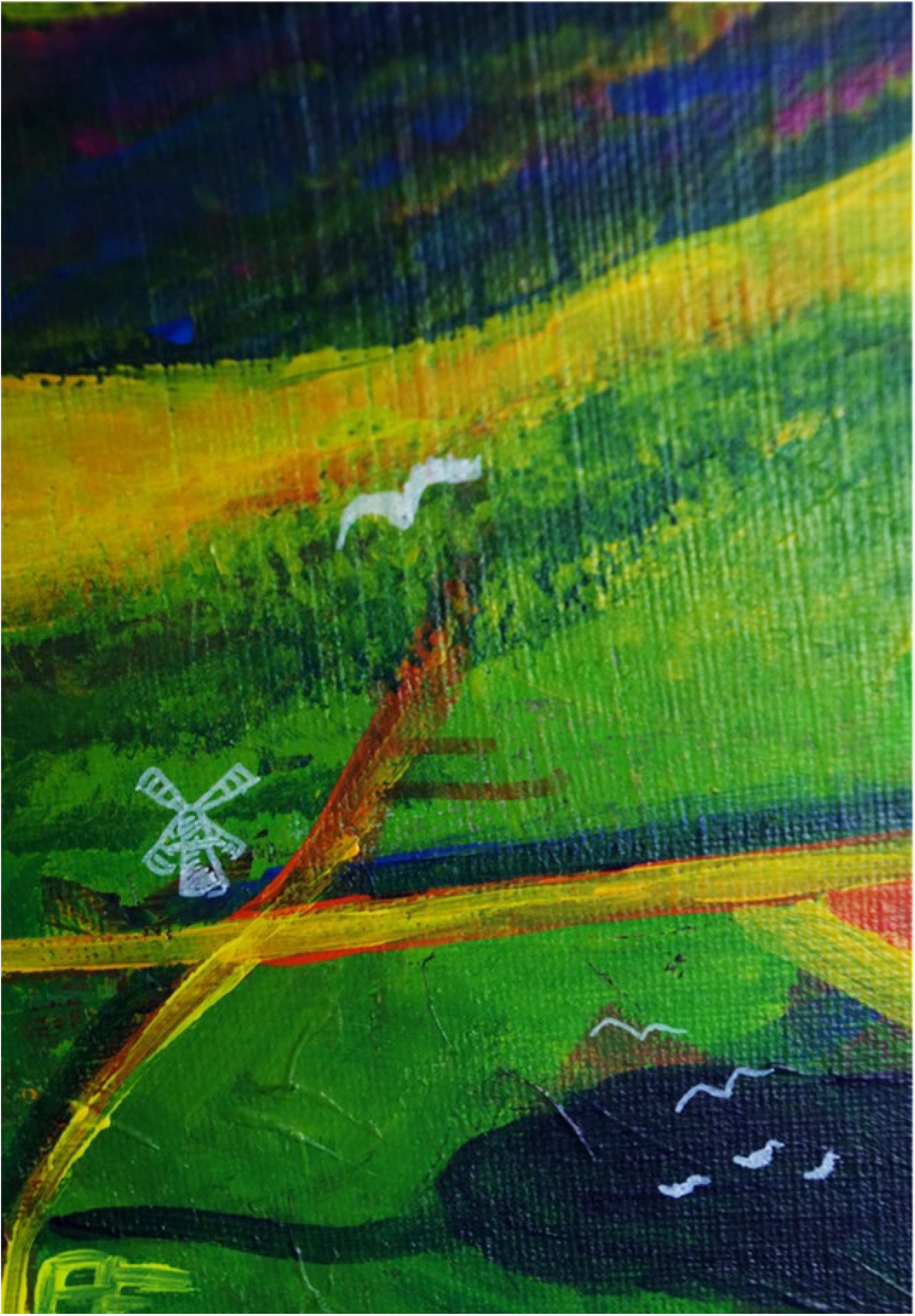
Wind energy for all!

The dynamic flight of gulls in human-engineered landscapes

Sage, E.L.

