Wind energy for all!
The dynamic flight of gulls in human-engineered landscapes
Sage, E.L.

Publication date
2022

Citation for published version (APA):
References


References


de Monte, S., Cotté, C., D’Ovidio, F., Lévy, M., le Corre, M., & Weimerskirch, H. (2012). Frigatebird behaviour at the ocean-atmosphere interface:
Integrating animal behaviour with multi-satellite data. *Journal of the Royal Society Interface, 9*(77), 3351–3358.


References


Spiegel, O., & Crofoot, M. C. (2016). The feedback between where we go and what we know—information shapes movement, but movement also impacts information acquisition. *Current Opinion in Behavioral Sciences, 12*, 90–96.


soaring migrant under changing atmospheric conditions along an entire flyway. *Journal of Avian Biology, 48*(6), 887-896


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
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 luchtlag rond de aarde, is echter een enorm dynamische omgeving, voldoende 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 verandert 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 rukzakje 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 vlucht karakteristieken 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 generaliseerbaar 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 vliegrange 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 luchtlag 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 thermiekbel te glijden, zonder de noodzaak te klapwieken. We laten hier opnieuw zien dat landschapsontwikkeling, 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 aannemelijk 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.
Author affiliations

Susanne, Åkesson  
Department of Biology, Centre for Animal Movement Research, Department of Biology, Ecology Building, 223 62 Lund, Sweden

Lee Barber  
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Willem Bouten  
Theoretical and Computational ecology, Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

Katherine A. Booth Jones  
British Trust for Ornithology Northern Ireland, Northern Ireland Environment Agency, Klondyke Building, Gasworks Business Park, Belfast, BT7 2JA, UK

Niall H.K. Burton  
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Richard Caldow  
Natural England, W4, Dorset Council, County Hall, Colliton Park, Dorchester, Dorset, DT1 1XJ, UK

Kees. C. J. Camphuysen  
Department Coastal Systems, NIOZ Royal Institute for Sea Research and Utrecht University, P.O. Box 59, 1790 AB, Den Burg, Texel, The Netherlands

Nigel A. Clark  
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Gary D. Clewley  
British Trust for Ornithology Scotland, Unit 15, Beta Centre, Stirling University Innovation Park, FK9 4NF, UK

Greg J. Conway  
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Anna-Marie Corman  
Research and Technology Centre (FTZ), Kiel University, Hafentörn 1, 25761 Büsum

Tom Evans  
Department of Biology, Centre for Animal Movement Research, Department of Biology, Ecology Building, 223 62 Lund, Sweden
Marine Scotland Science, Marine Laboratory, 375 Victoria Road, Aberdeen, AB11 9DB, UK

Stefan Garthe
Research and Technology Centre (FTZ), Kiel University, Hafentörn 1, 25761 Büsum

Ros M.W. Green
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Bart Hoekstra
Theoretical and Computational ecology, Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

Elizabeth M Humphreys
British Trust for Ornithology Scotland, Unit 15, Beta Centre, Stirling University Innovation Park, FK9 4NF, UK

Natalie Isaksson
Department of Biology, Centre for Animal Movement Research, Department of Biology, Ecology Building, 223 62 Lund, Sweden
Environmental Research Institute, North Highland College, University of the Highlands and Islands, Ormlie Road, Thurso KW14 7EE, UK
BirdLife Sweden, Stenhusa gård 386 62 Mörbylånga Sweden

Daniel T. Johnston
British Trust for Ornithology Scotland, Unit 15, Beta Centre, Stirling University Innovation Park, FK9 4NF, UK

Luc Lens
Department of Biology, Terrestrial Ecology Unit, Ghent University, B-9000 Ghent, Belgium

Ulrik Lötberg
BirdLife Sweden, Stenhusa gård 386 62 Mörbylånga Sweden

Elizabeth Masden
Environmental Research Institute, North Highland College, University of the Highlands and Islands, Ormlie Road, Thurso KW14 7EE, UK

Wendt Müller
Department of Biology, Behavioural Ecology and Ecophysiology Research group, University of Antwerp, 2610 Antwerp, Belgium

Leonardo Porcacchia
Theoretical and Computational ecology, Institute for Biodiversity and
Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

Lucy R. Quinn
NatureScot, Buidheann Nàdair na h-Alba, Great Glen House, Leachkin Road, Inverness, IV3 8NW, Scotland.

