This electronic thesis or dissertation has been downloaded from Explore Bristol Research, http://research-information.bristol.ac.uk

Author:
Spelt, Anouk

Title:
The secret life of urban gulls

Habitat use, foraging behaviour and flight energetics of urban-nesting lesser black-backed gulls, Larus fuscus

General rights
Access to the thesis is subject to the Creative Commons Attribution - NonCommercial-No Derivatives 4.0 International Public License. A copy of this may be found at https://creativecommons.org/licenses/by-nc-nd/4.0/legalcode This license sets out your rights and the restrictions that apply to your access to the thesis so it is important you read this before proceeding.

Take down policy
Some pages of this thesis may have been removed for copyright restrictions prior to having it been deposited in Explore Bristol Research. However, if you have discovered material within the thesis that you consider to be unlawful e.g. breaches of copyright (either yours or that of a third party) or any other law, including but not limited to those relating to patent, trademark, confidentiality, data protection, obscenity, defamation, libel, then please contact collections-metadata@bristol.ac.uk and include the following information in your message:

- Your contact details
- Bibliographic details for the item, including a URL
- An outline nature of the complaint

Your claim will be investigated and, where appropriate, the item in question will be removed from public view as soon as possible.

The secret life of urban gulls

Habitat use, foraging behaviour and flight energetics of urban-nesting lesser black-backed gulls, Larus fuscus

By

ANOUK SPELT

Department of Aerospace Engineering
UNIVERSITY OF BRISTOL

A dissertation submitted to the University of Bristol
in accordance with the requirements of the degree of
DOCTOR OF PHILOSOPHY in the Faculty of Engineering.

APRIL 2020

Word count: 44,880

ABSTRACT

Urbanisation generally negatively affects biodiversity, but some opportunistic animals, like gulls, are able to adapt to urban environments and are increasing in numbers in cities. At the same time, traditional non-urban gull colonies (especially in the UK) are declining. Different aspects of the - supposedly better - living conditions in the city have been proposed for this increase in urban areas, such as fewer predators, ample nesting sites, predictable anthropogenic food sources and favourable weather conditions. However, the impacts of urban living on gull behaviour and movement ecology is relatively unstudied and little is known about how they use urban environments. Therefore, the overall aim of this thesis was to study the movement ecology of urban-nesting gulls by quantifying their habitat use, foraging behaviour and flight energetics. Between 2016 and 2019, 12 lesser black-backed gulls, *Larus fuscus*, were tracked with UvA-BiTS GPS tracking devices during the breeding season. These tracking devices collected high-resolution positional and acceleration data, the latter used to identify gull-specific behaviours and energy budgets. Additionally, observations were conducted at the nesting areas to quantify their breeding status and at feeding grounds to observe their foraging behaviours in distinct habitats. These datasets were then combined with habitat maps of Bristol and weather data from weather stations to quantify habitat use, foraging behaviour and flight energetics of urban-nesting gulls. Firstly, it was found that urban-nesting gulls in Bristol spent the majority of their time during the breeding season in suburban and urban areas, but also utilised rural areas surrounding the city. Additionally, they used distinct foraging behaviours in different habitats, appearing to adapt their behaviour to suit resource availability. Secondly, it was found that gulls matched their foraging schedule to the timing of school breaks and the opening and closing times of a waste centre, but that gull activity in a park appeared to correspond with the availability of natural food sources. This suggests that gulls are able to adjust their foraging behaviour to artificial time schedules when beneficial. Thirdly, it was found that favourable weather conditions in the city, such as the potential for thermals and orographic updrafts, affected the gulls' flight behaviour, but surprisingly, did not result in substantial differences in time investment or energy costs. This suggests that gulls are able to modify their flight behaviour to keep a relatively consistent energy budget across a wide range of weather conditions. Overall, this work shows that urban-nesting gulls are highly flexible behaviourally and are able to take advantage of a wide variety of terrestrial habitats by using a range of foraging strategies. They also time their foraging behaviour with the peak availability of food sources and are able to maintain their energy costs over a range of weather conditions by shifting their flight style to optimise their use of the aerial environment. The multiple levels of behavioural flexibility demonstrated by gulls appear to enable them to be successful in the diverse dynamic urban environment.

DUTCH ABSTRACT

In het algemeen heeft verstedelijking negatieve gevolgen voor de biodiversiteit maar er zijn opportunistische dieren, zoals meeuwen, die zich kunnen aanpassen aan de stadse omgeving en de hoeveelheid meeuwen in steden neemt zelfs toe. Tegelijkertijd, in traditionele kolonies weg van steden nemen de aantallen meeuwen af (zeker in het Verenigd Koninkrijk). In de wetenschappelijke literatuur zijn er verschillende redenen voorgesteld voor de schijnbaar betere levensomstandigheden in steden, zoals minder roofdieren, een overvloedige hoeveelheid plekken om een nest te bouwen, voorspelbare antropogene voedselbronnen en gunstige weersomstandigheden. Echter, de relatie tussen gedrag en het overleven en voortbestaan van meeuwen in de stad is nog relatief weinig bestudeerd en er is nog maar weinig bekend over hun gebruik van de stadse omgeving. Het is daarom het doel van deze thesis om het gedrag van stadse meeuwen te kwantificeren om hun gebruik van de stadse habitat, hun foerageer gedrag en hun vliegkosten te bepalen.

Om dit te doen heb ik bij twaalf kleine mantelmeeuwen, *Larus fucus*, een GPS (UvA BiTS) apparaatje als rugzakje bevestigd en heb ik ze (digitaal) gevolgd tijdens de broedseizoenen tussen 2016 en 2019. Deze apparaatjes verzamelde ongeveer elke 5 minuten data over de positie en op- en zijwaartse beweging van de meeuwen. De bewegingsdata heb ik gebruikt om gedrag en vliegkosten van de meeuwen te bepalen. Naast het verzamelen van GPS data heb ik observaties gedaan bij de nesten om het broedstadium te bepalen en bij verschillende foerageergebieden om hun foerageer gedrag te bestuderen. Ook heb ik habitat kaarten van Bristol en omgeving gemaakt en heb ik informatie over het weer verzameld met behulp van weerstations binnen Bristol. Al deze datasets heb ik vervolgens gecombineerd om het gebruik van de stadse habitat, het foerageer gedrag en de vliegkosten van de meeuwen te bepalen.

Uit mijn resultaten blijkt, ten eerste, dat stadse meeuwen in Bristol tijdens het broedseizoen het merendeel van hun tijd in steden en buitenwijken spenderen, maar dat ze ook gebruik maken van het platteland rond de stad. Bovendien blijken de meeuwen verschillende foerageer strategieën toe te passen afhankelijk van het habitat type waar ze zich bevinden ‚Äì- ze lijken hun gedrag aan te passen aan de voedselbeschikbaarheid. Ten tweede, het blijkt dat meeuwen hun foerageer schema koppelen aan de pauzes op scholen en de openingstijden van afvalcentra, maar in parken hangt hun activiteit af van natuurlijke voedselbronnen (zoals wormen). Deze bevindingen suggereren dat meeuwen hun foerageer gedrag kunnen afstemmen op menselijke activiteit als dat voor hun voordelig is. Ten derde, de gunstige weersomstandigheden in steden ‚Äì- zoals de vergrote kans op thermiek en opwaartse windstromen ‚Äì- hebben invloed op het vlieggedrag van meeuwen maar verrassend genoeg leidt dit niet tot wezenlijke verschillen in hun tijdsinvestering of vliegkosten. Het lijkt er dus op dat meeuwen hun vlieggedrag kunnen

aanpassen zodat ze in een breed scala van omstandigheden een relatief constant energie budget behouden.

Alles bij elkaar genomen laat dit werk zien dat stadse meeuwen gedragsmatig zeer flexibel zijn en dat ze door een breed scala aan foerageer strategieën kunnen profiteren van een grote verscheidenheid aan habitatten. Ze stemmen ook hun foerageer gedrag af op de maximale voedselbeschikbaarheid en kunnen door het veranderen van hun vliegstijl hun omgeving optimaal benutten en daardoor hun energie kosten handhaven in een scala van weersomstandigheden. Het lijkt er op dat meeuwen zo succesvol zijn in de diverse en dynamische omstandigheden van de stad door deze meerdere niveaus van flexibiliteit in hun gedrag.

DEDICATION AND ACKNOWLEDGEMENTS

First and foremost, I would like to thank the **gulls** in Bristol for being part of my PhD and the Urban Gull Project, especially the twelve gulls who have been wearing their backpacks with proud during the four years of the project. The females that we tagged the first year in 2016: Sansa, Arya, Lady Brienne, Daenerys, Tyrion. And the females and two males we tagged in 2017: Jon Snow, Sam, Melisandre, Missandei, Margaery, Gilly and Ygritte. Without them I would not have been able to finish my PhD. I have become increasingly passionate about the life of gulls in general and their amazing capabilities both during the breeding season as well as their migration travels, something I will never forget and hope to keep learning about.

I want to thank the **European Research Council** for providing the funding to be able to track these gulls and conduct my PhD. The funding was part of the European Union's Horizon 2020 research and innovation programme (grant agreement No. 679355).

Shane, I want to thank you for giving me the opportunity to work with you and in such a diverse research group in the Aerospace Engineering department. You accepted me as a biologist in a group of mainly engineers, and provided me with guidance, knowledge, and motivation whenever I needed it. Thank you for your comments, perseverance, and positivism during my writing process and the several rejections of the papers we have submitted. I also really appreciate your encouragement to attend different courses and conferences all over the world where I learned so many things and met amazing people. Also, your support for developing outreach activities and organising art-science events was really valuable. Thank you so much for being my supervisor and mentor during these four years.

Judy and **Emily**, I want to thank you both for being my co-supervisors and providing me with continued support during my PhD. The various meetings and Skype calls were so valuable for receiving feedback, support and just to develop new, exciting ideas. Thank you for all your comments and suggestions on the many manuscripts I have sent your way. Judy, it was great to go on adventures such as bird watching and diving during conferences and I hope we can do that again. Emily, I was so happy to hear about the exciting news and wish you all the best. I hope we will see each other soon.