Publication date
2022



6

Synthesis

The research in this thesis demonstrates the enormous complexity of the atmospheric landscape traversed by avian species and deepens our understanding of the behavioural mechanisms birds adopt in order to traverse such a dynamic environment. The atmospheric landscape can be examined on different scales that reveal both stochasticity and predictability in atmospheric resources used by birds to save energy in flight. Lesser black-backed gulls are able to react to these dynamic changes in atmospheric resources on very fine scales, responding to stochasticity with opportunistic behaviours and to predictability with repeatable behaviours. Knowledge of atmospheric resources in the landscape allow gulls to create energy efficient routes between destinations via predictable atmospheric resources. In many respects, predictable atmospheric uplift is heavily influenced by human engineering of the landscape, which is revealed in this thesis by studying surface-atmospheric interactions on a very fine scale. 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.

The dynamic flight of lesser black-backed gulls

Opportunism and predictability

Throughout this thesis we have gained further insight into the flight behaviour of lesser black-backed gulls, particularly their ability to respond with plasticity to atmospheric conditions at varying scales. This plasticity fits into a wider pattern of generalist behaviours that lesser black-backed gulls exhibit, which allows them to adapt to changes in their environment and contributes to the wide variability we see across various aspects of their life-cycle. Lesser black-backed gulls breed in a wide variety of habitats from remote coastal areas to (increasingly) inland urban towns and cities (Calladine *et al.* 2006; Spelt *et al.* 2019) and they have a broad wintering range, from north-west Europe to west Africa (Klaassen *et al.* 2012; Brown *et al.* 2021). They also have a generalist diet that encompasses marine and terrestrial resources (Camphuysen *et al.* 2015; Tyson *et al.* 2015; Isaksson *et al.* 2016) and to some extent lesser black-backed gulls demonstrate an ability to switch between food resources when a reliable resource becomes unavailable (Langley *et al.* 2021). All this plasticity is likely to arise from an ability to respond opportunistically to ephemeral resources while also repeatably taking advantage of more reliable resources. An understanding of the scales over which they can respond to resources in their environment is likely to be very important in determining the degree to which they can adapt to change, or the costs of having to change strategy.

The opportunistic, generalist behaviour of the lesser black-backed gull goes some way to explaining the high variability in movement range and time spent at sea measured between breeding colonies in **Chapter 2**. Whilst the drivers of colony level variation were not explored in this thesis (but are an interesting potential direction for future research), we can speculate that the availability of resources such as suitable foraging areas is one of the likely drivers of variation. Urban populations will have more nearby access to urban food sources (Spelt *et al.* 2019, 2020), whilst more rural populations may rely more upon marine or agricultural food resources distributed further from their breeding sites. The reliability of different food resources can vary or shift throughout the season, as do the needs of the colony through the various stages of breeding, which may be reflected in individual or population-wide movement behaviour (**Chapter 2.A.2**, Camphuysen et al., 2015; Isaksson et al., 2016)**.** In order to properly understand the decisions taken by birds in relation to their surrounding resource landscape, we need to understand how the resource landscape changes. We therefore took an approach in subsequent chapters of this thesis to explicitly measure and study changes in a type of resource landscape, in this case not based on food availability, but on the resources gained from the atmosphere that facilitate energy saving flight. Here, by quantitatively modelling atmospheric uplift on a very fine scale based on an understanding of what drives atmospheric uplift, we can gain a much deeper understanding of the influence the atmosphere has on the decisions birds make at different scales.

In this thesis I find that lesser black-backed gulls respond to atmospheric uplift in the environment on a range of scales. The use of orographic lift by lesser black-backed gulls is measured in **Chapter 3**, where we see that lesser black-backed gulls (and herring gulls) respond to the presence of orographic lift by increasing their use of soaring, thereby taking advantage of uplift to reduce dependence upon flapping flight. This behaviour is opportunistic in real time, a seizing of the moment. Instantaneous responses to encountered uplift can be explained by an ability to respond to airflow around the wings, which can be a bio-mechanical response as well as a cognitive one (Cheney *et al.* 2020). A sudden loss of uplift, as is demonstrated in one example of orographic soaring in **Chapter 3** (Figure 3.3), can also incur an instantaneous response. In **Chapter 3** we also assume that a bird can detect uplift in its very immediate surroundings and on this basis make cognitive movement decisions on a scale that requires them to move a few meters to encounter uplift. In **Chapter 4** we identify a similar real-time response to thermal uplift; lesser black-backed gulls respond to the availability of higher thermal uplift by utilising more soaring flight and are also more likely to use distinctive circular soaring behaviours associated with thermals. Whilst there are overlaps in the types of soaring behaviour a bird may exhibit in response to either orographic or thermal uplift, there are also distinct differences, which raises the question of how gulls make decisions about which types of soaring behaviour to use. Sustained orographic uplift will typically follow linear landscape features at low altitudes above the surface, inviting a bird to soar at a relatively maintained altitude in the direction of a linear feature. Meanwhile significant thermal uplift typically occurs over areas of high sensible heat flux and extends upwards to the top of the boundary layer while being advected by the wind. In this case a bird typically uses thermal uplift to gain altitude until it reaches its desired altitude or for as long as the thermal remains. The extent to which different mechanisms, such as biomechanical flight control or cognition, enable gulls to respond instantaneously to uplift isn’t known; birds may detect differences in the types of uplift they encounter or take cues from other parts of their environment (such as broader environmental conditions or social cues). We can however conclude that lesser black-backed gulls are able to react opportunistically to uplift in their immediate environment over short time scales while also responding to different sources of uplift with distinct soaring behaviours.