Viola H. Ross-Smith
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Elspeth Sage
Theoretical and Computational ecology, Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

Emily S. Scragg
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Judy Shamoun-Baranes
Theoretical and Computational ecology, Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

Kozue Shiomi
Department of Biology, Centre for Animal Movement Research, Department of Biology, Ecology Building, 223 62 Lund, Sweden
Frontier Research Institute for Interdisciplinary Sciences, Tohoku University, Aramaki aza Aoba 6-3 Aoba-ku, Sendai 980-8578, Japan

Anouk Spelt
Department of Aerospace Engineering, University of Bristol, Bristol, BS8 1TR, United Kingdom

Eric W.M. Stienen
Research Institute for Nature and Forest, Havenlaan 88 bus 73, 1000 Brussels, Belgium.

Chris B. Thaxter
British Trust for Ornithology, The Nunnery, Thetford, IP24 2PU, UK

Walter van Dijk
Theoretical and Computational ecology, Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

Emiel van Loon
Theoretical and Computational ecology, Institute for Biodiversity and
Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

**Jens van Erp**
Theoretical and Computational ecology, Institute for Biodiversity and Ecosystem Dynamics, Faculty of Science, University of Amsterdam, PO Box 94240, 1090 GE Amsterdam, the Netherlands

**Cara Williamson**
Department of Aerospace Engineering, University of Bristol, Bristol, BS8 1TR, United Kingdom

**Shane Windsor**
Department of Aerospace Engineering, University of Bristol, Bristol, BS8 1TR, United Kingdom
Acknowledgements

I am prone to sentimentality but not succinctness, so I expect these acknowledgements to drag out a bit. Good job there’s no word count!

Firstly, thank you to my supervisors Judy and Willem. I can’t remember if I ever mentioned this, but the friendly and collaborative atmosphere I detected during my interview for this PhD was one of my main reasons for taking the job (and the gulls, of course the gulls). My first interactions with you both felt much more like an interesting conversation than an interview, and among all the reservations I had about taking on this PhD (moving abroad, blindly jumping into ecological research) fears about the quality of supervision I would get was never one of them. You proved my instincts absolutely correct; from my first week here when you each put me up in your homes at zero notice after my initial accommodation had come up a bit short, to all the fruitful, interesting, challenging and enjoyable conversations we’ve had every week.

Willem, thank you for turning questions on their head with a smile. You always bring a broad interesting perspective to the table, surprise me with your thoughts, create interesting conversations. You think everything is possible, and have managed to convince me of this on several occasions when I have felt otherwise! I’m particularly grateful for the support you have given throughout my teaching career. The trust you placed in me, whilst intimidating at times, gave me a huge amount of confidence, and as a result I thoroughly enjoyed working on Programming in Matlab throughout the years.

Judy, thank you for always finding ways to make me excited about science, for seeing something redeeming or at least interesting in every figure, and for helping challenge me to create interesting stories out of the science we carry out. You’ve been a great guiding force in my research throughout, from inspiring new ideas and developing them, to deciding when to wrap it up, or take a break. Most of all, thank you for being so supportive, and for being enormous fun!
Acknowledgements

Luuk, thank you, of course, for arranging the funding of this project, but also for the remarkable way in which you’ve worked with us. You set an example for university-industry partnerships. You’ve been so enthusiastic throughout my PhD and given us an amazing amount of freedom to take this research in perhaps unusual directions sometimes. Thank you for the faith you placed in us and thank you for valuing fundamental scientific research. I also must thank you for coming out to Schiermonnikoog 2019 because it was enormous fun (and I know you’d agree).