Cara, my partner in crime working on the Urban Gull Project and my good friend. Thank you so much for being there from the moment I arrived on my own in Bristol and taking me to the gorge to go climbing, meeting all your friends. You have been a great support both at work and in my personal life. The discussions, cup of teas, lunchtime climbs in the gorge and all the interesting (and stinky) places we have visited were the best experiences because I was with you and we always had fun. Also, during more difficult parts of my PhD I could talk to you and you were there to help me get back to the analysis or giving me tips on writing. Our continued friendship is so valuable to me and I could not have finished my PhD without you. It was great to go through the same PhD time with you and I am happy that you have finished your PhD too. I am going to miss you, but I am sure we will see each other soon.

Peter, or Pete (which never really stuck with me), thank you so much for introducing me to the intriguing world of urban gulls. You have shown me the best and weirdest places in and around Bristol where we could find gulls foraging and spot their rings. You have been my encyclopaedia full of knowledge about gulls in general and urban gulls, which was always useful if I needed to explain any interesting behaviour we observed in the GPS data or during observations. I really enjoyed the funny conversations we had and the experience of catching gulls and ringing chicks. Thank you also for your helpful comments and suggestions on the manuscripts I have been sending you. I wish you all the best with the urban gulls in Bristol and I will definitely help to ring some chicks in the future.

Oli, I want to thank you especially for all your hard work during the summer of 2018. Your dedication to the field work and collecting interesting data has been so valuable to me. I really enjoyed our conversations even at 4 am in the morning and thanks for giving me an awesome gull-related gift for my birthday. Your hard work will hopefully be rewarded when our manuscript will be published. I wish you all the luck in London and hopefully our paths will cross again.

I also want to thank other people at the University of Bristol for their continuous support and help during my PhD. **Luca**, thank you for the helpful discussions, comments, and suggestions during each annual review over the last years. They have been very helpful, and it was great meeting you. **Jane**, thank you for your guidance, tips, and suggestions for both the fieldwork methods and the manuscript writing. I also want to thank the **Stats Clinic team** from the School of Mathematics for their helpful comments and patience with my long list of statistical questions and problems. A special thanks goes to Simon, Aoibheann, Guy, Jonty and Peter.

I want to thank the people who made it possible to set-up the equipment to collect data. Firstly, the **Physics / ASSL team** who has been very patient and helpful while we were trying many different set-ups of our equipment. Special thanks to Mike and Alastair for their continuous interest in our project and always being enthusiastic and great company when I was doing observations. I also would like to thank the **Cotham Parish Church** for allowing us to place our equipment on their roof and providing us with endless cups of tea and biscuits. Also a great thanks to the **dBs Music team** which were pleasantly surprised to hear they had gulls on their roof but were always very welcoming and helpful in providing us access. I am also grateful to Kees, Willem and Edwin for their (ongoing) support and assistance during the set-up of the project and tagging the gulls in the first year of this project.

A great thanks goes to all the people involved with the important places we have visited for conducting observations which included farms, waste centres, landfills, Avonmouth Docks, reservoirs, golf clubs, and private houses. Specifically, I want to thank Christabel Brightly from Henbury school and Katie Ganfield from Viridor Waste Centre to let us conduct multiple observations over the course of a summer.

I will always remember my fellow labmates from the **BIF group** and the whole **Flight lab** who made working at the University a better place and a fun time. I have learned so much from you about a field I thought I would never know more about. Thank you so much for the lunches, tea breaks, chats, company, and enthusiasm for the many lab activities I tried to organise, especially the yearly Dutch celebration of Sinterklaas.

A huge thanks goes to my new friends in Bristol. To my climbing friends, thank you for taking me outside to discover a whole new world of climbing. I will never forget the many trips to the pub, (pizza) dinners, playing games, conversations, gardening, cider making, comedy shows, wine evenings and fun times I have had with my friends in Bristol which made PhD life much better. My time in Bristol would have been very different without you. I also want to thank my (old) friends from around the world who have been supporting my move to the UK and starting a PhD. Thank you for the many Skype calls or even the (multiple!) visits to Bristol. It has been great to be able to share my successes and struggles during the PhD and show you the amazing city which has been my home for the last four years.

A special thanks to my family for continuous support and love during my PhD. **Remco** and **Karolina**, it has been an honour to be part of your wedding last summer and I am so happy we see each other as much as we can while living in other countries. **Mom** and **Dad**, you have been so supportive, enthusiastic, concerned and proud of me during my PhD and I really appreciate the many holidays you have taken to visit me here in Bristol. It has been great to have shared my life in Bristol with you. I have really enjoyed the many Skype family calls over the years while we were sometimes even in four different countries. Thank you for being my family and being there whenever I need it.

Last but certainly not least, **Maarten**, I cannot thank you enough as you decided to move with me to Bristol so that I could start this PhD and we would (finally) be living together in the same place for longer than 3 months. You have been encouraging me, giving me support and love, reading my work with dedication and giving constructive comments like a teacher (with a red pen). You have been so understanding during my PhD especially in moments when it felt it was too much. I am so grateful that you are here with me and enjoying (but also making fun of) this country as much as I do. I am thankful for all the holidays we spent exploring the country which cleared my mind and sometimes gave me new ideas for my PhD. I cannot imagine my life without you and I would certainly not have been able to finish this PhD in time.

AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: ANOUK SPELT
DATE: 16-04-2020

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

GENERAL INTRODUCTION

In 2019, the world population was estimated to be 7.7 billion people and is expected to grow to around 10.9 billion in 2100 (DESA, 2019). Currently, 55% of that population lives in urban areas and this is also expected to increase to 68% by 2050 (DESA, 2018). More natural areas will have to make place for cities, transportation and other related anthropogenic utilities such as agricultural lands. This phenomenon – urbanisation – is negatively affecting animal and plant populations all over the world (Marzluff, 2001; Shochat et al., 2006). However, urban cities can also create new ecological niches and some animals have been able to adapt to life in or near cities (Marzluff, 2001; Luniak, 2004). The increase in some animal numbers can result in an increase of human-wildlife interactions and to minimise these conflicts many city councils and wildlife organisations have focused on managing and controlling these urban populations. In order to be able to apply management and conservation policies properly, we need to study the effect of urbanisation on species populations and individuals to understand the behaviour of animals which are able to adapt to urban environments. This chapter will introduce the background of the effects of urbanisation on animal populations and focus on a specific case-study of a successful urban animal, the gull.

1.1 Urbanisation

Urbanisation refers to an increase in the amount of people living in urban areas shifting the population from rural to these urban areas. Urbanisation results in a change in landscape caused by urban development. Urban development has been increasing in the last century and the concentration of people living in cities can be visualised by looking at the radiation of light at night (Figure 1.1). Increasing urbanisation of the landscape will have an affect on the natural

Figure 1.1: Global map of the earth at night showing the light pollution from cities. Credit: NASA Earth Observatory images by Joshua Stevens, using Suomi NPP VIIRS data from Miguel Roman, NASA's Goddard Space Flight Center.

areas surrounding cities, resulting in habitat destruction and fragmentation. These habitats have to make place for buildings for housing people, structures such as roads for transportation and agricultural land for cultivating food (Luniak, 2004). This will negatively affect animals currently living and residing in these natural areas, and they will either have to adapt to urban environments or move away. Many different animals ranging from birds, butterflies, mammals, amphibians and carnivores have been negatively affected by urbanisation but some have managed to adapt to cities or even thrive (Blair, 2001; Marzluff, 2001; Luniak, 2004; Bateman & Fleming, 2012). Behavioural flexibility traits such as being able to use a wide variety of habitats, having an opportunistic diet, higher rates of feeding innovation, and other physical characteristics such as a medium body size and large brain have been proposed to contribute to successfully adapting or invading novel environments such as cities (Sol et al., 2002; Möller, 2009; Bateman & Fleming, 2012).

1.1.1 Effects of urbanisation on animals

Animals respond differently to urbanisation and previous studies have characterised different group types along the urban-rural gradient (Blair, 1996; McKinney, 2002): urban avoiders, urban adapters and urban exploiters. Urban avoiders reach highest densities away from cities and will only occasionally enter urban areas, whereas urban adapters are more abundant in moderately developed areas. Lastly, urban exploiters are living in urban areas and are mainly dependent on this environment with diets consisting of mostly anthropogenic food sources. Recently, this categorisation has been challenged and new categories have been proposed which are not based on densities but on the relative importance of natural and developed areas to population dynamics (Fischer et al., 2015): urban avoiders (rarely occur in developed areas), urban utilisers (presence in developed areas is dependent on natural areas) and urban dwellers (persistence in developed areas is independent of natural areas). However, categorisation is not always the best tool to quantify the effects of urbanisation on animals (Soulsbury & White, 2016) as species and populations will vary in their response to urbanisation. Additionally, the degree of specialisation might be an important factor in how animals react to landscape changes such as urbanisation. Specialist species might perform better under favourable conditions, whereas generalist species might be more flexible in changing novel environments such as during urbanisation (Andrén et al., 1997). Indeed, in general the number of specialist predators decreased and the number of generalist predators increased along a rural to urban gradient (Sorace & Gustin, 2009). The effects of urbanisation on communities, animal behaviour and life-history traits are broad and beyond the scope of this thesis, but I will shortly illustrate the effect of urbanisation on the following areas: (A) Community composition, (B) Diet and feeding behaviour, (C) Movement behaviour, (D) Reproductive success, and (E) Survival and mortality.