Lesser black-backed gulls also respond to orographic and thermal uplift on scales which suggest they have knowledge of reliable uplift areas in their atmospheric environment. We discovered in **Chapter 3** that gulls select for orographic uplift in the landscape throughout their flight routes, indicating their knowledge of where uplift is higher in real time. We also see that by examining orographic uplift over a seasonal time scale, spatial patterns of reliable orographic uplift emerge; corridors of uplift created by wind repeatedly deviating over linear structures, such as dikes, buildings and even tree lines, which create continuous paths of uplift in the landscape that are repeatedly used by gulls and shape their flight routes. Similarly, we see that reliable patterns in thermal uplift also influence gull flight behaviour, albeit in a more indirect way. Urban areas are particularly reliable hotspots of thermal uplift; rather than providing continuous corridors as is the case for orographic uplift, thermal hotspots provide stepping stones for soaring. Lesser black-backed gulls converge upon thermal uplift hotspots, use them for circular soaring to gain altitude, and are then able to glide between them. The relationship between route choice and reliable atmospheric conditions demonstrate that lesser black-backed gulls are able to utilise knowledge about their surroundings to reduce their flight costs.

In **Chapter 5** we continue to examine the drivers of fine-scale energy saving flight behaviour in an environment that provides a stark contrast to the human-engineered terrestrial landscape of North-Holland studied in **Chapters 3 and 4**; here we focus on thermal soaring over the North Sea**.** The marine landscape is far more homogenous than the terrestrial North-Holland landscape, with much less differential heating of the surface. It was therefore expected that the sea will be less conducive to thermal soaring and that conditions for thermal soaring are driven by broader weather conditions. We observed that lesser black-backed gulls use thermal soaring when the environmental conditions are suitable, again demonstrating their opportunistic response to ephemeral atmospheric resources. We don't go as far as in previous chapters into measuring whether a gull's knowledge of the environment can shape flight routes between movement goals in relation to uplift at sea. There are oceanographic factors which may influence the spatial distribution of thermals over the sea, particularly factors influence local sea surface temperatures such as oceanic fronts or river outflows, which could be explored in future research. However, since thermal uplift over a temperate sea is relatively rare and lacking regular features which could provide reliable hotspots of uplift, we expect that gulls are unlikely to be able to use thermal uplift on sea as a predictable resource in comparison to land.

Costs and benefits of energy saving flight

We have established that lesser black-backed gulls respond to dynamic patterns in fine-scale atmospheric uplift by opportunistically taking advantage of immediate uplift while using reliable sources of uplift in the landscape to shape their routes. How then do gulls make decisions about how and where to move in relation to the atmospheric landscape? Whilst opportunities for soaring provide energy saving benefits, they also pose potential costs; for example, how large a deviation in route is worth an energetic saving due to soaring with atmospheric uplift? How reliable does a source of uplift have to be to justify a deviation in flight route? Here we can speculate upon some of the cost-benefit trade-offs that may be important in shaping the flight decisions of lesser black-backed gulls in response to fine-scale atmospheric uplift. We can also discuss some of the potential consequences of behavioural trade-offs and provide direction for future research.

