain altitude, and to reduce the energetic cost of flight. Some soaring birds are almost entirely dependent upon these uplift sources to stay airborne, while other birds may make use of uplift opportunistically as and when they encounter it.

Since these fine scale atmospheric dynamics are so dependent on the Earth's surface, they are highly sensitive to landscape change and development, which are greatly affected by human activity. Very few areas of the Earth remain untouched by human influence and in many cases the land is heavily engineered to meet humanity's wants and needs. Deforestation, agricultural intensification and urbanisation have all radically changed the literal face of

the Earth and therefore have also influenced the dynamics of the atmosphere above it. If future modifications to the landscape are to be made with conscientious and informed consideration of the potential to impact other species, there is a need to better understand how the landscape influences the atmospheric environment and the flight of birds that depend upon it.

Lesser black-backed gulls are flight generalists, meaning they can switch readily between different modes of flight, such as flapping and soaring, as and when it suits them. This ability makes them a fascinating but tricky species to study when it comes to the influence of the atmosphere on flight, as lesser black-backed gulls may adjust their behaviour depending on their environmental conditions and energetic needs. As a species, lesser black-backed gulls are highly opportunistic in many other aspects of their life cycle, displaying great behavioural plasticity, i.e. the ability to adapt their behaviour to different resources and situations. From their historic coastal habitats and marine foraging grounds they have increasingly been found nesting and foraging in towns and cities, and are highly dependent on anthropogenic sources of food such as fishery discards, agricultural landscapes, refuse sites and urban food opportunities. Many aspects of their behaviour are highly variable, so by studying how they respond to different aspects of their environment, such as the atmosphere, we can gain insight into how lesser black-backed gulls make decisions in relation to their surroundings.

By learning more about how lesser black-backed gulls make decisions, it becomes more feasible to predict how they may behave under different conditions. This knowledge is highly useful when making conservation decisions in relation to certain species. For lesser black-backed gulls, a current conservation area of concern is their potential to interact with wind farms, particularly their risk of colliding with turbines during flight. Improved understanding of lesser black-backed gull behaviour contributes towards quantifying these risks more effectively, from knowing where lesser black-backed gulls are present in an area and where they originate from, to being able to predict the altitudes at which they fly in relation to the altitude of wind turbine blades. To some extent we can measure these sorts of

important metrics, but we need to understand how they vary with environmental change in order to predict them for future conservation decisions.

In this thesis we aim to gain a deeper insight into how atmospheric conditions influence the movement behaviour of lesser black-backed gulls, particularly in human-engineered landscapes and in the context of wind farm development. We study questions surrounding these aims using GPS tracking of individual lesser black-backed gulls in combination with environmental modelling of terrestrial and marine landscapes and the atmospheric features they generate. UvA-BiTS GPS trackers, attached via a backpack harness to individual lesser black-backed gulls, provide information on geographical position and three-dimensional movement, allowing us to identify the geographical position of a bird as well as its flight behaviour. Fine-scale environmental models quantify the atmospheric conditions a bird is experiencing in real space and time in relation to its surrounding landscape. We focus upon the daily movements of lesser black-backed gulls during the breeding season and gain insight into how lesser black-backed gulls respond opportunistically to the atmosphere on an instant, as well as how they forge energy efficient routes through familiar atmospheric landscapes over time. We also examine how measuring movement at very broad scales and very fine scales can be used in conservation contexts, particularly in making conservation decisions during the planning and approval stages of wind farm development.

In **Chapter 2** we examine the movement behaviour of lesser black-backed gulls at a very broad scale. Our aim is to gain insight into species-wide patterns of movement range during the breeding season and to develop ways of using generic metrics of movement range in spatial conservation scenarios. During the breeding season lesser black-backed gulls are typically central placed foragers; travelling to and from their breeding colony regularly. By measuring how far gulls typically range from their colony throughout the breeding season across 25 different populations, we can see if any generalisable patterns emerge, or measure the degree to which different populations vary. We also measure the movement range and time

spent in either marine or terrestrial areas, as lesser black-backed gulls are known to use both habitats and such knowledge is useful in developing conservation policy for different regions, such as for onshore and offshore wind farm developments. Our results show that on a species-wide level, lesser black-backed gulls spent 95% of their time within 70.5 km of their breeding colony, but variation in movement range across colonies was high. Movement range at sea and land was very similar on a species level, but this was because there was a lot of variation across colonies. Without knowing which factors drive variation across colonies, we advocate for using local information about movement where feasible when making conservation assessments.

