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General Introduction
The impact of human behaviour on Earth’s ecosystems can be traced back as far as humanity itself (Boivin et al. 2016). Many of these impacts are linked to human engineering of the landscape, where the Earth’s surface is physically modified by creating or removing structures and habitats to the point of altering entire ecosystems. Agricultural development, deforestation and post-industrial land-use intensifications are all prime examples of human landscape modifications which have had significant global impacts (Ellis et al. 2013). Many species have evolved alongside human engineering of the landscape for millennia (Sullivan et al. 2017), but the rate of human induced landscape change has rapidly increased over the last few centuries, particularly in the wake of the industrial revolution of the 18th and 19th centuries, followed by the mechanisation of agriculture and urbanisation of the 20th and 21st century (Steffen et al. 2011; Corlett 2015). As a result, many species and ecosystems have faced greater environmental pressures, leading to increased rates of extinction (Pimm & Raven 2000; IPBES 2019). Habitat loss, alongside climate change, is now viewed as the main threat to species and ecosystems (Pimm & Raven 2000). Human engineering of the landscape now continues to play a role in our attempts to mitigate the catastrophic ecological impacts of past (and ongoing) human landscape modifying behaviour, from engineering projects (artificial reefs, fish friendly dams, (Schilt 2007; Bulleri & Chapman 2010) to conservation-based land use management (Antrop 2005), and, conversely, to rewilding practices which aim to minimise human interaction with the landscape entirely (Perino et al. 2019). In order for any of these interventions to be effective there needs to be conscious and informed considerations of the impacts of continuing landscape modification on organisms and ecosystems. In particular, there is a need to develop our understanding of how different species respond to environmental changes at a range of scales.

Movement is a critical biological function which nearly all organisms use to respond to environmental change. Movement allows individuals or populations to interact with different environments that meet different survival needs, or to leave environments which are not meeting these needs. Some environments offer safety for breeding or resting, others provide food resources for replenishing energy, or environmental conditions that
minimise metabolic costs. Through movement an organism can encounter these resources as and when it needs them. Just as organisms move in order to change their external environment, these external environments change how and where an organism moves, either by influencing their motion capacity, navigation capacity, or even by affecting their internal state, i.e. their drive to move in the first place (Nathan *et al.* 2008). The external environment also influences information acquisition, whether that is sensed in the environment, remembered from previous experience, genetically inherited, or gained from the social environment of other organisms (Spiegel & Crofoot 2016). The landscape through which an organism moves is important not just in determining where an organism moves to, but also how it gets there, and the costs it takes to do so. There are many costs and benefits associated with movement that depend on the environment, which can generally be linked in some way to the energetic impact they have on an organism, such as the energy used to move, or the energy gained from a beneficial feeding habitat. The distribution of these costs and benefits can be expressed as an energy landscape which can then be used to evaluate the quality of a landscape for different species and ecological functions (Wilson *et al.* 2012; Shepard *et al.* 2013; Gallagher *et al.* 2017). Energy landscapes are influenced by human modifications to the landscape and can impact movement in a range of ways, some positive, some negative. Landscape modifications create barriers to movement (Panzacchi *et al.* 2016), but may also facilitate more efficient movement (Dickie *et al.* 2017). Habitat removal can increase the distances organisms must travel to find food, shelter, or a mate (Fahrig 2007), but animals who can adapt to new habitats, such as urban habitats, may find their transport costs reduced (Fuirst *et al.* 2018).

There are global indications that human impacts on the landscape are reducing movement in many species (Tucker *et al.* 2018), however there is also a need to more deeply understand the influence of the landscape on movement at a species level.