The key benefit of soaring flight is that it is energetically cheaper than flapping flight. In fact, for lesser black-backed gulls, soaring flight is nearly 4 times cheaper in terms basal metabolic rate, and is more comparable to walking than flapping (Baudinette & Schmidt-Nielsten 1974; Brown 2022). In **Chapter 3** we estimated that lesser black-backed gulls made energy savings of around 20% when comparing their true flight routes with equivalent random routes in terms of the orographic uplift provided. Large gulls have variously been referred to as flapping birds (Ainley *et al.* 2015), flight generalists (Shamoun-Baranes *et al.* 2016) and facultative soarers (Shepard *et al.* 2016)**,** which perhaps goes to highlight their recorded variability in flight mode. In this thesis we can conclude that soaring makes up a substantial portion of the lesser black-backed gull flight repertoire (mainly over land) and provides considerable benefits in terms of energy savings.

A critical cost of soaring flight is its dependence on the atmosphere. Aerodynamic flight theory predicts that the minimum sink rate for lesser black-backed gulls is 0.469 m s^{-1} (Pennycuick 2008), meaning they require uplift strength of at least this amount to maintain altitude in soaring flight. In **Chapters 3 and 4** we confirm predictions from aerodynamic theory in the patterns of soaring under orographic uplift and thermal uplift that we observe; gulls are hardly ever using thermal soaring below this uplift strength and low altitude soaring occurs at very low rates in relation to the landscape (low altitude soaring at low uplift strength is likely to be associated with gliding flight, where altitude is not maintained). The relationship between atmosphere and bird movement is also a foundational concept in optimal migration theory, particularly with respect to horizontal winds, whereby individuals may orientate themselves towards a goal, or may orientate themselves with the wind, or compensate to some degree in between (Alerstam 1979). Harvesting energy from the atmosphere as a bird frequently necessitates moving in the direction the atmosphere dictates. This raises the question of how much deviation in route is worth the benefits associated with soaring? The movement goal of an individual, and particularly the specificity of that movement goal, may influence the relative costs and benefits of responding to the atmosphere. For example, the need for a bird to reach a predetermined goal area such as a nest or a reliable foraging site within a restricted amount of time may outweigh the need to potentially save energy during that flight by taking a detour (Shamoun-Baranes & van Loon 2006). Conversely, a bird with a less specific goal, less dependent on minimising time, (perhaps undertaking exploratory movements), or with a greater need to minimise energy, may be more likely to detour in favour of energetic benefits.

Another cost to consider when studying the dependence of soaring flight on the atmosphere is the reliability of atmospheric resources. If, in our case, a lesser black-backed gull takes a detour in its route based upon expected predictable atmospheric uplift, only to find no uplift where it is usually present, how much does this cost versus never taking the detour in the first place? Predictability of resources has been widely studied in foraging theory in the context of reliable foraging patches as well as in the context of conditions for migration (Bauer *et al.* 2020; Riotte-Lambert & Matthiopoulos 2020). These same concepts are applicable to atmospheric resources influencing the daily movement patterns examined in this thesis. Predictability of atmospheric resources may be improved by taking cues from the environment, for example regarding future movements. In the context of orographic lift, it may be possible to take cues from local wind strength and direction, whilst in the context of thermal lift cues could be taken from solar radiation or temperature. If birds are able to use these sorts of cues before departing on daily foraging trips, they may be able to use fine-scale atmospheric uplift with greater reliability. Social cues can also provide added information within a relatively short field of detection; for example, birds can use visual cues of other individuals to gain information on thermal soaring conditions (Williams *et al.* 2018b).