I have been incredibly lucky to collaborate with many wonderful people during my research here at IBED. Firstly I had the pleasure of initiating parts of my PhD research off the back of some brilliant student projects. Bart and Walter, I’m really glad I got to work with both of you, you’re both amazing scientists. Bart, thank you for commenting your code so well, there are few people whose code I think I could jump into and make sense of in the time I did, but you are one of them. Walter, I really enjoyed collaborating with you from the start of your thesis, with all the interesting conversations we had, and especially our attempts to present each others research! Thanks also to both of you for your contribution to Programming in Matlab, along with the many other amazing teachers we worked with: Cynthia, Casper, Catherine, Lisa, Lars, and Jens. It was a privilege to work alongside you all.

To Kees Camphuysen, thanks for your support and collaboration throughout my PhD. I think I had a tendency to pop up out of nowhere with a question or manuscript draft and disappear again, but you always helped with my various questions! Firstly with your introductions to field research in the colony and your direction in developing the protocols at Schiermonnikoog, then with the whistle stop introduction to dietary analysis you gave to Marceline and me, and then to all the thoughtful and insightful input you’ve provided on manuscripts. I really appreciate the thorough and critical insight you always gave to my writing, especially when it comes to forming a watertight story.

My second research chapter evolved into a large collaboration with many individuals, and I’m very grateful to everyone who got involved in the work and gave their insight, especially when dealing with all the different
directions a dataset can take you in. Thank you Lucy, for all your help in setting up this collaboration and to your initial ideas and suggestions. Thanks also to Natalie for the insightful input into this project (I still hope we'll get a chance to talk more and develop this dataset further sometime). Special thanks to the BTO team, Liz, Niall and especially Chris, for all your insightful conversations and opportunities to share ideas.

My final research chapter was an ambitious undertaking against the clock, so firstly I must thank Judy and Willem again, as well as Emiel, for giving me and Jens the go ahead to attempt it! Emiel, thank you for all your support throughout my PhD, from quick Dutch grammar lessons to discussions of different statistical approaches I could take in my research (I’m not sure which was more confusing), you always approach tricky questions with a sense of optimism and opportunism, which I really appreciate. Leonardo, thank you for your input and commitment to making sense of the meteorological landscape Jens and I were trying to investigate, even when we weren’t really sure what it was we were looking for. Jens, I am so so glad we got to collaborate on a project. After so much time being a bit trapped in my own head (and in my own house) it was a breath of fresh air to really work together on something, especially in such direct collaboration with a very good friend. It’s been some of the most fun I’ve had doing research, and I think we achieved some really cool science under a lot of pressure! Thank you for the ideas, the last minute discussions, tolerating all the teasing from Maja, Morgan and me, and most recently for all those memes.

I also had the opportunity to work with some brilliant collaborators when undertaking field work on Schiermonnikoog. We gathered a lot of useful data, most of which hasn’t made it into this thesis, but which I know will provide value to the long term goals of studying lesser black-backed gulls in the Netherlands. Kees Oosterbeek, thank you so much for all your hard work and guidance in the field. I can imagine I was a bit of an unknown liability when I started, especially with my tendency to declare chicks missing and presumed dead, only for you to find them miraculously risen again. I still remember painfully how gruelling that earliest cycle to the colony was when I first met you at the end of the 2017 season, (I hadn’t grown my Dutch
cycling legs yet and definitely felt I had something to prove). Nevertheless (I think), our work together evolved smoothly in the end. I really enjoyed my time on Schiermonnikoog and I learned a lot that I will take with me (whether that’s how to spot an oystercatcher chick in a ditch, how to pick up an angry gull with minimal bloodshed, or how to squash 500 flies in a minute). Thanks also to Martijn, for the friendship and company throughout the long field season days, (especially when sitting in that office doing data entry). Petra, I’m also really glad I got to experience field work with you. Thank you for inviting me to help with the spoonbills, I had an absolutely magical time out on the saltmarsh with you. Thank you also for all your advice and support, both practically and emotionally, you are a real pioneer! Rosanne, Marceline and Laura, thank you so much for all your hard work and dedication. Rosanne I will remember all the meaningful conversations we had. Marceline, thank you for your ingenuity with our less than optimal field lab equipment, and for the barnacle goose cinema! Laura, thank you for your hard work and good humour!

I also want to thank the staff that supported this research: Edwin for all the work you do with UvA BiTS (and your help with some dodgy relays last year), Ander for all your infrastructural support, and Stacy for all your help with setting up the field work database (and your enduring patience when something inevitably needed adding or altering).