A. Community composition

Urbanisation changes the landscape resulting in habitat loss and fragmentation (McKinney, 2002) which negatively affect the animal communities residing along the urban-rural gradient. A community's composition can be defined by the species density (number of individuals from a given species), species richness (number of species present) and species evenness (how evenly spread in an area), with the latter two combined referred to as species diversity. Marzluff (2001) found that a small majority of studies in birds showed that urbanisation increased species density, but decreased species richness and evenness indicating that in urban areas only a few species with high but varying numbers remain. Another study on birds showed that although species richness, diversity, abundance and total biomass was lowest in urban areas, suburban areas showed the highest values suggesting that these areas might be providing more opportunities for food and/or nesting areas (Blair, 1996, 2001). Not only birds, but also several urban carnivores can reach higher population densities in urban areas compared to rural areas (Bateman & Fleming, 2012). A specific example is the population of urban red foxes, *Vulpus vulpus*, in the city of Bristol, which are estimated to have a population density of around 37 individuals per km^2 (Baker et al., 2000). Luniak (2008) collated data of most taxonomic animal groups living in Warsaw, Poland, and found a decrease in species richness with increasing urbanisation. Besides species diversity, there is also a lower amount of native species present in cities (McKinney, 2002) and increased numbers of non-native species (Marzluff, 2001).

B. Diet and feeding behaviour

The urban environment provides a range of different anthropogenic food sources for animals foraging in these areas, which can affect their diet and foraging behaviour. For example, Florida scrub-jays, *Aphelocoma coerulescens*, in suburban areas were observed to be more efficient in foraging than their rural counterparts as they foraged for less time but handled more food, which was possibly a result of the easy access to predictable anthropogenic food (Fleischer et al., 2003). Additionally, Cooper's hawks, *Accipiter cooperii*, in urban areas were observed to deliver more prey to their offspring than hawks in rural areas (Estes & Mannan, 2003). Animals that are living closer or have more access to anthropogenic food sources, generally have a higher amount of this type of food in their diet indicating an increase of consumption of anthropogenic food (Prange et al., 2004). For example, the diet of urban coyotes, *Canis latrans*, which had access to anthropogenic food sources, consisted of a higher percentage of human food than the diet of rural coyotes (Murray et al., 2015). On the other hand, for some species the urban environment does not provide sufficient food resources. Although urban European starlings, *Sturnus vulgaris*, had more human refuse in their diet, they fed less food items with a lower volume at a higher rate to their offspring than their non-urban counterparts (Mennechez & Clergeau, 2006).

C. Movement behaviour

The biological rhythms of animals and hence their movement behaviour, can also be affected by urbanisation. Several bird species have adjusted their natural rhythms, such as being more active at night or starting to sing earlier in the morning which could be due to street lighting in urban areas (Luniak, 2004; Russ et al., 2015). Additionally, large urban carnivores, like coyotes, changed their activity patterns to forage at night in order to avoid human disturbance during the day (McClennen et al., 2001). In contrast, racoons, *Procyon lotor*, foraging in urban environments do not seem to change their activity pattern in urban areas (Prange et al., 2004), however they showed smaller and more stable home ranges than in rural areas. This could have been a result of the type and distribution of anthropogenic food they consume, which was abundantly available in specific patches. In their review of urban carnivores, Bateman & Fleming (2012) showed that the majority of the urban carnivores showed a decrease in territory size compared to rural carnivores, however this was not always consistent between and within a species. Several bird species in urban areas have been observed to reduce their migratory behaviour during winter and some urban mammals showed a more sedentary life (Luniak, 2004).

D. Reproductive success

Generally it is thought that reproductive success is higher in urban areas due to the favourable conditions of cities (see section 1.1.2). However, in his review Marzluff (2001) found that the effects of urbanisation on birds' reproductive success were not consistent. Although the breeding success of the majority of the bird species increased with urbanisation, for some species it either decreased or no change was found at all. These differences between bird species is likely to reflect the adaptability of the species to urban areas and how they can benefit from human-related activity and food availability. Additionally, some birds and mammals seem to have prolonged breeding seasons, they either start breeding earlier or continue breeding in the winter (Luniak, 2004). For example, breeding Florida scrub-jays started laying their eggs three weeks earlier than rural breeding scrub-jays (Fleischer et al., 2003) and female urban black bears, *Ursus americanus*, have been observed to become reproductively active 2 to 3 years earlier than rural black bears (Beckmann & Lackey, 2008).

E. Survival and mortality

Urbanisation can also affect survival and mortality rates. Bird species are found to have higher survival rates in urban areas (Marzluff, 2001; Luniak, 2004), but this depended again on their ability to adapt to urban areas and make use of the resources available (e.g. nesting sites and food). Bateman & Fleming (2012) showed in their review that coyotes, foxes, raccoons and opossums also showed higher survival rates in urban environments compared to rural environments. Additionally, they showed that urban skunks, raccoons, black bears, foxes and badgers were on average heavier or in better physical condition than their rural counterparts, most likely due to the favourable conditions in cities (see section 1.1.2). On the other hand, higher densities of animals in urban areas can result in higher chances of disease spreading. In Cooper's hawks, the mortality rate of chicks was higher in urban nests (regardless of the more prey items delivered) due to the diseases associated with the main prey in the urban diet (Estes & Mannan, 2003). In addition, mortality rates in urban areas might be higher in some cases as a result of increased road kills (Forman & Alexander, 1998) or collisions with buildings (Loss et al., 2014).

1.1.2 Favourable conditions in cities

The previous section illustrated negative and positive changes in behaviour and life-history traits possibly due to the conditions in urban areas. Several factors have been put forward as reasons why animals would favour urbanised landscapes over their traditional habitat: abundant food availability, predator reduction, warmer temperatures, vegetation complexity, urban enhancement (e.g. providing novel structures for nesting), and artificial lighting (Marzluff, 2001; Luniak, 2004). However, the primary factors considered and studied in urban ecology are the bottom-up effect of predictable food sources and the top-down effect of lower predation pressure (Shochat, 2004).

Anthropogenic food sources, such as waste food at landfills and bird feeders in gardens, are highly available and predictable in urban environments (Belant et al., 1995; Oro et al., 2013). Higher food availability could increase reproductive success such as higher clutch sizes and eventually lead to the observed higher population densities (Shochat, 2004). However, although food can be more abundant overall, other aspects of food sources might be important too. For example, the quality of food might be low (Murray et al., 2015) or inappropriate to feed to offspring (Pierotti & Annett, 2001). Additionally, due to the high population densities in cities, competition might be too high resulting in a lower amount of food available per individual (Sol et al., 1998). In terms of the top-down effect of predation, in general less natural predators exist in urban environments possibly explaining the observed higher survival rates. Additionally, predator-prey interactions might reduce in urban areas, due to the fact that predators shift from their natural prey to anthropogenic food sources (Rodewald et al., 2011). Although natural predators are either in lower numbers or changing their foraging behaviour, new predators such as pets and feral cats are an increasing issue causing high mortality rates both in urban birds (Lepczyk et al., 2004) and other smaller animals like lizards (Koenig et al., 2002).

1.1.3 Human-wildlife interactions

High animal population densities in cities inevitably result in interactions between wildlife and people living in the cities. These interactions will likely be higher at intermediate urbanisation levels (i.e. higher species densities and favourable green spaces), higher during specific times (i.e. breeding season), and higher when opportunistic species with a wide variety in diet are involved (Soulsbury & White, 2016). Human-wildlife interactions can be either positive, providing people with pleasant experiences such as feeding birds, or negative – so called human-wildlife conflicts (Soulsbury & White, 2016).

Damage to property is an example of human-wildlife conflicts. In their review, Bateman & Fleming (2012) indicated that several carnivores may damage buildings, gardens, roads and waterways by conducting digging activities and living inside these structures. For example, badgers, *Meles meles*, digging dens are causing major problems for buildings and infrastructure in the UK (Davison et al., 2008). Additionally, bin-raiding, general noise or urination increased the nuisance and mess made by these carnivores (Bateman & Fleming, 2012). However, most of the nuisance and damage problems can be minor and with adequate education and control measures they can be prevented or reduced (Soulsbury & White, 2016). Additionally, although animals mostly avoid contact with people, living in or close to the city might result in aggressive encounters between animals and people. Although specific incidents where urban carnivores and birds were aggressive towards people resulting in injuries or fatalities do exist (Jones & Thomas, 1999; Rock, 2005; Bateman & Fleming, 2012), these attacks are rare and mainly related to territorial or defensive aggression (Soulsbury & White, 2016). Besides attacking humans, some urban carnivores can also injure or kill domestic dogs and cats (Soulsbury & White, 2016). Lastly, animals are able to carry different diseases and when living in similar areas to people, these diseases can be carried over either directly or indirectly via their pets (Mackenstedt et al., 2015). For example, urban carnivores and birds can carry multiple bacteria, parasites and diseases such as rabies and tuberculosis (Bateman & Fleming, 2012; Soulsbury & White, 2016; Borges et al., 2017) and the possibility of transferring these to humans could be a hazard to human health.

As urbanisation will increase in the future, so will human-wildlife conflicts. There is a need to understand the ecology, behaviour and demography of urban species as they seem to differ from their rural counterparts. Additionally, to mitigate human-wildlife conflicts, we need to develop proper control measures and educate the public about urban animals. Currently, due to limited knowledge of urban animals, some mitigation efforts are more based on data derived from rural populations resulting in lower effectiveness (Ditchkoff et al., 2006).

1.2 Urban-nesting gulls

An example of an urban animal which is highly successful in the city, is the gull (Figure 1.2). Members of the genus *Larus* are known to be flexible in their behaviour and can exploit novel environments (van Toor et al., 2017). Traditionally, gull species breed on islands or coastal areas and spend the majority of their life close to the sea. However, recently, gulls have been nesting in cities around the world and the term "urban gull" or "urban-nesting gull" is now increasingly used by scientists and the media. The expansion to urban environments is resulting in an increase in human-gull conflicts indicating the need for proper mitigation measures and adequate education about urban gulls. In order to develop these measures, we need to understand the ecology and behaviour of these urban-nesting gulls. This section will provide an overview of the current literature available regarding urban-nesting gull populations.