In **Chapter 3** we focus upon the influence of the environment on lesser black-backed gulls at a specific colony in North-Holland, by investigating the extent to which orographic uplift influences flight behaviour and route choice during daily flights of gulls between their breeding colony and various terrestrial foraging locations. We model the orographic uplift generated by features in the North-Holland landscape using a high resolution digital terrain model and data on wind speed and direction, identifying pathways of orographic uplift created by dunes, buildings and tree lines. We then measure the modelled orographic uplift experienced by gulls in real time and identify that gulls are more likely to use soaring flight over flapping flight when experiencing greater orographic uplift strengths. We also find that gulls experience high orographic uplift at a greater rate than is distributed randomly through the landscape, indicating that lesser black-backed gulls make flight decisions in order to encounter more beneficial uplift conditions. Overall we conclude that small changes to the topography of the typical flat Dutch polder landscape impact the atmospheric landscape traversed by gulls.

Aside from orographic uplift, thermal uplift may also provide atmospheric energy to lesser black-backed gulls during their daily flights over Noord-Holland. Therefore, we continue in **Chapter 4** by investigating the extent to which lesser black-backed gulls use thermal uplift and the extent to which the Noord-Holland landscape supports thermal soaring flight. Once again we

model uplift, this time solving the energy balance at the Earth's surface to model the amount of energy released from the surface into the atmosphere, which produces thermal uplift. We quantify the thermal uplift experienced by lesser black-backed gulls in time and space and learn that, as for orographic uplift, lesser black-backed gulls increasingly use soaring flight as thermal uplift strength increases. Additionally, we learnt that thermal uplift is regularly generated over urban areas: roads, buildings, especially where concentrated in towns and cities, serve as reliable hotspots for thermal soaring. Lesser black-backed gulls congregate over these urban thermal hotspots in order to soar and gain altitude that they then use to glide onward to the next soaring opportunity, all by hardly flapping their wings. Again the treatment of the landscape, not just topography but also land use practices, influences the atmospheric landscape and the flight strategies gulls utilise.

Thermal soaring among birds is most regularly associated with warm arid environments, so to some extent it was surprising to see how regularly it enabled soaring in lesser black-backed gulls over a wet temperate region like Noord-Holland, largely thanks to the energy reflected by urban areas. However, there are other regions where thermal soaring is expected to be even less available and where human-engineering of the terrain is far less prevalent, such as temperate marine environments. Alongside foraging inland, lesser black-backed gulls breeding along the Dutch coast regularly forage at the North Sea, where atmospheric conditions are considerably different compared to over land. There are few features to generate orographic uplift, and thermal uplift is far less prevalent over this temperate sea. Therefore, in **Chapter 5** we investigate the environmental conditions under which gulls utilised thermal soaring over the North Sea during the summer months of June and July. Because birds typically gain altitude during thermal soaring and the flight altitude of birds is of high importance when modelling the potential effects of wind farms on bird populations, we also wanted to identify whether thermal soaring influenced the degree to which birds flew at wind turbine height. For this study we experimented with using two different data sources in a complementary way. GPS tracking of individual gulls from two breeding colonies on the North Sea provided fine-scale information on flight altitude, whilst bird tracking radar located at two

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offshore wind farms gathered continuous information on all the thermal soaring inside and outside of a wind farm area. We learnt that soaring behaviours in general occurred rarely in lesser black-backed gulls at sea, and that thermal soaring behaviour was rarer still. Whilst thermal soaring was relatively more likely to occur at wind turbine height compared to the rest of flight, its overall effect on flight altitude was low. However, thermal soaring was influenced by environmental conditions, specifically the difference between air temperature and sea surface temperature. Over periods when air temperature consistently dropped below sea surface temperature, rates of thermal soaring increased considerably, meaning there are windows of time, driven by synoptic weather patterns, in which thermal soaring has a larger influence on flight altitude, which may affect collision risk estimates.

Throughout this research we have discovered some of the ways in which lesser black-backed gulls harness energy from the Earth's atmosphere in order to save energy in flight. In many ways the movements of the atmosphere are highly dynamic and unpredictable, but when we examine the relationship between the landscape and atmosphere on a very fine scale, we learn that some landscape features generate reliable sources of atmospheric uplift that gulls can use repeatedly to save energy in flight. Some of these landscape features are the result of human engineering of the landscape, from urban developments to agricultural practices. Lesser black-backed gulls are able to react to dynamic changes in atmospheric resources on very fine scales, responding to uplift opportunistically whilst undertaking repeatable flight paths in response to reliable sources of uplift in the landscape. Just as we find that bird flight behaviour in relation to the atmosphere is moderated by human activity, we identify ways in which an understanding of the environmental drivers of bird flight can be used to inform future landscape modifications.