Organisms differ hugely in their movement capacity and the degree to which they are constrained by the landscape. Flying organisms, such as most birds, could at first glance appear to bypass the constraints of the landscape by moving through the atmosphere with apparent ease. However, this is not the
case; there are many ways in which landscapes influence bird movement. Just like many other organisms, birds rely upon different habitats for survival, whether that is a safe place to breed or rest, or a reliable feeding habitat. If changes to landscapes alter the quality or density of these habitats, birds might not be able to get the resources they need from them, or will have to spend more energy travelling to habitats where they can. Flight itself can also be inhibited or facilitated by the landscape. Structures which interact with typical flight altitudes of birds, such as buildings, powerlines and wind turbines, are all known to pose as collision risks for flying animals with direct mortality consequences, or to create obstacles which birds must adjust their flight paths to avoid, again increasing their transport costs (Loss et al. 2015; Davy et al. 2017). On the other hand, landscape structures can facilitate movement by providing navigational landmarks (Mann et al. 2011).

The landscape also has indirect effects on flight via its influence on the atmosphere. Avian flight takes place in the troposphere (Davy et al. 2017), and whilst some birds have adapted to travelling at remarkably high altitudes (Sherub et al. 2016), the majority of animal flight occurs in its lowest level, the boundary layer. This is the section of the atmosphere most directly influenced by warming and friction effects of the Earth’s surface, from the ground up to spatio-temporally varying altitudes of between hundreds and thousands of metres (Stull 1988). Most transport processes occur here, with convection being the primary mechanism driving the movement of air, creating strong mixing and high winds. These air movements take place over a range of spatio-temporal scales, from sub-kilometre microscale movements that change within an hour, to large scale synoptic weather fronts that form over days or weeks (Shamoun-Baranes et al. 2017). Birds then respond to these atmospheric processes accordingly at varying scales, sometimes via an instantaneous behavioural adjustment in response to changing conditions (Elliott et al. 2014), or by altering timing or departure according to broad scale weather conditions (Bragaric et al. 2020). Birds adjust their flight speed or movement routes in response to wind conditions (McLaren et al. 2016; Collins et al. 2020), use vertical atmospheric uplifts to maintain or gain altitude (Kerling 1989; Leshem &
Yom-Tov 1996), and exploit changes in wind magnitude throughout the layers of the boundary layer to select beneficial flight altitudes or undertake dynamic soaring (Sachs 2005; Serres et al. 2019). Atmospheric movements are highly stochastic, but there are fine-scale patterns and features in the atmosphere which are consistently influenced by human engineering of the landscape. Thermal uplift, which many birds use to gain altitude by soaring, is dependent on the energy balance at the Earth’s surface, which may be altered by treatment of the land, including urbanisation and land management. Orographic uplift, whereby wind is deflected upwards over landscape features, is another source of uplift for birds and is influenced by topography, which in many regions is heavily affected by human developments. As such, bird flight is highly dependent on the boundary layer of the atmosphere, and the boundary layer is highly dependent on the landscape.

The atmospheric landscape influences the mode by which a bird flies, which then influences the energetic cost of flight and is itself also dependent on morphological, internal and navigational characteristics. These interacting factors are highly species dependent; some species are better able to display behavioural plasticity in their mode of flight due to the range of motion available to them. Flapping flight, whilst far more energy intensive, is available in any atmospheric condition. Gliding flight is far less energy intensive, but results in a loss of altitude, and an increased risk of grounding (Horvitz et al. 2014). Soaring flight allows a bird to retain or even gain altitude without the need to flap its wings and expend energy, but is dependent upon uplift in the atmosphere. Generally smaller birds are more likely to be limited to flapping flight, despite the energy savings they could make by gliding or soaring, which indicates that minimising energy consumption is not the only concern for them (Hedenstrom 1993). Many of the largest flying birds are highly dependent on soaring flight with atmospheric support (Williams et al. 2020), but some birds, often referred to as flight generalists, are more able to switch between modes of flight and may choose to do so based on internal and external drivers. Internal drivers, for example relating to breeding, or migration, can affect flight mode as a bird prioritises the need to minimise energy over time (Alerstam 1991).
External drivers influence the amount of energy birds can draw from the atmosphere to stay aloft, which may influence the energy saving strategies they use (Bohrer et al. 2012; Santos et al. 2017). These internal and external factors will therefore influence the degree to which a bird is dependent on the atmospheric landscape to support its movement.