1.2.1 History of urban-nesting gulls

The first roof-nesting gulls (herring gulls, *Larus argentatus*) were recorded at a port close to the Black Sea around 1894 (Kumerloeve, 1957; Goethe, 1960) and in Bulgaria between 1890-1893 (Reiser, 1894; Nankinov, 1992). Since these first recordings, large gulls have colonized urban environments in other countries both in Europe: Belgium, Croatia, Denmark, Finland, France, Italy, Ireland, Latvia, Montenegro, Netherlands, Norway, Poland, Russia, Serbia, Spain, Sweden, United Kingdom, and outside Europe: Canada, the United States and Australia (for an overview see Cramp 1971 and Rock 2005). However, for most countries this colonisation did not start until the 1960s and 1970s and the first recordings in Northern America were only in the early 1970s in Ontario, Canada (Blokpoel et al., 1990). Multiple gulls species can now be found breeding in urban areas: lesser black-backed gulls, *Larus fuscus*, great black-backed gulls, *Larus marinus*, common gulls, *Larus canus*, yellow-legged gulls, *Larus michahellis*, ring-billed gulls, *Larus delawarensis*, glaucous-winged gulls, *Larus glaucescenwere*, western gulls *Larus occidentalis*,

Figure 1.2: Four lesser black-backed gulls, *Larus fuscus* standing on a roof in the city of Bristol, UK. © Anouk Spelt and Cara Williamson

and slaty-backed gulls, *Larus schistisagus*. Additionally, non-laridae but related gull species such as the black-legged kittiwake, *Rissa tridactyla*, have been observed nesting on suitable ledges along artificial vertical structures, especially in the United Kingdom (Coulson, 1963).

In Europe, estimates of the number of breeding pairs for most of the urban colonies are limited, outdated or non-existent. In France, 11,700 urban-nesting gull pairs were estimated in 2000 (Cadiou et al., 2004), whereas Spain contained around 50 colonies in 2003 but no estimations of number of breeding pairs were made (Marti & Del Moral, 2003). Belgium accommodated 861 herring gulls and 1,745 lesser black-backed gulls breeding in Ostend and Zeebrugge in 2015 (Stienen et al., 2016). The Netherlands accommodated 2,622 herring gulls and 4,626 lesser black-backed gulls breeding in Vlissingen and the Hague in 2015 (Lensink et al., 2010; Strucker et al., 2015). Although Poland has three different species of large gulls, only herring gulls have been observed nesting on roof-tops with estimations of 300 breeding pairs in Gdansk-Gdynia-Sopot in 2003-2004 and 150 breeding pairs in Utska (Neubauer et al., 2006). Recently, the first observations of two breeding pairs of common gulls in an urban area of Malmo, Sweden, have been published (Villavicencio & Bahamonde, 2019). Outside Europe, in the United States, around 7,922 nesting pairs at 30 colonies in four states bordering the Great Lakes were documented on roofs in 1994, consisting of 71% ring-billed gulls, 24% herring gulls and 4% unknown (Dwyer et al., 1996). In Vancouver, British Columbia, Canada, numbers of roof-nesting glaucous-winged gulls were estimated at 500 breeding pairs in 1986 (Vermeer et al., 1988). Additionally, a recent survey in Victoria, Canada showed that the number of glaucous-winged gulls here increased three-fold from 114 to 346 breeding pairs between 1986 and 2018 (Blight et al., 2019).

Interestingly, the numbers of urban gull populations in the United Kingdom and Ireland seem to be a lot higher with estimations of 100,000 urban-nesting large gull pairs in 2004 based on previous counts and growth rates (Rock, 2005). From the 1940s, large gulls started to relocate from coastal areas inland and into urban environments, starting in Cornwall, followed by Dover and other surrounding areas (Parslow, 1967). One of the first counts of urban-nesting gull populations in 1969-70 showed that herring gulls nested in 55 urban locations in the UK and Ireland of which five locations had over 100 nests (Cramp, 1971). This was an enormous increase compared to a count in 1939 when only six urban locations consisted of nesting herring gulls with approximately one to nine nests per site (Cramp, 1971). Contrastingly, lesser black-backed gulls have been slower to colonise urban areas in the UK and Ireland and during the same count in 1969-70 only 61-62 breeding pairs were found at seven sites (Cramp, 1971). However, in 1976 lesser black-backed gulls had moved to several other areas in the UK including Bath, Bristol, South Shields, Sunderland and Newcastle (Monaghan & Coulson, 1977). This increase in number of gulls was probably a result of the implementation of the Clean Air Act in 1956 which prevented waste companies from burning their waste and resulted in an increased amount of waste food available for gulls on landfills. This extra source of anthropogenic food could have strengthened the increase of urban-nesting gulls and could have led to an overall increase in gull numbers in the UK after that point (Parslow, 1967; Mudge & Ferns, 1982). In the last decades, urban-nesting gull populations in the UK have been growing with estimates of 16,900 herring gull and 3,200 lesser black-backed gull breeding pairs in 1994 (Raven & Coulson, 1997) and numbers of around 31,000 gull breeding pairs during the last seabird census "Seabird 2000" between 1998-2002 (Mitchell et al., 2004). This number of breeding pairs is closer to the estimations from Rock (2005), however, the numbers are thought to be an underestimation as it is difficult to monitor nests in urban areas in comparison to traditional rural colonies due to unreliable vantage points (Monaghan & Coulson, 1977). In their study in Dumfries, Coulson & Coulson (2015) showed that vantage point surveys (used in the estimation of 1999-2002) only detected 78% of the actual nests present. Adjusting the counts of the "Seabird 2000" census would result in around 40,000 gull breeding pairs which is still a lower amount than estimated by Rock (2005). Recently, unmanned air vehicles (drones) have been used to survey an urban-nesting population of glaucous-winged gulls in Victoria, Canada, which proved to be a promising method for estimating breeding pairs (Blight et al., 2019).

1.2.2 Reasons for urban-nesting in gulls

In general, urban gull populations are increasing all over the world. On the other hand, especially in the UK, non-urban gull populations (island or coastal areas) have experienced declines over the

Figure 1.3: Overview of the possible reasons for urban-nesting in gulls. © Anouk Spelt and Cara Williamson

same period (Balmer et al., 2013; Eaton et al., 2015). The population patterns do differ per colony and show both decreasing and increasing trends in the three main gull species residing in the UK; herring gulls, lesser black-backed gulls and greater black-backed gulls (Nager & O'Hanlon, 2016). However, overall the numbers are decreasing leading to the amber listing of the lesser black-backed gull and the red listing of the herring gull on the Birds of Conservation Concern (BoCC) assessment of the British Trust of Ornithology in the UK (Eaton et al., 2015). Gulls are expanding their range to cities and seem to successfully adapt to these novel environments. Therefore, the question arises whether the living conditions in the city are currently better for gulls than in traditional non-urban areas.

Several reasons have been proposed for why gulls live and breed successfully in the urban environment (Figure 1.3). Firstly, food is readily available due to abundant predictable anthropogenic food sources, such as waste in the streets, feeding of birds in gardens and parks, and close proximity to landfills within and surrounding the cities (Monaghan & Coulson, 1977; Belant et al., 1998; Cannon, 1999). Gulls are opportunistic foragers with a wide variety of food sources in their diet and can therefore take advantage of all the different food types that become available in the city. Secondly, cities have fewer natural predators for gulls (Monaghan & Coulson, 1977; Raven & Coulson, 1997) and especially roof-nesting gulls build their nests high on buildings away from potential predators, such as foxes. However, some urban gull colonies which are not located on roofs but on the ground, have shown high predator pressure where red foxes killed all the chicks in the port of Zeebrugge, Belgium (Stienen et al., 2016). Thirdly, some cities have ample roof structures suitable for nesting (Monaghan, 1979; Belant, 1993) resulting in relatively low nest densities in urban areas (Petit et al., 1986). This can be advantageous as it would reduce the chick mortality due to intra-specific predation common at non-urban gull colonies (Monaghan, 1979; Perlut et al., 2016). Fourthly, artificial street lighting in cities might provide the opportunity for gulls to change their natural rhythm and start foraging at night, increasing their opportunity to encounter food sources and potentially their daily energy intake (Rock & Vaughan, 2013). Fifthly, urban environments are generally warmer than their surrounding areas due to the unequal heating of the artificial surfaces in the city compared to the surrounding areas, which results in the so-called "Urban heat island" (UHI) effect (Kim, 1992; Arnfield, 2003). This warmer temperature could provide gulls with better breeding conditions, such as a prolonged breeding season and early breeding opportunities (Raven, 1997; Rock, 2005). Lastly, the weather conditions in the city are quite complex and unique. The UHI effect could result in higher probabilities of thermals, columns of rising air. Gulls are known to make use of thermals to save energy during flight (Shamoun-Baranes et al., 2016; Williamson et al., 2020). Additionally, the wind conditions in the city could provide sources of orographic lift when wind is deflected upwards by structures such as buildings and trees. Gulls are also known to be able to make use of these orographic updrafts to save energy by switching from energetically expensive flapping to the more cheaper flight strategy soaring flight (Shamoun-Baranes et al., 2016; Shepard et al., 2016; Sage et al., 2019; Williamson et al., 2020).

1.2.3 Current knowledge of urban-nesting gulls

The favourable conditions in the city can affect or change the life-history traits of urban-nesting gulls. Several studies have looked into nesting behaviour (A), reproductive success (B) and diet characteristics (C) of urban-nesting gulls, some comparing the results to non-urban colonies, however, only a few studies have looked at their movement behaviour (D). Here, I summarise the current knowledge of urban-nesting gulls.