There are several factors not accounted for in this thesis which also have potential to influence the costs and benefits of interacting with the atmospheric landscape for lesser black-backed gulls, which could provide insightful future research directions. Firstly, the atmospheric environment is not consistent throughout the year. Seasonal variation in the environment and in land management, as well as migration by lesser black-backed gulls, results in a complex environmental envelope that gulls inhabit throughout the annual cycle. The breeding season is the most energetically demanding time of year and lesser black-backed gulls regularly skip breeding (Camphuysen 2013); it is expected that they save considerable energy when they do so, as has been observed for herring gulls (van Donk 2020). Lesser black-backed gulls also have varying activity budgets across different wintering strategies (Brown et al 2022). Therefore, by studying flight response to the atmosphere throughout the annual cycle we may gain more insight into whether gull flight decisions are more energetically constrained at different points in the year. Secondly, inter-individual variation in energy saving flight behaviour may exist. This could be particularly interesting to examine in relation to foraging preferences; marine and terrestrial areas present different atmospheric environments and individuals that show a preference for either region may develop different flight strategies. Thirdly, the influence of landscape familiarity could be investigated. Spatial memory allows an individual to reduce its uncertainty with respect to its environment and this thesis focuses upon central-placed movement behaviour, which typically generates memorised locations and reoccurring space use patterns (Fagan *et al.* 2013). We see evidence in **Chapters 3 and 4** that lesser black-backed gulls have some level of knowledge about their atmospheric landscape that is likely gained by experience over time. Studies of juveniles, or of individuals in novel environments, may be able to answer questions about how birds acquire environmental knowledge, or how flight decisions driven by the atmosphere develop into repeatable behaviours over time. Finally, whilst we have identified that the atmospheric environment plays a role in shaping routes, foraging opportunities are critical to shaping route destinations, so by integrating the flight and foraging environments it will be possible to investigate how birds make trade-off decisions in relation to flight and foraging costs. These foraging costs can be influenced by the cost of travelling to different foraging areas, but also by the energetic consequences of utilising different food resources. Among a generalist gull diet there is large variation in calorific content of food (van Donk *et al.* 2017). Without knowing exactly what the energetic consequences of varying flight costs are in relation to the rest of annual energy expenditure, it is hard to determine the overall significance of the costs and benefits relating to using atmospheric uplift. If lesser black-backed gulls are able to reduce their daily energy budgets significantly by selecting reliable uplift sources in the landscape, there is the potential for the energy landscape of flight to influence exploration and even range expansion (Bonte *et al.* 2012).

The human-engineered landscape

In this thesis we see how small changes to the landscape can impact the fine-scale dynamics of the atmosphere, which propagate into the energy landscape and flight behaviour of lesser black-backed gulls. Small landscape changes alter not just the presence of uplift, but also its predictability in time and space, potentially influencing the behaviour of gulls who use environmental information to perform repeatable behaviours. We also identified that small landscape changes are heavily linked to human engineering of the landscape; from the creation of orographic corridors when a line of trees is planted, which we observe in **Chapter 3,** to the influence of urban developments on creating thermal uplift hotspots that we observe in **Chapter 4.** Beyond land cover, we see how the treatment of the soil, the levels of moisture in the soil, the choice of crop and crop management all influence thermal uplift in North-Holland.

By contrasting the heavily managed quantile landscape of North-Holland studied in **Chapters 3** and **4** with the areas of the North Sea studied in **Chapter 5,** we can gain some insight into the scale of influence that human-engineered terrestrial landscapes have on the atmosphere and therefore also on gull behaviour**.** The orographic uplift and thermal uplift landscapes studied in **Chapters 3 and 4** display high heterogeneity in uplift availability and certain areas, very much tied to attributes of the landscape, produce reliable sources of uplift. At sea the picture is quite different; whilst we did not study orographic uplift at sea, marine landscapes are comparatively homogenous in their surface and there are no structures that provide continuous corridors of uplift in the way that terrestrial landscape features do. Birds may follow in the wakes of boats (Brewster 1912) or make use of certain structures in the sea (e.g. offshore platforms, which they are also known to rest on (Vanermen *et al.* 2020)), but these areas are unlikely to provide the types of reliable uplift we see in **Chapter 3.** Regarding thermal uplift, once again the terrestrial landscape demonstrates high heterogeneity and the most important thermal lift areas for lesser black-backed gulls are associated with urban areas. At sea there are no such sources of reliable thermal uplift and thermal conditions are more tied to weather systems coming through the area, likely resulting in more opportunistic behavioural mechanisms in relation to the soaring of lesser black-backed gulls. It should be noted that the scale on which we measured conditions for thermal soaring at sea was far more coarse than on land and future studies which measure conditions for soaring on an even more fine-scale may find more features in the atmospheric landscape at sea. However, whilst a fine-scale model of uplift at sea might be able to resolve some more detail, we still do not expect to find the same degree of reliable, closely spaced uplift sources at sea as on land. Is flight over land therefore less energetically costly for lesser black-backed gulls in comparison to sea? This is likely when we note that across all soaring behaviours lesser black-backed gulls spend far less time soaring over sea compared to land; around 38% of flight time is spent in soaring at land (**Chapters 3 and 4**), but less than 7% at sea (**Chapter 5**). Does the cost of flight at sea then influence foraging decisions, especially in a generalist seabird such as the lesser black-backed gull who makes use of both marine and terrestrial foraging areas? The answers to these questions must once again be addressed by integrating the costs and benefits of all aspects of the energy landscape, from the energetic cost of flight to the energy gained from different food sources.