Birds are not the only organisms that harness energy from atmospheric winds; humans have long been taking advantage of wind energy too. In particular, the wind energy industry has grown exponentially in recent decades (Esteban & Leary 2012), as we attempt to address the critical need for a clean and just transition to renewable energy sources. Wind farms are a substantial modification to the landscape, especially where large areas of land and sea are developed for wind energy generation, so there is a need to understand the potential impacts wind farms may have on species and ecosystems. For birds, there are various threats to movement that wind farms pose, resulting in direct and indirect consequences. A direct consequence of wind farms is bird collisions, whereby birds collide with wind turbines causing injury or death. Indirect consequences may arise if birds use avoidance behaviours (from avoiding individual turbines to entire wind farm areas). Cumulatively, avoidance can have a range of effects, from increasing movement costs for individuals, to reducing available habitat if birds are unable to forage in or move through wind farm areas. Bird reactions to wind farms may vary considerably between individuals, species, and locations, so there is a need to understand the drivers of bird flight behaviour in these different contexts. This knowledge can then be used to make more informed decisions throughout the planning and operating of wind farms, from using existing knowledge of species movements when positioning new wind farm developments, to applying knowledge of how birds interact with the landscape when developing new policy for wind farm development, to predicting where when and how different species move through wind farm areas in changing environmental conditions.

**Lesser black-backed gulls: flight generalists**

Lesser black-backed gulls *Larus fuscus* are long lived generalist seabirds that display enormous behavioural plasticity from the individual to species level,
resulting in high variability in their movement behaviour. As a species through which to examine questions surrounding the relationships between human engineered landscapes, the atmosphere, and flight behaviour, lesser black-backed gulls are an excellent candidate for a variety of reasons. These birds have a generalist diet, feeding on a wide range of natural and anthropogenic food resources from marine and terrestrial habitats, which results in high variability in their foraging movements. Some of their foraging resources are highly linked to human landscape use, such as agricultural fields, refuse sites, and fishery discards (Ramírez et al. 2015; Tyson et al. 2015; Isaksson et al. 2016; Langley et al. 2021), and whilst lesser black-backed gulls are often regarded as a highly adaptable species with the capacity to shift between different strategies, this is not without cost (Bicknell et al. 2013; Langley et al. 2021). Lesser black-backed gulls have a long history of responding to human pressures with both positive and negative effects (Camphuysen 2013) so it remains important to monitor the impacts of the landscape on their movements and to understand how lesser black-backed gulls make decisions with respect to the landscape. This also extends to the need to understand how lesser black-backed gulls make decisions in response to the atmospheric landscape.

Lesser black-backed gulls are flight generalists; despite primarily using flapping flight, these gulls regularly engage in soaring when conditions are suitable. During flight they respond dynamically to atmospheric features, adjusting their flight behaviour in response to wind conditions (Shamoun-Baranes & van Loon 2006; McLaren et al. 2016; Serres et al. 2019) and fine-scale atmospheric uplift (Shamoun-Baranes et al. 2016; Shepard et al. 2016; Williamson et al. 2021). By investigating the influence of external and internal drivers on flight mode in lesser black-backed gulls it becomes possible to understand the energy landscape they move through and determine how these birds budget their time and energy. The energetic consequences of these movement trade-offs can then be examined throughout other aspects of the lesser black-backed gull’s ecology as well as in conservation contexts.
In relation to the specific case of monitoring the impacts of wind farms on bird species, lesser black-backed gulls are also a species of interest. They have been identified as a species at risk of collision with individual turbines (Furness et al. 2013; Marques et al. 2014) and show variability in their attraction to wind farm areas (Cook et al. 2018). Therefore there is a specific need to understand the degree of variation in lesser black-backed gull movement behaviour and the drivers of gull movement in the context of their interactions with wind farms. There is a lot that can be learnt from lesser black-backed gull movements which will support informed decision making regarding landscape development, providing we have the right tools to investigate the dynamic interactions between the landscape, the atmosphere, and animal movement.