Samenvatting

Wanneer je naar boven kijkt op een wolkeloze dag, lijkt het wel alsof er een soort leegte is tussen jezelf en de eindeloze ruimte. De atmosfeer, de luchtlaag rond de aarde, is echter een enorm dynamische omgeving, vol activiteit en van vitaal belang voor de voortbeweging van organismen van alle domeinen van het leven. Sporen van paddenstoelen en zaadjes van paardenbloemen dansen op de wind. Insecten, vogels en vleermuizen migreren met de wereldwijde windpatronen mee, en zwaluwen kunnen tot wel 10 maanden in de lucht blijven zonder ook maar even te landen. De atmosfeer moet daarom, net zoals het water en het land, beschouwd worden als een habitat en natuurbescherming zou ook rekening moeten houden met de rol van de atmosfeer bij het ondersteunen van soorten. Om het belang van de atmosfeer te begrijpen, zou je dus precies moeten bestuderen hoe deze de voortbeweging van dieren faciliteert, zowel op de schaal van wereldwijde patronen als bij fijnschalige interacties tussen organismen en de atmosfeer die slechts enkele minuten of seconden duren.

Het atmosferische habitat staat niet op zichzelf: de onderste laag is continu onder invloed van het aardoppervlak, die de atmosferische dynamiek op fijne schaal beïnvloedt. Elementen in het landschap, van bergen tot bomen, kunnen de wind opwaarts afbuigen en zo opstijgende lucht veroorzaken, zogenoemde “orografische lift”. Het opwarmen en afkoelen van het aardoppervlak beïnvloedt atmosferische turbulentie en veroorzaakt thermische lift (thermiek genoemd) die zich tot honderden of zelfs duizenden meters hoog uitstrekt. Lift is een bron van energie voor vliegende dieren. Ze maken er gebruik van om te zweven of om hoogte te winnen, en zo energie te besparen. Sommige zwevende vogels maken bijna uitsluitend gebruik van lift, terwijl andere vogels alleen opportunistisch gebruik maken van lift wanneer deze voorhanden is.

De fijnschalige atmosferische dynamiek is nauw verbonden met het aardoppervlak, en dus met de landschapsverandering en -ontwikkeling, die versneld wordt door menselijke activiteit. Slechts enkele gebieden op aarde zijn niet beïnvloed door de mens; meestal is het land zwaar bewerkt om aan onze eisen te voldoen. Ontbossing, landbouw, en verstedelijking hebben het

landschap wereldwijd radicaal veranderd en daarmee ook de dynamiek van de atmosfeer. Als we toekomstige aanpassingen van het landschap weloverwogen en verantwoord willen uitvoeren vanuit het perspectief van dieren, dan is er meer kennis nodig over hoe het landschap de atmosfeer beïnvloedt en over het vlieggedrag van vogels, die hiervan afhankelijk zijn.

Kleine mantelmeeuwen zijn generalisten qua vlieggedrag, hetgeen betekent dat ze direct kunnen wisselen van hun manier van vliegen, zoals klapwieken en zweven, waar en wanneer het hen schikt. Deze vaardigheid maakt hen een fascinerende maar lastige soort om te bestuderen als het over de invloed van de atmosfeer op hun vlieggedrag gaat, aangezien kleine mantelmeeuwen hun gedrag kunnen aanpassen afhankelijk van hun omgeving en energetische behoeften. Als soort zijn kleine mantelmeeuwen ook zeer opportunistisch in andere aspecten van hun leven; ze vertonen een sterke plasticiteit, oftewel een vaardigheid om hun gedrag aan allerlei situaties aan te passen. Vroeger hadden ze hun foerageergebieden aan de kust en op zee, maar nu worden ze ook vaak gezien in dorpen en steden om te foerageren en te broeden. Ze zijn erg afhankelijk van antropogene voedselbronnen zoals visafval, akkers, vuilstort en voedsel in de stad. In hun gedrag zijn ze zeer variabel, dus door te bestuderen hoe ze reageren op verschillende aspecten van hun omgeving, zoals bijvoorbeeld de atmosfeer, kunnen we een beter beeld krijgen van de manier waarop kleine mantelmeeuwen beslissingen nemen in relatie tot hun omgeving.