Despite being a flat wet temperate landscape, the region of North-Holland presents a reliable energy landscape to lesser black-backed gulls. North-Holland is in many ways a unique landscape that provides a stark example of the levels to which human behaviour can alter a landscape. North-Holland has undergone enormous geomorphological change as a result of human activity in the last 2000 years, which I briefly summarise here based on Hoeksema (2007) in the hope that an understanding of these changes will present insight into how the flight environment for birds may have altered over time. In the first millennium CE, land reclamation via the draining of peat bog resulted in peat oxidation and land subsidence, bringing the landscape below sea level and by the medieval period leaving it vulnerable to flooding from the sea, storms and encroaching lakes. Drainage of lakes via pumping was aided by technological development in wind mills, which performed the continual maintenance pumping need to keep the land dry, resulting in a landscape of outlet canals, protective dikes, and fertile clay soil from the lake beds beneath the now eroded peat. The North-Holland landscape as it is seen today is a continuation of historic land management practices as well as new developments. The land continues to be pumped of water, maintaining strict irrigation levels which, alongside the fertile clay soils, facilitate intensive agricultural practices (**Chapter 4**). Urbanisation has also continued throughout the region, leading to many urban population centres among the agricultural landscape. We can therefore conclude that the features we identified as important sources of uplift for facilitating energy saving flight may be quite recent landscape developments in many cases and that the historical flight environment for lesser black-backed gulls in North-Holland would have looked quite different in the past. This historical view of the human-engineered landscape also provides perspective when considering how the flight environment might change in the future. For example, continued increases in urbanisation may create more uplift opportunities for lesser black-backed gulls, which may have knock on effects on their flight behaviour, potentially even facilitating range expansions.

The importance of scale

Throughout this synthesis we have seen that the concept of scale has come up repeatedly as being important in studying the response of lesser black-backed gulls to their environment. The scale over which we observe movement and the environment influences the degree of variation we observe. This was found to be the case when measuring the difference in movement range between land and sea in **Chapter 2**; results on the species-wide scale indicated that little difference existed between movement range at land and sea, while between colonies there was in fact very high variation that got negated at the species wide level. This doesn't mean that broad scale generalised results aren't useful in certain contexts, but it does mean being mindful of the scale upon which certain results are applied, such as the example of using movement range to support spatial conservation decisions concerning wind farm developments given in **Chapter 2.**

In order to study ecological questions regarding the environmental drivers of flight on very fine-scales, we must measure flight and the environment at the scale relevant to the ecological question. In this thesis we made attempts to model the atmospheric landscape on the most detailed scale available, using hourly time scales and spatial scales as small as 5 m by 5 m. These scales allowed us to maximise the variability captured in atmospheric models and we were then able to aggregate the models to scales relevant to our ecological questions. In **Chapter 3** we spatially aggregated modelled orographic uplift to a 25 m by 25 m scale, which was partly based on our expectations regarding the scales upon which gulls would perceive uplift in their surroundings and the diminishing range of orographic uplift as distance from landscape features increased (Shepard *et al.* 2016). In **Chapter 4** we aggregated modelled thermal uplift to a 105 m by 105 m scale based on our expectation of the likely footprints of thermal columns forming in the landscape and the circling radii of tracked lesser black-backed gulls. High resolution environmental models therefore allow us to properly tailor our environmental information to the scale of our ecological question.

How can we then scale up our knowledge of drivers of flight behaviour on a fine scale to answer questions about behaviour on a larger scale, such as population level behaviour, species level behaviour, or changes in behaviour over long time periods? In particular, how does individual decision-making impact wider patterns of movement beyond the individual? To address these questions in future research, we need to develop our understanding of the many ways in which the environment drives movement, whether that relates to the atmosphere and weather, climatic conditions, foraging, or breeding opportunities. We need to understand how all these drivers interact with one another and how they change over long time periods. Mechanistic models of movement can go a long way to probing the impact of individual behavioural mechanisms on the behaviour of populations (Aarts et al., 2021; Brandes & Ombalski, 2004). Here the variation of conditions over long time periods can be studied for many individuals in relation to generalised environmental proxies. In empirical research, long term tracking data sets, including many individuals, and fine-scale comprehensive environmental datasets provide opportunities to measure how complex behaviour-environment interactions evolve over time. There is also a need for high-quality complementary ecological data in relation to animal tracking, such as knowledge of the breeding status, breeding success, or partnerships of individuals, which will help us to identify how energetically demanding phases of the annual cycle influence the drivers of movement.