Figure 1.4: Examples of several nests of urban-nesting lesser black-backed and herring gulls in the city of Bristol, UK. © Anouk Spelt and Cara Williamson

A. Nesting behaviour

The nesting behaviour of urban-nesting gulls have been studied in different parts of the world and gulls seem to use a wide variety of places to construct their nests (Figure 1.4). In the UK, large gulls in the city of Dumfries, Scotland, mainly nested on flat roofs of commercial buildings and within a few meters of each other (Coulson & Coulson, 2009). This was similar to a study in a mixed-colony on a large industrial building where the distance to the nearest neighbour was 5 m for herring gulls and 6.5 m for lesser black-backed gulls (Raven, 1997), indicating that urban gulls do have a type of colony structure. However, many individuals were observed to nest solitary typically on chimney stacks but even these individual nests were not more than 100 m apart from each other (Coulson & Coulson, 2009). Indeed, other gull species were observed to be nesting either in small colonies or have isolated nests on roofs such as the glaucous-winged gull (Vermeer et al., 1988) and the slaty-backed gulls (Zelenskaya, 2019). In contrast, due to the fact that the urban-nesting population of yellow-legged gulls in Barcelona is low in numbers and wide-spread over several roofs, Petit et al. (1986) argued that they do not consider these urban-nesting gulls as a colony but as individual nesting areas. Lastly, there seems to be a difference between gull species in preference for the roof structure used for nesting as the majority of herring gulls nested on chimney stacks and sloping roofs but lesser black-backed gulls preferred to nest on the ground and both flat and sloping roofs (Sellers & Shackleton, 2011). It also seems that glaucous-winged gulls preferred flat roofs but nests were mostly placed against structures found on the roof (Hooper, 1988).

B. Reproductive success

Reproductive output of urban-nesting gulls has been studied and compared to gull populations in traditional non-urban habitats in several countries (Table 1.1). One of the first studies, comparing the reproduction effort in large gulls between roof-top and island-nesting colonies was done by Mudge (1978). In this colony, clutch size and hatching success were lower on roof-top colonies, which was probably a result of higher human disturbance on these roofs. Recently, a study in Portland, Maine, USA, observed the same low clutch size and hatching success in a herring gull roof-top colony, however, the egg volume was similar and chicks had a higher chance to survive to day 30 than in a traditional colony (Perlut et al., 2016). This is in contrast with a study on herring gulls in Ohio, USA, where clutch size and hatching success were equal between roof-top nesting and island populations but eggs were larger and hatched later on roof-tops (Belant, 1993). Similarly, the clutch size and hatching success in herring gulls nesting on rooftops in South Shield and Sunderland, UK, were similar to published data from other UK island colonies, but they found higher fledging success on the roof tops (Monaghan, 1979). A generally high fledging success of both herring gulls and lesser black-backed gulls was also found in several towns in Cumbria, UK (Sellers & Shackleton, 2011). In another gull species, the glaucous-winged gull in Victoria, British Colombia, Canada, there was no difference found between gulls nesting on rooftops and on islands for several reproductive variables: date of clutch initiation, clutch size, incubation period, hatching success, fledging success and mortality rate (Hooper, 1988). However, in Vancouver, Canada, post-hatch fledging success in the same urban gull species was higher than previous observations in non-urban populations in the same region (Kroc, 2018). Clutch size was similar but hatching success was lower in urban gull populations of western gulls compared to non-urban populations in the United States (Pierotti & Annett, 2001). In Venice, Italy, the clutch size was smaller for yellow-legged gulls nesting on rooftops than of a population in a lagoon nearby, but the breeding performance (i.e. fledging success) did not differ (Soldatini et al., 2008a). Lastly, very recently a long-term study on slaty-backed gulls showed that urban gull colonies in the city of Magadan, Russia, had a higher fledging success than surrounding natural gull colonies (Zelenskaya, 2019).

It is apparent that the difference in reproductive output between urban and non-urban populations are contrasting (Table 1.1). A possible explanation for these contradictory findings could be that urban populations differ in nest densities, with some gulls nesting close to each other and others individually. Lower nest densities on roof-top colonies could simply mean less aggression from neighbouring birds and thus result in lower intra-specific chick predation (Monaghan, 1979; Perlut et al., 2016). Indeed, rooftops that contained fewer nests of glaucous-winged gulls had a higher reproductive success than rooftops with higher nest density (Vermeer et al., 1988). Additionally, disturbance is generally less in rooftop colonies due to lower predation pressure, however birds can be disturbed by humans visiting or working on the roofs (Mudge, 1978).

Table 1.1: Overview of the differences in reproductive success between urban and non-urban gull populations of different species of gulls. + = higher values in urban populations, - = lower values in urban populations, x = no difference between populations, CS = clutch size, EV = egg volume, HS = hatching success, FS = fledging success, HG = herring gull, LBBG = lesser black-backed gull, GWG = glaucous-winged gull, WG = western gull, YLG = yellow-legged gull, SBG = slaty-backed gull.

Country	Species	CS	EV	HS	FS	Reference
United Kingdom	HG/LBBG	-		-		Mudge (1978)
United Kingdom	HG	x		x	+	Monaghan (1979)
Canada	GWG	x		x	x	Hooper (1988)
United States	HG	x	+	x		Belant (1993)
United States	WG	x		-		Pierotti & Annett (2001)
Italy	YLG	-			x	Soldatini et al. (2008a)
United Kingdom	HG/LBBG				+	Sellers & Shackleton (2011)
United States	HG	-	x	-	+	Perlut et al. (2016)
Canada	GWG	-			+	Kroc (2018)
Russia	SBG				+	Zelenskaya (2019)

Figure 1.5: An urban-nesting gull feeding bread to its chicks on a roof in the city of Bristol, UK. © Anouk Spelt and Cara Williamson

C. Diet

Large gulls are considered to be opportunistic foragers making use of a wide variety of food sources including anthropogenic food (Annett & Pierotti, 1999; Kim & Monaghan, 2006; Camphuysen et al., 2015) (Figure 1.5). Gull colonies located on coastal areas or islands rely mainly on marine food sources (Camphuysen, 1995; Oro et al., 1997; Tyson et al., 2015), although this differs per species (Washburn et al., 2013). Nevertheless, it seems that these non-urban gulls are increasingly using terrestrial environments and have been observed foraging in cities, at landfills, at sewage outfalls and on agricultural fields (Mudge & Ferns, 1982; Greig et al., 1986; Washburn et al., 2013; Isaksson et al., 2016). At one colony of inland breeding lesser black-backed gulls, individuals were only using terrestrial food resources with refuse dumps as the most used site, followed by agricultural fields and freshwater bodies (Gyimesi et al., 2016).

When looking at urban gull colonies, the diet of common gulls nesting on a roof in Northern Germany consisted mainly of terrestrial natural food sources including cherries, earthworms and insects (Kubetzki & Garthe, 2007). Earthworms and insects were also found in the majority of the pellets in roof-nesting lesser black-backed gulls and herring gulls in the UK followed by food waste and marine food sources (Raven, 1997; Coulson & Coulson, 2008). Food items in the diet of herring gulls nesting on rooftops in Cardiff, UK, mainly consisted of mammalian tissue, chicken and bread which were probably obtained at refuse tips (Mudge & Ferns, 1982). Herring gulls and ring-billed gulls nesting on roofs in Ohio, USA, showed differences in their diet, with herring gulls mainly feeding on fish and ring-billed gulls having anthropogenic food as the major contributor to their diet (Belant et al., 1998). The diet of these roof-nesting herring gulls in Ohio showed a relatively similar diet compared to gulls nesting on a nearby island, except that the occurrence of medium-sized birds in the diet of roof-nesting gulls was greater than in the diet of the island-nesting gulls (Belant et al., 1993). Also, comparing the diet of ring-billed gull chicks between urban and non-urban areas in Quebec, Canada, showed that both diets contained mostly waste, but the type of waste was different (Brousseau et al., 1996). The diet of urban chicks contained more household waste and the diet of non-urban chicks more agricultural waste which was probably linked to the surrounding environment of their nests.

Anthropogenic food waste seems to be a bigger part of the diet of urban-nesting gulls than of non-urban gulls, but the contradictory results show that the proportion depends on the species, location and the resources available to them. Additionally, the quality of anthropogenic food waste obtained at landfills and waste centres is under debate with some studies showing its low quality and difficulty for small chicks to digest (Pierotti & Annett, 1987; Hillstrom et al., 1994) and other studies linking it to a higher reproductive success (Hunt, 1972; Pons, 1992) and a higher body conditions (Auman et al., 2008). A reason for these contradictory results could be the fact that anthropogenic food waste consists of complex carbohydrates which contain many

Figure 1.6: Lesser black-backed gull with GPS backpack flying in the city of Bristol, UK. © Anouk Spelt and Cara Williamson

nutrients but might also be difficult to digest for gulls and therefore not providing them with enough energy (Pierotti & Annett, 1987). Additionally, the important factor might not be the quality of the food, but the quantity that parents are feeding to their offspring (Sotillo et al., 2019a). Sibly & McCleery (1983a) suggested that gulls are able to obtain food more efficiently at landfill tips, but this may depend on the age of the gulls as feeding at landfills is thought to be an acquired skill and it might take some years to become competent (Greig et al., 1983).

D. Movement behaviour

Most of our knowledge about urban-nesting gulls is known from ringing data, observations and diet samples as discussed previously. In the 1960s, methods for tracking animals with portable radio transmitters were designed, however only since the end of the last century, miniature, light-weight Global Positioning System (GPS) devices (Figure 1.6) have been used extensively resulting in a more detailed understanding of the movement behaviour of animals (Cooke et al., 2004; Sokolov, 2011). Although GPS devices have been deployed on gulls nesting on islands and coastal areas (Klaassen et al., 2012; Camphuysen et al., 2015; Thaxter et al., 2015; Isaksson et al., 2016; Shamoun-Baranes et al., 2016), only a few studies have looked into the movement and foraging behaviour of urban-nesting gulls.