**Measuring movement in a dynamic landscape**

Studying movement behaviour in relation to complex atmospheric dynamics and landscape characteristics requires an understanding of the relevant scale at which research questions should be investigated, advanced technologies and methods with which to address these questions at the relevant scale, and close interdisciplinary collaboration in order to incorporate knowledge of ecological, atmospheric and earth systems (Kunz et al. 2008; Shamoun-Baranes et al. 2010). This thesis attempts such an approach, looking at movement and the environment over multiple scales and paying particular attention to how high-resolution tracking data and fine-scale environmental modelling allow us to probe the atmospheric drivers of flight. An overview of the key issues relating to study design and data collection encountered during this thesis and an overview of the main data sources used is given below.

First there is the issue of choosing the relevant spatial and temporal scale at which ecological research questions should be answered (Shamoun-Baranes et al. 2010). Such choices require an understanding of the scale at which an environmental system is influencing animal movement as well as the scale of the resulting animal movement behaviour itself. This often ends up being a somewhat tricky circular question as movement and environment are so interdependent. It is therefore helpful to incorporate as much existing
knowledge about the ecological and environmental systems as possible, ideally using interdisciplinary expertise, in order to generate expectations regarding the scales over which animal movement and the environment vary or influence each other. An iterative approach can then be taken using animal movement data to inform use of environmental data and vice-versa at multiple steps in the research process.

Next there is the issue of measuring bird flight behaviour. Here the relatively recent advancement of biologging technology has been transformative in its ability to track individuals closely across the annual cycle. Radio telemetry was first developed for animal movement studies in the mid twentieth century (LeMunyan et al. 1959) and today there exist a large array of animal tracking techniques, of which a comprehensive overview is given by (López-López 2016). The use of geographical positioning systems (GPS) has gained particular traction in movement ecology, being equipped with the capacity for high data storage, long battery lives, and presenting the opportunity to eliminate the need for recapture of an individual to retrieve a tag (Bouten et al. 2013). Miniaturisation has allowed such devices to be deployed on increasingly small animals and has facilitated the inclusion of other technologies into tags, such as accelerometers (Shamoun-Baranes et al. 2012), magnetometers (Williams et al. 2018a) and pressure sensors which can provide additional information. The lesser black-backed gulls who were studied for the majority of this thesis were fitted with UvA Bird Tracking System (UvA-BiTS) GPS trackers (Bouten et al. 2013). These loggers can track individuals throughout the year and even for multiple years, collecting positional and 3D acceleration information which can be used to track movement at high enough resolutions (up to 3 second measurement intervals) in order to measure fine-scale flight behaviours.

Finally there is the question of how to measure or model the environment that birds fly through. Having identified the relevant scale upon which the environment is influencing animal movement, ecologists generally draw from large existing data sets describing the landscape and atmosphere. These include remote sensing techniques such as using satellite imagery or LiDAR (Actueel Hoogtebestand Nederland 2022) or large scale weather
models such as those developed by the European Centre for Medium Range Weather Forecasting (ECMWF). These sorts of data can be integrated with tracking data to examine the influence of weather and environment on movement behaviour, however many of these datasets focus on broad scale conditions over large extents and do not capture fine-scale atmospheric dynamics. Instead, high-resolution environmental models might need to be developed for specific animal movement systems, especially those which operate over fine spatio-temporal scales.

One of the major challenges when assembling such large amounts of movement and environmental data is the need to find ways to appropriately store, explore, and analyse such data. Centralised relational databases and virtual labs facilitate safe storage and data exploration (Bouten et al. 2013) and have been essential for this thesis, whilst analysis methods increasingly take on techniques at the forefront of data science, utilising high performance computing and machine learning (Shamoun-Baranes et al. 2012). Collaboration between ecologists and computational scientists is therefore increasingly necessary for the growing complexity of the data we work with.