Wind energy for all! Conservation implications in the context of bird-wind farm interactions

In this thesis we aim to deepen our fundamental understanding of the influence of the atmosphere on flight behaviour. We also aim to gain insight into how interactions between lesser black-backed gulls and the atmosphere may influence bird-wind farm interactions, using the fundamental knowledge we gained and providing examples of how this knowledge can be applied to conservation contexts. Below we outline the key findings of this thesis which offer greater insight into bird-wind farm interactions.

Over the last twenty years, ever increasing quantities of animal tracking data have been collected; as a result, there exists a practical and ethical responsibility to utilise existing data to its utmost potential. In **Chapter 2** we demonstrated an example of this by making use of existing data to improve movement metrics that can have an immediate impact on conservation policy. We show that when large enough tracking datasets exist for a species, relatively robust measures can be quantified using straightforward techniques. The time-distance function approach we take in **Chapter 2** is modelled on existing wind farm environmental impact assessment protocols (NatureScot 2018), meaning it is easily transferable to current conservation policy, yet it incorporates more comprehensive information and improves upon metrics currently used in practice. It does however remain important to maintain an understanding of how species-wide data can be applied. We see in **Chapter 2** that movement range varies a lot between breeding colonies and recommend that species-wide information only be used when no local information on specific colonies is available. Where possible, colony-specific information should be obtained in order to improve the reliability of impact assessments. However, it is not feasible to track every existing gull colony; even if it were, movement range varies within a colony as well as over time, so tracking every colony has many other limitations. We therefore need to develop methods which enable us to predict movement range, species presence, and even fine-scale movement behaviour, as all of these behaviours influence potential interactions with wind farms. In order to be able to predict species occurrence and behaviour, we need to understand how birds respond to their environment at different scales.

In the context of supporting conservation decisions relating to wind farms, a particularly important aspect of lesser black-backed gull ecology to understand and eventually work towards predicting is their use of marine and terrestrial environments. Lesser black-backed gulls live on an interface between land and sea; we have already discussed how their surrounding resource landscape influences their foraging movement decisions and this can have a big impact on where they fly. As urban gull populations have been growing and moving inland, it becomes increasingly important to gain insight into how breeding location and food availability shape the degree to which populations use land and sea areas, which many existing wind farm conservation policies do not fully account for (Quinn 2019). In **Chapter 2** we quantified the proportion of time lesser black-backed gulls spent at sea throughout the breeding season across many colonies of varying proximity to the coast. We found that the proportion of time spent, as well as movement range, varied considerably between land and sea for different colonies, even though on a species level little difference was measured. Therefore, where possible, colony wide information on land and sea utilisation should be gathered and taken into account when making estimates of colony range, or when estimating the origin of gulls in wind farm areas. Whilst over longer time periods, food availability or foraging specialization is likely to be the largest predictor of land and sea use in lesser black-backed gulls, the atmospheric flight environment may contribute to predicting daily or seasonal fluctuations of area use at land and sea, which can be relevant for wind farm planning decisions.

By studying the atmospheric flight environment, we also gain insight into small changes in lesser black-backed gull behaviour which have implications for wind farm interactions. Flight altitude determines whether a bird flies within the rotor swept zone of wind turbines and therefore where it is at risk of collision. In this thesis we have identified ways in which flight altitude is influenced by the atmosphere, specifically the presence of thermal uplift studied in **Chapters 4 and 5.** Whilst we make a link between the influence of thermal lift on flight altitude and potential wind farm interactions at sea in **Chapter 5**, there is also potential for thermal uplift to influence onshore wind farm interactions, based on the altitude range of thermal soaring we measure in **Chapter 4.** This means there is once again a need to understand differences in flight behaviour between land and sea, specifically with regards to flight altitude. Lesser black-backed gulls tend to fly at lower altitudes over sea than over land (Ross-Smith *et al.* 2016), which based on the findings of this thesis is likely to be partly influenced by differences in uplift availability. A comprehensive understanding of the underlying processes which promote changes in flight altitude among lesser black-backed gulls will make it possible to identify circumstances where potential wind farm conflicts may increase.