I cannot imagine life at IBED without the amazing people in AME, TCE and the wider IBED community. Thanks so much to all of you and now I will attempt an exhaustive list. To the AME members who welcomed me when I first arrived: Wouter, Bart, Thomas, Liesbeth, and to those who turned up with me (Morgan!) and those who joined along the way: Laura, Ji, Iris, Bart, Berend, Stacy, Johannes, Nelleke, Kees, Roos, Maja, Jens, Fiona, Leonardo, Hans. Thank you for making AME a warm welcoming environment, thank you for your scientific imaginations, and thank you for your friendship!

In particular, I have to thank Morgan and Maja for being the most amazing squad I could have asked for, especially these last couple of years when we have been a bubble in many aspects of life. Morgan, thank you for being there
from day one, for all the ways you’ve supported me, whether it’s listening to my half baked thoughts, throwing me references, taking me on gentle NS walks complete with google translated local interest stories, or yelling me up the bouldering wall, you’ve made my time here fun and manageable in countless ways. Maja, thank you for all the laughter, for your dedication to finding good deals, (especially involving the spa), and of course for all the rakia. You’ve both been a shoulders to cry on and to stand on, and I will miss you both so much! Thank you also to Avery and Dado, mainly for just being around to keep us sane, usually through Avery’s cooking, Dado’s storytelling, or either of your enthusiasm to planning fun days out!

Thanks also go to the wider TCE community for your friendship and support over the years. It was wonderful getting to know you all: Hanna, Vincent, Romain, Cata, Greg, Floor, Jun, Catherine, Tom, Jasper, Andre, Yael, Harry, Daniel and Kenneth. Lotte, Jacques and Kat for your ability to insult the British so eloquently, Louise for being vibrant and hilarious and for having amazing style and for that chestnut crème tart that I still think about regularly, Silke for your wonderful friendship, for placard making and for being a brilliant comrade and council co-chair. Hal, thank you for the friendly welcome, good conversation and support over the years, from Tai Chi classes to lending books and buying beers. Also, thanks for being on my thesis committee! Sietze, thank you just for being so cheerful, it’s very infectious. Zsofi, thank you for always smiling and laughing, regardless of what was happening with our research! To all of you, for your hilarious (and usually bizarre) lunch time conversation.

We zoom out again and I must thank other members of IBED for enriching my time here. To the EPB gang: Jacques, Kat, Tom, Max, Rachid, Giudi, Eileen, Naomi, Elise, and to the cake club gang, which heavily overlaps, for all your good conversations and tasty cakes over the years. Thank you to the secretaries and thank you to the IBED management, particularly Amber, Monique and Anne-Marie, for all your hard work and support. Especially during the first wave of Covid, you showed a great commitment to keeping the flow of communication open, even when it was very difficult. To the members of the IBED PhD and PostDoc council, thank you for your
commitment to supporting our research community, for helping to plan fun events and for all the endless meetings! Ernesto, Naomi, Rachid, Jacques, Kat, Silke, Sebastiaan, Sara, Carl, Max, Maja, Jasper, it was a pleasure to serve with you all. Thanks also to the members of the FNWI PhD council for all your hard work, and for your efforts to bring together an enormous scientific community within the UvA. It’s no small feat, and we’ve come a long way!

I am also very grateful to have met and befriended many astronomers from API throughout my PhD. Dating Vatsal certainly went a long way in helping me muscle my way in, but even before then you were all a lovely bunch to hang out with at our mutual coffee corner. I may have academically walked away from astronomy, but it never walked away from me! Vlad, Frank, David, Ben, Kenzie, Inés, Alex, Deniz, all the rest of you, thanks for having me around! Kenzie and Gregor, thanks for all the cat sitting, sorry Sisi is a lowkey bully. Ben, thank you for organising the horrifically long bike rides that brought us out of our lockdown slump. Vlad, thank you for always being up for a chat and for organising so many fun activities (especially inter-institute events with Rachid!)