**Thesis overview**

The overall goal of this thesis is 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 address questions within this theme at different scales using animal tracking technology, (predominantly UvA-BiTS GPS trackers, Bouten et al. 2013), focusing on localised breeding season movements, and using the insights gained to explore ways in which a deeper understanding of gull movement behaviour can be used to inform future landscape modifications, particularly in the context of wind farm development.

In Chapter 2 we begin by carrying out a comparative analysis of lesser black-backed gull movements across populations and the implications for environmental assessments, particularly prior to wind farm development.
Diversity in movement patterns has been observed among colonies, but there is a need to quantify movement and variation in movement in such a way that differences among colonies can be accounted for to support land use planning. To address this, continuous estimates of lesser black-backed gull breeding season movement range are developed, using GPS data from 25 lesser black-backed gull colonies around the North, Baltic and Irish seas, and applied to examining the consequences of variation in movement range on environmental assessment outcomes.

Beyond measuring movement and examining the effects of movement variability on conservation policy, the need to understand the drivers of variation in movement behaviour is identified, part of which requires investigation into the response of birds to their aerial environment on fine scales. We therefore continue in Chapters 3-5 by focusing on the fine-scale flight of lesser black-backed gulls in response to atmospheric conditions at land and sea, examining how gulls are able to respond to dynamic change through opportunism and knowledge of their landscape. Chapters 3 and 4 use detailed environmental modelling and high-resolution GPS tracking to investigate two typical energy saving flight behaviours, thermal and orographic soaring, in terrestrial human engineered landscapes. In Chapter 3 we determine the extent to which two morphologically similar flight generalist species (lesser black-backed gull and herring gull, *Larus argentatus*) utilise orographic lift across their terrestrial surroundings in a flat landscape, and examine the extent to which orographic lift shapes their flight behaviour and routes on a fine scale. In Chapter 4 we investigate the roles of the environment and behavioural decision making during thermal soaring in lesser black-backed gulls, describing both the characteristics of their thermal soaring flight and exploring the role of a wet mosaic landscape in shaping soaring behaviour. Altogether in Chapters 3 and 4 we identify different ways in which modification of the Earth’s surface can influence the flight behaviour of gulls and their resulting movement costs.

In Chapter 5 we identify the conditions needed to undertake thermal soaring at sea, quantifying the occurrence of thermal soaring flight and the
local to synoptic weather conditions driving thermal soaring opportunities at sea. The marine landscape offers many contrasts to the terrestrial landscapes studied in previous chapters, both in terms of environmental conditions and the ways in which marine landscapes are influenced by human behaviour. The sea surface is relatively untouched compared to urbanised terrestrial landscapes, but developments such as offshore wind farms are altering sea landscapes considerably. To understand how thermal soaring flight may influence interactions with wind farms the effect of thermal soaring on flight altitude profiles is quantified alongside identifying whether thermal soaring occurs inside wind farms. We also provide an example of how multiple animal tracking sources (GPS and bird radar) can be used in a complementary way to study fine-scale flight behaviours.

In Chapter 6 we summarise the findings of this thesis in various contexts; exploring our new found ecological insight into the flight capacity and behaviour of lesser black-backed gulls, grounding this insight in the effects of the environment on gull flight behaviour, discussing the role of environmental scale in probing ecological questions, and examining the implications of this on issues across spatial conservation and wind and wildlife interactions.

This thesis forms part of a research collaboration with Gemini wind farm entitled ‘Offshore space use of lesser black-backed gulls (Larus fuscus) from the Schiermonnikoog breeding population’ which aims to quantify the potential impact of offshore wind farms on local breeding populations of lesser black-backed gulls, as well as a larger collaborative project entitled ‘Interactions between birds and offshore wind farms: drivers, consequences and tools for mitigation’ which aims to develop knowledge and tools to support sustainable co-existence between birds and wind energy. Therefore, the knowledge gained in this thesis offers species-specific insights into movement behaviour that can be incorporated into a wider research framework to offer direct conservation insights.