A radio-tracking study in Ohio, USA, showed that adult urban-nesting ring-billed gulls used landfills more frequently (77% of locations) than urban-nesting herring gulls (34% of locations) (Belant et al., 1998) which was also reflected in their diet. Another study in ring-billed gulls nesting on an island in the city of Montreal found that the birds preferred to forage in agricultural lands (40% of their time) and the nearby river (42% of their time) compared to anthropogenic habitats (14% of their time) (Caron-Beaudoin et al., 2013). Four herring gulls nesting on rooftops in St. Ives (a coastal town in the UK), were highly variable in their activity patterns visiting both marine and agricultural lands (Rock et al., 2016). A study with the same species nesting along the east coast of the USA on three different islands varying in degree of urbanisation showed that gulls at more urbanised colonies visited urban areas more frequently, had a lower diversity of habitat types, had shorter trip durations and showed higher rates of site fidelity (Fuirst et al., 2018). These four short-term (1 year) studies are the only studies published to my knowledge that have followed the movement behaviour of urban-nesting gulls during the breeding season with tracking devices.

Movement patterns of urban-nesting gulls outside the breeding season have not been published yet to my knowledge. Individuals from non-urban colonies in the UK and the Netherlands showed a range of migration strategies from migrating to warmer countries like Portugal and Spain to residing more locally close to the breeding grounds (Klaassen et al., 2012; Thaxter et al., 2014a). Ross-Smith et al. (2014a) reported that their preliminary analysis of ringing data from urban-nesting gulls might imply that there are different migration strategies between gulls from non-urban and urban populations suggesting that urban populations might be more sedentary.

1.2.4 Human-gull conflicts

The favourable conditions in the city discussed in section 1.2.2 seemed to have led to an increase in numbers of gulls in cities worldwide. Urbanisation and the colonisation of gulls into cities also led to an increase in conflicts between gulls and people. City councils are receiving numerous complaints about gulls even resulting in the Aberdeen City Council publishing a "Survivors guide: Living with urban gulls" in the UK (Aberdeen City Council, 2019). Additionally, there are many stories in the media about city residences being attacked by gulls and information about how to avoid gull attacks (Ellis, 2014; D'Albiac & Gibbons, 2019).

The main perceived problems of gulls residing in cities are general nuisance, aggression, damage to property, and health risks (Belant, 1997; Rock, 2005; Villavicencio & Bahamonde, 2019). Especially in the breeding season, gulls nesting on buildings can produce a high level of noise and mess due to creation of nests, communication between individuals, destruction of rubbish bags or bins, and raiding food (Rock, 2005; Huig et al., 2016). Additionally, parents can be very protective during this stage and aggressive towards any person or animal getting close to their nest. This generally results in an increase in complaints about aggression and attacks when the breeding season starts (Rock, 2005). Gulls nesting on rooftops are observed to damage property by using materials for nests, defecating on buildings and cars, and obstructing drainage on roofs due to blockage by nesting materials (Monaghan & Coulson, 1977; Belant, 1993). For example, Vermeer et al. (1988) found that a roof containing nests of gulls had a shorter life span due to both drainage obstruction and defecation of the gulls. Lastly, gulls are known to carry many different bacteria either related to human diseases or resistant to antibiotics (Belant, 1997; Smith et al., 2014). Although threats are generally minimal, gulls that carry for example the *Salmonella* or *Clostridium botulinum* bacteria can cause a threat to human health when they visit contaminated sites such as landfills and sewage outlets before visiting potable water reservoirs (Ortiz & Smith, 1994; Hatch, 1996; Ferns & Mudge, 2000).

Several non-lethal and lethal control measures are being used to control the numbers of gulls in urban areas. Examples of non-lethal measures are covering the waste on landfills and separating the food waste from other types of waste (Belant, 1997). This will reduce the access to food sources on landfills and waste centres, however within cities food availability, such as waste on the street and the intentional feeding of gulls, should be also reduced. This can be achieved by educating people to stop feeding, however it seems that this does not always work (Clark et al., 2015). Additionally, using frightening devices such as distress calls, loud noises, Mylar flags and birds of prey at waste centres could be effective (Belant, 1997; Rock, 2004a), however it seems that the effect is only temporary until the gulls habituate (Baxter & Robinson, 2007; Soldatini et al., 2008b). Another method to prevent gulls from entering waste centres is placing wires over the area where food waste is deposited. However, the effectiveness is dependent on the spacing between the wires and the species visiting the waste centres (Belant & Ickes, 1996). In cities, nesting of gulls can be prevented by installing netting on roofs. This is very expensive and is only effective when it is well designed, properly installed and looked after (Rock, 2005). When this does not happen, netting can have detrimental consequences resulting in gulls getting trapped in netting and eventually dying (BBC, 2018). Additionally, netting on buildings forces the birds to relocate, possibly creating problems for adjacent buildings. Lethal control measures include the culling of gulls which can happen only with appropriate licences (Ross-Smith et al., 2014b). At a landfill site near Montreal, Canada, culling was more effective than the non-lethal method of rubber shots as the latter showed signs of habituation during the trials (Thiériot et al., 2012). Less invasive but still lethal are egg manipulation and nest removal. Oiling or pricking the eggs can prevent the eggs from hatching and parents from relaying eggs (Belant, 1997). This will result in prolonged incubation period and avoid the noise related to the chick-rearing stage (Rock, 2005). For example, removal of nests and eggs at high-density urban gull colonies in Dumfries, Scotland, resulted in complete desertion of the nesting area and reduction of breeding pairs in the vicinity in the next year (Coulson & Coulson, 2009).

Although there are several control measures being implemented, it seems that most of these measures do not work on the larger scale, and only are effective locally and temporarily (Belant, 1997; Rock, 2012). This could be a result of the habituation which has been observed in several studies (Baxter & Robinson, 2007; Soldatini et al., 2008b; Thiériot et al., 2012). Additionally, birds seemed to move and relocate to adjacent landfills when deterred from one landfill (Rock, 2004a). Lastly, in Ontario, control measures did reduce the problems related to nesting gulls, but the overall population of urban gulls was not reduced (Blokpoel et al., 1990). In order to understand human-gull conflicts and apply control measures properly, understanding the ecology and specifically the movement behaviour of gulls nesting in urban environments is crucial.

1.3 Study aim and research questions

In the UK, numbers of gulls at non-urban populations are generally decreasing whereas numbers of gulls breeding in cities are increasing. Several advantages of urban-living for gulls have been proposed but the exact reasons for their success in cities is still disputed. Alongside the increase in number of gulls in cities, conflicts between gulls and humans are also increasing. Research has mainly focussed on nesting behaviour, reproduction and diet of urban-nesting gulls and only a few short-term studies have looked at their movement behaviour. There is a need for fine-scale and long-term studies looking at the behaviour of these urban birds to understand their life-history traits and be able to mitigate human-gull conflicts. Therefore, the overall aim of this project was to study the movement behaviour of urban-nesting gulls by quantifying their habitat use, foraging behaviour and flight energetics.

1.3.1 Research questions

This study aims to answer the following questions:

1. To what extent do urban-nesting gulls use urban environments and does this change with breeding stage?
2. Are there temporal patterns in the foraging behaviour of urban-nesting gulls and how are these linked to human-related activity and food availability?
3. How do weather conditions affect both time investment and energy costs of urban-nesting gulls?

1.4 Thesis outline

Chapter 2 will outline the general methods used in this thesis (Figure 1.7). The study area and species, lesser black-backed gulls, will be described alongside the GPS tracking system used in this study and the catching and tagging procedures of the gulls. Both field and nesting observations will be explained in detail and the quantification of the behaviour of the gulls based on accelerometer data is described. Preparation of other datasets such as habitat data, elevation data and weather data will also be clarified.

Chapter 3 will focus on the general habitat use of urban-nesting gulls in Bristol based on the GPS tracking data and field observations. This will be discussed in light of the different breeding stages. Additionally, specific time-activity budgets in different foraging habitats will be described also in light of the breeding stages, and eventually how this could potentially inform management and conservation policies.

Chapter 4 will follow up on chapter 3 by looking into more detail at the use of specific urban feeding grounds and the anthropogenic food predictability in cities. This chapter will look into one possible reason of why gulls might be successful in cities, namely if they are able to adjust to artificial temporal cycles in food availability in urban feeding grounds. The time schedules of gulls will be investigated by field observations and GPS tracking data to look into the temporal patterns in foraging behaviour and relationship with human-related food availability and activity.

Chapter 5 will describe how urban-nesting gulls deal with the specific weather conditions in the urban environment to follow up from Chapter 3 where I found that the gulls spent the majority of their time in the city. The possibility of utilising the weather conditions in the city, such as thermals and orographic lift, could potentially be another reason of why gulls are thriving in cities. The effects of weather on time investment and energy costs will be discussed on both a daily and a trip level.

Chapter 6 will summarise the findings of this thesis and discuss their wider implications, limitations and future directions.