Door meer te leren over hoe kleine mantelmeeuwen beslissingen nemen, kunnen we beter voorspellen hoe ze zich gedragen onder verschillende omstandigheden. Deze kennis is zeer nuttig bij het natuurbehoud en de bescherming van specifieke soorten. Een van de huidige zorgen met betrekking tot de bescherming van kleine mantelmeeuwen is hun interactie met windparken en met name het risico dat ze door rotoren van windturbines uit de lucht geslagen worden. Om deze risico's te kwantificeren is meer kennis nodig van het gedrag van kleine mantelmeeuwen, van het begrijpen waar ze zich binnen een gebied bevinden en waar ze vandaan komen, tot het voorspellen van de hoogte waarop ze vliegen in relatie tot de rotoren van turbines. Tot op zekere hoogte kunnen

we dit soort variabelen meten, maar we moeten ook begrijpen hoe veranderingen in het landschap hier invloed op hebben om toekomstig natuurbeheer te verbeteren.

Het doel van dit proefschrift is een beter beeld te krijgen van hoe atmosferische omstandigheden invloed hebben op het bewegingsgedrag van kleine mantelmeeuwen, specifiek in de context van antropogene landschappen en de ontwikkeling van windenergie. We onderzoeken dit door middel van het volgen van individuele kleine mantelmeeuwen met GPS-trackers en dit te combineren met het modelleren van atmosferische omstandigheden boven land en zee. UvA-BiTS GPS-trackers, als ruzzakje op individuele kleine mantelmeeuwen gebonden, meten de geografische positie en driedimensionale bewegingen van de vogel en daarmee het gedrag. Omgevingsmodellen met fijne schaal kunnen de atmosferische omstandigheden, die een vogel ervaart, kwantificeren. Door dagelijkse bewegingen van kleine mantelmeeuwen tijdens het broedseizoen te meten, krijgen we inzicht in de manier waarop kleine mantelmeeuwen in een oogwenk opportunistisch reageren op de atmosfeer in hun directe nabijheid en ook hoe ze energiezuinige routes ontwikkelen in een atmosferisch landschap dat ze langzaam maar zeker hebben leren kennen. Ook kijken we hoe het meten van bewegingsgedrag op zowel zeer grove als fijne schaal gebruikt kan worden in de context van natuurbeheer, voornamelijk met betrekking tot het nemen van beslissingen bij het plannen en goedkeuren van windparken.

In **Hoofdstuk 2** onderzoeken we bewegingspatronen van kleine mantelmeeuwen op de schaal van de Noordzee. Ons doel is om voor de soort inzicht te krijgen in de “vliegrange” tijdens het broedseizoen en methoden te ontwikkelen om deze generieke vluchtkarakteristieken te gebruiken voor ruimtelijke beheer-scenario’s. In het broedseizoen foerageren kleine mantelmeeuwen normaliter vanuit een centrale broedlocatie, en vliegen ze heen en weer vanuit hun kolonie. Door in 25 verschillende populaties te meten hoe ver meeuwen in het algemeen van hun kolonie wegvliegen (het genoemde vliegrange), kunnen we kijken of er generaliseerbare patronen zijn en de verschillen tussen de populaties vaststellen. Ook kunnen we meten

welk deel van hun tijd ze besteden op zee en op land, aangezien kleine mantelmeeuwen in beide gebieden voorkomen en deze kennis nuttig is voor het ontwikkelen van natuurbeleid, bijvoorbeeld met betrekking tot windenergie op land en op zee. Onze resultaten laten zien dat op soort-niveau kleine mantelmeeuwen 95% van hun tijd doorbrengen binnen een afstand van 70.5 km van hun kolonie, maar de variatie tussen de kolonies was groot. Er waren geen aantoonbare verschillen in de vlieggrange voor land of zee, maar dat kwam ook door de zeer grote verschillen tussen de kolonies. Omdat we nog geen kennis hebben omtrent omstandigheden die deze variatie veroorzaken, adviseren we, waar mogelijk, lokale kennis over het bewegingsgedrag van de meeuwen te gebruiken voor natuurbeheer.