My first summer in Amsterdam was a bit weird and lonely. I will always be grateful to you Verena, when you turned up in September and we started going on adventures together. Bike rides, nights at Mezrab, rants about pigeons; I had a lot of fun in my first two years here thanks to you, even if it was just to chat after a long day. I will always remember to leave a moka pot out as a reassuring gesture to potential housemates. Ruyue, I really enjoyed living with you until covid ruined everything! No instant ramen will ever be as eye-wateringly spicy and I fondly remember our many attempts to fix that useless toilet. I must also thank Deniz and Johannes for accepting me as a lockdown interloper, I’d happily hunker down inside with either of you for weeks on end should the need ever arise again (although happily may be too strong a word). Deniz, thank you for all the company, the philosophical conversations, and for your solid guitar performance in our short lived but chart topping lockdown band. Johannes, thank you for your amazing cooking, music, and of course for the majority of your worldly possessions.
Loz, thank you for your witty, beautiful conversation and company, for your cooking, free coffee, and exotic minibreaks to Utrecht. I’m so glad my brother palmed you off on me. There will always be a bath in my house for you.

Alicia, thank you for your unwavering support and thoughtfulness, also for your cooking, especially baking (I see now that I benefit a lot from other people’s culinary skills). Thank you for joining me in making fools of ourselves on rollerskates in Park Frankandael. Alex, thank you for having such a cool girlfriend- naaah I’m kidding, thank you for your friendship and hospitality, for being a companionable fellow bike-tripper (even when the sun is unforgiving and the punctures are unending), and for sending so many cat pictures.

To the gull gang! It’s been so lovely to have a network of other gull researchers to connect with: Susanne, Anouk, Marwa, Cara, Liam, thank you for your gull stories, camaraderie, and especially your dance moves. Anouk and Marwa, I’m really glad to have seen you back in Amsterdam, you gave me some very motivating final pep talks in my final weeks.

There are also many people who have supported me from a distance. Richard, thank you for the philosophical letters and phone calls and unwavering long distance friendship. Simon, thank you for being my go to procrastinating friend who I can always chat to on a slow work day, and for always having something interesting to say. Will, thank you for being a great sightseeing companion on our last minute holidays in suburban holiday lets and for our shared loved of tortellini! Lizzy, thank you for your endless love and affection, whether you deliver it through hugs or through soup, I miss them all! Thank you for always being there. Rob, thank you for sticking around this long, for the lazy Macc walks over familiar ground. Kate, thank you for sharing in my ups and downs, for the quick check ins, long texts, and for your impeccable taste in books. Thanks to the art gang, Arianne, Emma and Morgan, especially for our lockdown games, I miss you all a lot! That international come dine with me will happen some day.

I am lucky and thankful to have the support of a wonderful family, as far flung as they are. Thank you all for the zoom calls and messages. Thanks especially
to all my grandparents for your love and support over the years. Esmond, thank you for being my best friend and standard bearer throughout (well my entire life but particularly the last 5 years since that is what this whole book is about). Thank you for laughing at what I laugh at. Thank you for the weekly Saturday morning lockdown cartoons that have genuinely really grounded me during the last two years.

Vatsal, where to start. Thank you for lecturing me on the difference between muggles and Mughals. Thank you for following me on twitter. Thank you for being with me every step of the way since then. I can’t imagine the last few years without you, nor would I want to, because intertwining our lives has been such a wonderful adventure. Thank you for all your love, for your solidarity, for helping me with questions that had cornered me, for telling me to get back to work when you knew I needed to, and of course for all your delicious cooking. I am so very proud of you and I can’t wait to find out what we get up to next. Of course, thank you for taking on a feline friend with me, and for being much more confident than me when it comes to brushing her teeth. Sisi, thank you for being the best of cats.

Finally, thank you to my parents, for setting a beautiful example of love and for nurturing my curious, creative, and analytic minds. Dad, thank you for your thoughtfulness, your patience, your help with all the homework, and for your off-beat creativity and sense of humour. Thank you also for being my first teacher when it comes to the wonderful world of birds.

To mum, who gave so freely to all around her, who was ingenious and resourceful, who loved nature, particularly the delicious parts of it, who had an unwavering dedication and focus for the things that she loved, and who was utterly herself every day. Thank you for everything you shared with me.