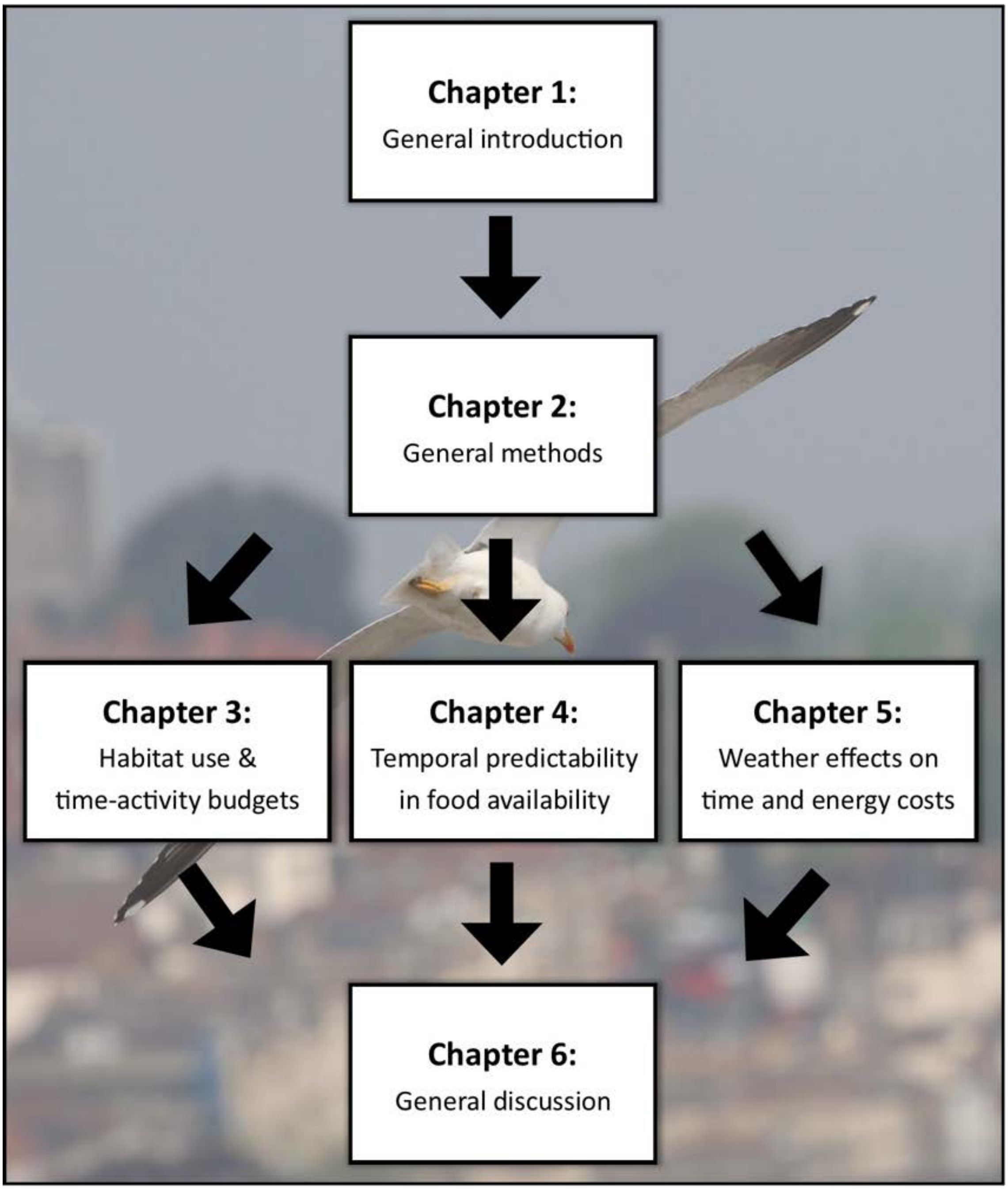

Figure 1.7: Overview of the structure of the thesis.

CHAPTER 2

GENERAL METHODS

This project was conducted in Bristol, United Kingdom, from May 2016 until August 2019 including four breeding seasons (2016, 2017, 2018, 2019). Several datasets were collected and prepared to answer the aim of this study. This chapter will give an overview of the general methods used to collect the different datasets to be able to understand the habitat use, foraging behaviour and flight energetics of urban-nesting gulls in Bristol.

2.1 Study area and species

Bristol is the largest city located in south-west of England, UK, covering an area of approximately 110 km^2 with a human population of 463,400 (Bristol City Council, 2019b). The city has a small city centre which is highly urbanised surrounded by a wider area with suburban housing. Around the city, the landscape is characterised by agricultural lands, lakes and some forests. The river Avon flows through the city centre to the Severn Estuary which is located ~10 km from the centre.

The urban-nesting gull population in Bristol has been monitored since 1980 by Peter Rock, but the first gulls (herring gulls) nesting on roofs were recorded in 1972 (Rock & Vaughan, 2013). After this first reporting, the population of both lesser black-backed and herring gulls (ratio 3:1) has increased quickly from 100 breeding pairs in 1980 and 1,000 pairs in 1990 to 1,922 pairs in 2004 and 2,954 in 2010 based on personal observations from Peter Rock (2004b, 2010). The nation-wide count census of seabirds "Seabird 2000" recorded 482 apparently occupied nests (AONs) of herring gulls and 1,210 AONs of lesser black-backed gulls in Bristol between 1998-2002 (Mitchell et al., 2004). Since 1980, Peter Rock has implemented a colour-ring scheme for gull chicks in Bristol and surrounding areas with currently around 6,340 chicks being ringed.

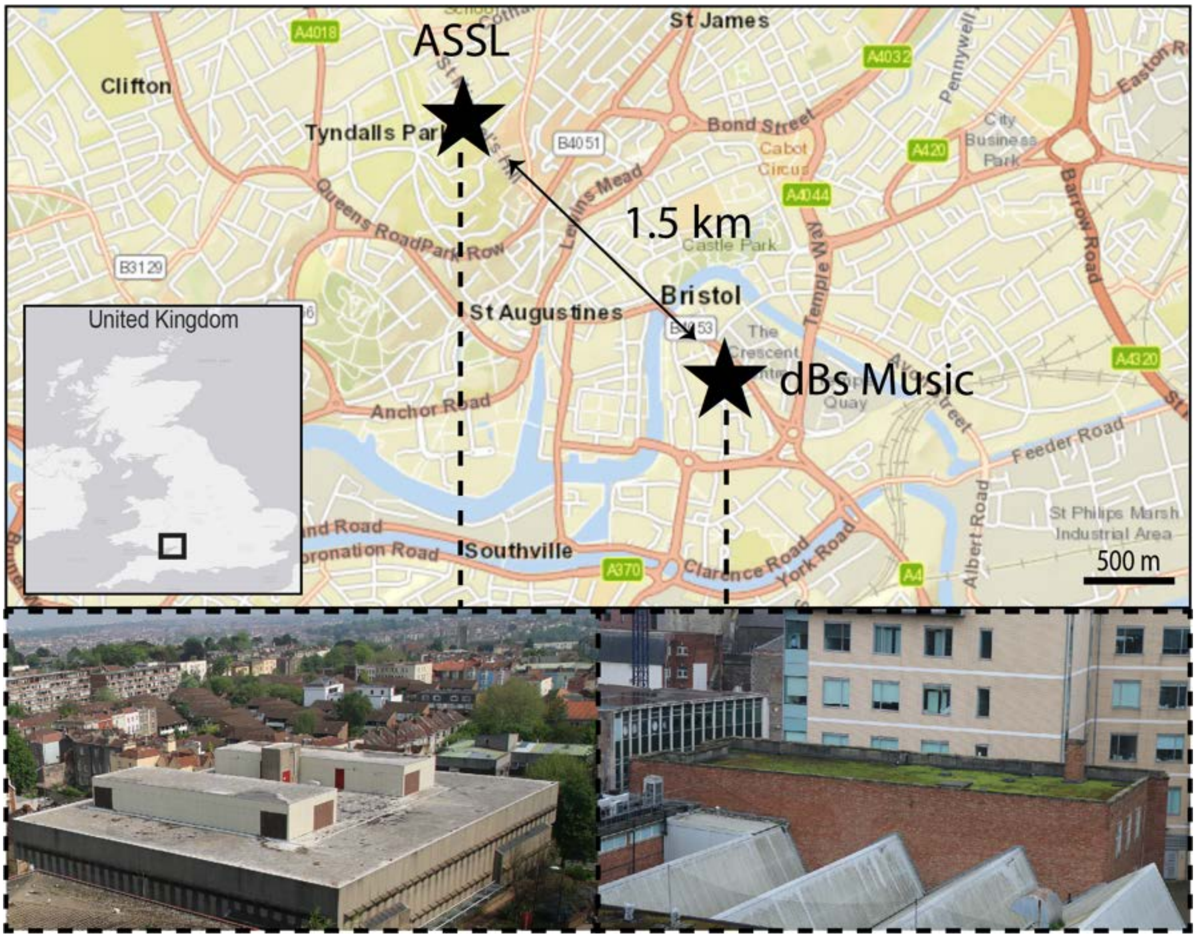

Figure 2.1: The two study locations in Bristol, UK. The Arts and Social Science Library (ASSL) is situated at the University of Bristol and the dBs Music centre is situated in the city centre. The two locations are situated approximately 1.5 km from each other. © Anouk Spelt and Cara Williamson. Base map sources: Esri, DeLorme, HERE, USGS, Intermap, iPC, NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Thailand), MapmyIndia, Tomtom.

Gulls are nesting on roofs throughout Bristol either solitary or in small colonies. Two roofs were selected as study locations which had at least five breeding pairs; the Arts and Social Science Library (ASSL) at the University of Bristol and the dBs Music building in the centre of Bristol (Figure 2.1). Both buildings were located in the the city centre at approximately 1.5 km from each other. ASSL is a large building (LxWxH is 41x48x13 m) in the middle of the University of Bristol has two plant rooms on the top of the roof. Nesting has been recorded since at least 2004 (P. Rock, personal observation) and on average six to eight gulls were nesting on this roof during 2016-2019. Nests were spread out (>15 m between nests) and built upon the roof structure. dBs Music is a smaller building (LxWxH is 34x16x11 m) in the centre of Bristol. Nesting has been recorded since 1980 (P. Rock, personal observation) and on average eight to ten gulls were nesting on this roof during 2017-2019. Nests were closer to each other on this roof (>5 m between nests) and the roof structure contained a mossy layer on which the nests were built.

2.2 GPS tracking

2.2.1 The system

This study used high-resolution tracking global positioning system (GPS) devices to understand the movement behaviour of urban-nesting gulls. The GPS devices were obtained from the University of Amsterdam Bird Tracking System (UvA-BiTS) which was developed by the Institute for Biodiversity and Ecosystem Dynamics (Bouten et al., 2013). These trackers are small (61x25x10 mm), lightweight (~13.5 gram), solar-powered with rechargeable batteries, have an internal antenna and high memory capacity (~220 mAh, Figure 2.2). Moreover, they contain a tri-axial accelerometer, and speed, altitude and temperature sensors. A special feature of this system is the communication via a Zigbee two-way radio transceiver which provides automatic data transfer and data processing, plus the settings on the GPS devices can be changed remotely according to the needs of the project at that moment. The spatial resolution of the GPS devices depends on the GPS interval ranging from 1.13 m (interval 6 s) to 29.95 m (interval 600 s, Bouten et al. (2013)).