Throughout this thesis we have explored the flight environment of lesser black-backed gulls by defining it as an energy landscape, i.e. looking at where and when gulls are able to harness energy from the landscape to reduce their flight costs (**Chapters 3 and 4**). Incidentally, a very similar approach is taken when decision makers select areas for potential wind farm development. This creates a potential conflict, as suitable wind conditions for wind farm areas and for soaring flight frequently overlap (Katzner *et al.* 2012; Hanssen *et al.* 2020; Marques *et al.* 2020). In this thesis we identified that even very small changes to landscape features can influence soaring conditions for lesser black-backed gulls, so any consideration of the overlap between suitable soaring landscapes and wind farm landscapes should not be limited to the most prominent landscape features (e.g. ridges and hills). Detailed knowledge of how and when features create areas of concentrated bird movement provide information that can be used to designate areas less suitable for development and identify where wind farm and soaring habitats might have the greatest conflict.

It is also important for future research to consider the possible influence of wind farms on the energy landscape itself. Wind turbines create wakes which reduce downwind wind speeds, usually within a wind farm but in some cases influencing wind profiles over many kilometres beyond (Platis *et al.* 2018). Immediately upwind of turbines, wind speed is also reduced

(Porté-Agel *et al.* 2020) and there are many fine-scale stochastic vortices and eddies created by turbines. There is even evidence that the presence of wind turbines impacts the stability of the atmospheric boundary layer (Lu & Porté-Agel 2015). The influence of atmospheric fluctuations due to wind turbines on bird flight behaviour is not known; wind deflections and eddies may offer energy savings, but may bring birds into dangerous proximity to turbines, while large scale wind wake effects may alter flight costs over longer time periods. Overall, more research is needed into these interactions, but could offer insight into fine-scale flight behaviour in close proximity to wind turbines.

Future directions for fine-scale flight behaviour studies in a conservation context could aim to look more explicitly at the interactions of the environment and features which pose potential risks, such as wind turbines. Lesser black-backed gulls are generally considered at risk in relation to wind farms due to their potential for collision with turbines (Furness *et al.* 2013; Marques *et al.* 2014). To some degree, lesser black-backed gulls are expected to be able to perform avoidance behaviours within a wind farm (Thaxter *et al.* 2017c), but the degree to which they are able to avoid collision is not fully understood. A deeper understanding of the internal and external drivers of fine-scale flight movements may firstly make it easier to outright identify distinctive avoidance patterns, and may also enable us to better predict the conditions under which birds will be more (or less) capable of performing avoidance behaviours.

Conclusions

The aim of this thesis was to gain a deeper insight into how atmospheric conditions influence the movement behaviour of lesser black-backed gulls, particularly in human-engineered landscapes in the context of wind farm development. We achieved this by studying GPS tracked lesser black-backed gull flight behaviour at different scales, across and within populations, and by measuring and modelling flight behaviour and atmospheric dynamics on very fine scales. In **Chapter 2** we measured movement range across colonies throughout the lesser black-backed gull range and examined how variability across relatively simple movement metrics could influence spatial conservation outcomes. In **Chapter 3** we found that lesser black-backed gulls respond to orographic lift in their terrestrial surroundings on a fine-scale and demonstrate knowledge of predictable corridors of uplift. In **Chapter 4** we learnt that lesser black-backed gulls also regularly undertake thermal soaring and identified how the mechanics of different flight behaviours, such as circling and gliding, interact with the spatio-temporal dynamics of the thermal landscape to facilitate energy efficient flight. In **Chapter 5** we quantified thermal soaring in lesser black-backed gulls over the North Sea, identified the environmental conditions under which thermal soaring occurs in a marine landscape where soaring opportunities are expected to be scarce, and made links between thermal soaring and flight altitude in the context of interaction with offshore wind farms. Overall, the knowledge in this thesis can be used to better understand how human behaviour, even on very fine-scales, influences the flight environment for a generalist bird species, and can therefore also be applied to shaping future landscape engineering decisions.