In **Hoofdstuk 3** richten we ons op de invloed die de omgeving heeft op kleine mantelmeeuwen van een specifieke kolonie in Noord-Holland, door te kijken naar de mate waarin orografische lift invloed heeft op hun vlieggedrag en op de route die ze kiezen voor hun dagelijkse vlucht tussen de kolonie en verschillende foerageergebieden op land. We modeleren de orografische lift, veroorzaakt door landschapselementen in Noord-Holland, door gebruik te maken van een hoge resolutie digitaal hoogtemodel en informatie over windsnelheid en -richting, en daarmee de orografische lift te berekenen langs duinen, gebouwen, rijen van bomen en bosranden. Zo kwantificeren we de orografische lift die meeuwen ervaren in real-time, en zien we dat meeuwen vaker zweven dan klapwieken naarmate de orografische lift toeneemt. We zien ook dat meeuwen meer orografische lift ondervinden op hun routes dan wat ze bij toeval zouden tegenkomen in het landschap. Dit geeft aan dat ze hun route zo kiezen dat ze vaker van deze voordelige lift gebruik kunnen maken. We concluderen dat kleine aanpassingen in het typisch platte Nederlandse landschap al invloed hebben op de atmosferische omgeving die meeuwen doorkruisen.

Naast orografische lift zou thermiek ook atmosferische energie kunnen leveren voor de kleine mantelmeeuw tijdens zijn dagelijkse vluchten over Noord-Holland. Daarom gaan we in **Hoofdstuk 4** door met het onderzoeken van het gebruik van thermische lift door kleine mantelmeeuwen, en de manier waarop het Noord Hollandse landschap het zweefgedrag

ondersteunt. We modeleren opnieuw lift, maar deze keer door de energiebalans aan het aardoppervlak op te lossen en daarmee de hoeveelheid energie, die van het aardoppervlak de luchtlaag instroomt, te modeleren en daarmee de thermiek. We kwantificeren de thermiek die kleine mantelmeeuwen ondervinden in tijd en ruimte en leren dat ze, net als bij orografische lift, meer zweven naarmate de thermiek toeneemt. Bovendien bleek dat thermiek vaak aanwezig is in stedelijk gebied: wegen en gebouwen, zeker wanneer ze geconcentreerd zijn in dorpen en steden, zijn betrouwbare bronnen voor thermisch zweven. Kleine mantelmeeuwen gebruiken deze thermische “hotspots” om te zweven en hoogte te winnen, die ze daarna kunnen gebruiken om naar de volgende thermiekbelt te glijden, zonder de noodzaak te klapwieken. We laten hier opnieuw zien dat landschapontwikkeling, niet alleen de topografie maar ook het gebruik van het land, invloed heeft op het atmosferische landschap en de vliegstrategieën die meeuwen gebruiken.

Thermisch zweven van vogels wordt vooral geassocieerd met warme, droge landschappen in een warm klimaat. Het was daarom verassend om te zien dat kleine mantelmeeuwen vaak konden zweven in een gematigd klimaat en een nat landschap zoals in Noord-Holland. Zoals beschreven hing dit in hoge mate samen met de energie die opsteeg vanuit stedelijke gebieden. Echter, er zijn gebieden waar thermisch zweven nog minder aantrekkelijk is en waar de menselijke invloed op het landschap veel kleiner is, zoals op zee in gematigde klimaten. Naast het foerageren op land zijn kleine mantelmeeuwen, die langs de Nederlandse kust broeden, ook vaak op zee te vinden om te foerageren. De atmosferische condities verschillen daar sterk met die op land. Er zijn weinig elementen die orografische lift kunnen genereren, en thermiek komt veel minder voor bij een gematigd zeeklimaat. Om dit verder te verkennen kijken we in **Hoofdstuk 5** naar de omstandigheden waaronder meeuwen thermisch zweven op de Noordzee in de zomermaanden juni en juli. Aangezien vogels tijdens thermisch zweven stijgen naar grotere hoogte en de vlieghoogte van groot belang is voor het modeleren van de mogelijke effecten van windparken op vogelpopulaties, wilden we ook vaststellen op welke hoogte vogels vliegen tijdens thermisch zweven op zee en of dit overeenkomt met de rotorhoogte van windturbines.

Voor deze studie hebben we twee verschillende databronnen gebruikt die elkaar aanvullen. GPS-metingen van individuele meeuwen van twee kolonies op de Noordzee gaven ons informatie over de vlieghoogte met hoge tijdsresolutie, terwijl vogelradars bij twee windparken op zee continu maten hoe vaak vogels zweven binnen en buiten het windpark. We leerden dat kleine mantelmeeuwen op zee bijna altijd klapwieken en dat thermisch zweven zeldzaam is. Hoewel thermisch zweven vaker plaatsvond op rotorhoogte, was de bijdrage van zweefgedrag op de gemiddelde vlieghoogte erg klein. Wel werd thermisch zweven duidelijk beïnvloed door omgevingsfactoren, specifiek het temperatuurverschil van de lucht en het wateroppervlak. Wanneer de luchttemperatuur voor langere tijd lager was dan de temperatuur van het zeeoppervlak nam het zweven toe. Dit wijst erop dat er specifieke perioden zijn, beïnvloed door de synoptische weersomstandigheden, waarin thermisch zweven een grotere invloed heeft op de vlieghoogte en dus een invloed kan hebben op risicoschattingen dat vogels botsen met turbines.

In dit onderzoek hebben we een aantal manieren ontdekt waarmee kleine mantelmeeuwen de energie in de atmosfeer benutten om zelf energie te besparen tijdens het vliegen. In veel opzichten is de atmosfeer zeer dynamisch en onvoorspelbaar, maar wanneer we op een zeer fijne schaal kijken naar de relatie tussen het landschap en de atmosfeer erboven, leren we dat sommige elementen in het landschap als betrouwbare bronnen van atmosferische lift dienen en meeuwen deze gebruiken om energie te besparen tijdens hun vlucht. Sommige van die elementen zijn het resultaat van menselijke aanpassingen in het landschap, zoals stedelijke ontwikkeling en landbouw. Kleine mantermeeuwen kunnen reageren op zeer fijne dynamische veranderingen in de atmosfeer en opportunistisch gebruik maken van lift terwijl ze herhaalde vliegroutes ontwikkelen als reactie op voorspelbare bronnen van lift in het landschap. Net zoals we zien dat het vlieggedrag van vogels en hun afhankelijkheid van de atmosfeer beïnvloed wordt door de mens, kunnen we ook onze kennis van de invloed van de omgeving op vlieggedrag aanwenden om weloverwogen beslissingen te nemen omtrent aanpassingen in het landschap.

Author contributions

Chapter 2 Incorporating variation in movement range into conservation measures for a central-place forager

ES, JSB and WB conceptualised the study and designed the methodology. ES analysed the data and led writing of the manuscript. JSB, NHKB, WB, RC, TE, EMH, LRQ and CBT were involved in discussions throughout stages of the work. JSB, WB, CJC, SW, AS, CW, EWMS, LL, WM, SG, SÅ, UL, CBT, EMH and NHKB provided data. TE, JSB, KS, AC CBT, DTJ, ESS, GDC, GJC, KABJ, LJB, NAC, RMWG, VRS, NI, SÅ, UL, ES, were instrumental in the collection of data. All authors provided feedback on drafts and gave final approval of the manuscript.

Chapter 3: Orographic lift shapes flight routes of gulls in a virtually flat landscape

ES, JSB WB and BH conceived the study. Field work was carried out by KC and tracking data collection by KC & JSB. WB and BH developed the initial orographic lift model, ES developed random movement model and undertook all data analysis. Writing was led by ES supported by WB and JSB, and all authors provided comments and discussion.

Chapter 4: Thermal soaring of lesser black-backed gulls *Larus fuscus* supported by a human engineered landscape

ES, WB and JSB conceived and designed the study. WB and WvD conceived the sensible heat flux model with WvD carrying out the modelling, and validation of the sensible heat flux model. ES implemented the model on GPS data and carried out all other analysis. Field work was carried out by CJC and long term tracking research by CJC and JSB. Funding was acquired by JSB. Writing was led by ES, supported by WB and JSB, with all authors providing comments and discussion.

Chapter 5: Conditions supporting thermal soaring over the North Sea and implications for wind farm interactions

This study was conceived and designed by ES, JAvE, JSB, WB and EEvL. Funding was acquired by JSB and tracking data collection was led by JSB. Tagging at IJmuiden was led by CJC. Data preparation and processing of radar data was carried out by JAvE, whilst data preparation and processing of GPS data was carried out by ES. Meteorological data processing and interpretation of pressure charts was carried out by LP. JAvE and ES took equal roles in the final data analysis, supported by JSB, WB and EEvL. JAvE and ES led the written manuscript equally, with all authors providing comments and discussion.

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