The GPS devices communicate via a Zigbee connection (2.4 GHz) with a base-station and/or a relay antenna when inside their reception area. The base-station consists of a base antenna, a 15 m cable attached to a field laptop which is the main system manager (Figure 2.3). The relay station contains an antenna, 15 m cable and a battery pack which lasts for 50-100 days (Figure 2.3). At the ASSL, one relay antenna was used to provide a broader reach of reception, whereas at the dBs just the base-station antenna was sufficient. The base-station communicates with the relay antenna via the same Zigbee connection and both have a 70° horizontal and 30° vertical range. The field laptop from the base-station contains the Birdtracking programme where data are downloaded and stored. In this programme the user can also change the settings of the GPS devices when necessary and can remotely access this field laptop by a programme called *LogMeIn*. Furthermore, this system provides an online environment, *'Virtual lab'*, where data can be handled, downloaded and visualized. Bouten et al. (2013) have published a paper where more detailed information can be found about this useful system.

2.2.2 The set-up

During the breeding seasons of 2016 and 2017, different set-ups of the system were examined in both study locations. Although the UvA-BiTS system has been used in a wide variety of landscapes, this was the first time it was used in an urban environment. The system can communicate with the GPS devices over a distance up to six km in rural areas, but sometimes in Bristol the system did not work at a distance of five metres. After several tests, we discovered that the problem was most likely due to the interference with Wi-Fi networks, which use the same frequency as our Zigbee connection. This resulted in intermittent connection between the base-station, relay

Figure 2.2: A GPS device from the University of Amsterdam Bird Tracking System (UvA-BiTS) used in this study with a £2 coin as reference. The GPS device is small (61x25x10 mm), lightweight (~13.5 gram), solar-powered with rechargeable batteries, has an internal antenna and high memory capacity (~220 mAh).

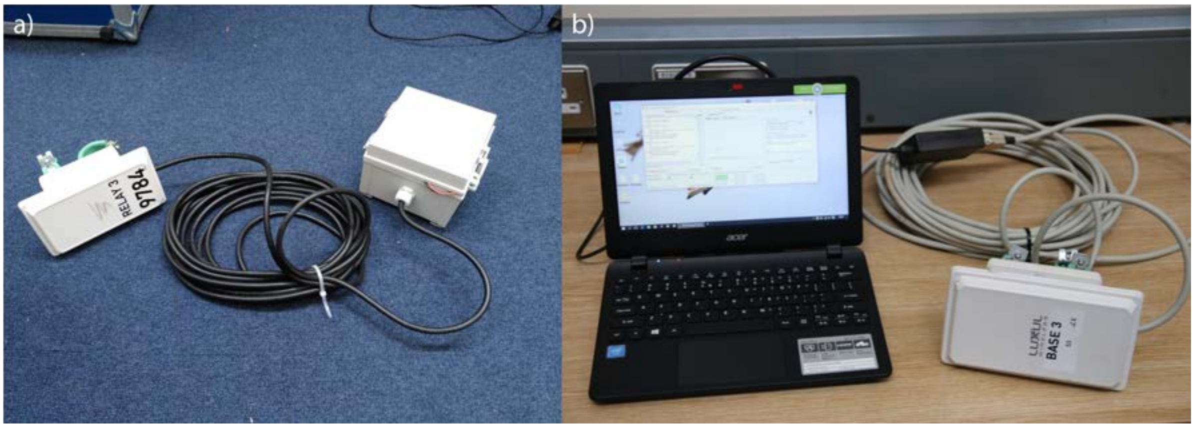

Figure 2.3: The equipment used in this project to communicate with the GPS devices, including a) relay station with antenna, 15 m cable and battery pack, and b) base-station with antenna, 15 m cable and a field laptop as main system manager. The antennae and GPS devices communicate with each other via a Zigbee connection (2.4 GHz).

antenna and GPS devices (mostly working at night when the University students were using Wi-Fi networks to a lesser extent). Several set-ups were investigated in both study locations including placing antennae on high buildings surrounding the locations and on the roof of the study locations themselves. The quality and speed of the connection between the base-station and GPS devices were compared between the set-ups. Figures 2.5 and 2.6 demonstrate the final set-ups with the least interference at the two study locations.

The ASSL building has two plant rooms on top of the roof which limited the placement of the base-station on the roof itself because not all the nest were covered by its range (Figure 2.5). Therefore, the base-station was placed on a high building in proximity of the ASSL building (Physics building). Some of the gulls' nests were on the back side of the ASSL building where the plant rooms were blocking the line of sight from the base-station antenna located at the front. Therefore, a relay antenna was placed on a high building on the opposite side of the ASSL building compared to the base-station. The base-station antenna was placed on a two-metre pole attached to a railing on the roof of the Physics building (south of ASSL) whereas the relay antenna was placed on top of the Cotham Parish Church (north-west of ASSL). Both base-station and relay antennae were placed in line of sight with each other and with the roof of ASSL.

The dBs building has medium parapets and is relatively lower than its surrounding buildings (Figure 2.6). Initially, the base-station was placed on top of one of the surrounding buildings to the south but due to the interference with Wi-Fi networks in the area, no connection could be made with the GPS devices. Placing the base-station on the roof of the dBs building itself resulted in better connections in every corner of the roof. Therefore, no extra relay antenna was needed as the base-station could cover all the nests on the roof. To minimise the access to the roof and disturbing the gulls, the laptop was placed in a waterproof box on the roof close to the base-station antenna. A USB dongle with internet was included to be able to access the laptop remotely and to download the data.

2.2.3 The settings

The interval of data collection could be changed remotely in the system manager and was adjusted based on the time in the year, the location of the bird and the weather conditions. In general, outside the breeding season data was collected every 30 minutes for all birds in the first year, after which the settings were changed to every 60 minutes in order to save battery life. During the breeding season and when the birds were in the nesting area, data was collected every 10 minutes. This interval was chosen to save battery life as we were not particular interested in the birds' behaviour at the nest. Outside the nesting area, the interval of data collection was generally five minutes which was increased to four seconds depending on the battery voltage (above 4.05 V). Sunny weather increased the voltage of the (solar-powered) battery and thus the interval of data collection. The nesting area was defined by setting a GPS fence around each

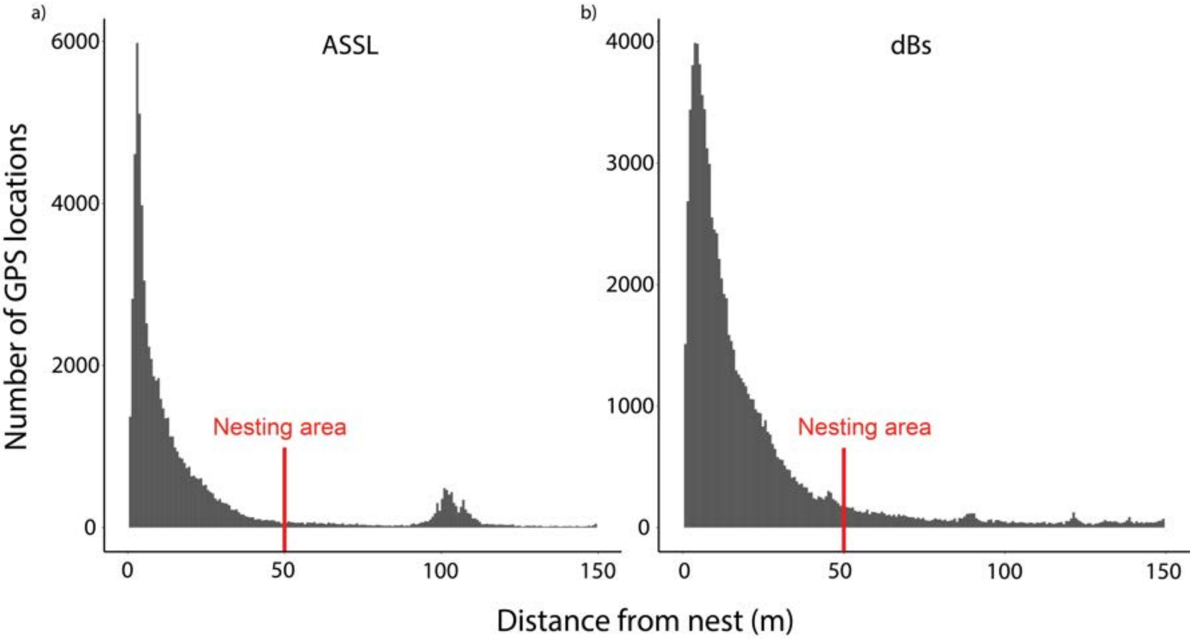

Figure 2.4: The frequency of distance from each nest (m) per GPS measurement. a) Arts and Social Sciences library (ASSL). b) dBs Music Centre (dBs). The cut-off for defining the nesting area was determined visually and was defined as a radius of 50 m for all nests. The peak at 100 m at the ASSL location was a result of some individuals roosting on the same nearby building.

study location based on a cut-off radius of 50 metres. This value was chosen based on visual inspection of the number of GPS locations plotted against the distance from the nest (Figure 2.4).

Data was collected from the beginning of May for the five individuals tagged in 2016 and for the additional seven individuals tagged in 2017. Unfortunately, one GPS device (ID 1) failed after one week resulting in only a small amount of data from this individual and was therefore excluded from the dataset. A second GPS device (ID 4) was not working properly and rebooted itself every time it had a low battery voltage resulting in a lower amount of tracking days especially during the winter. Two individuals (ID 7 and 8) died during the breeding seasons of 2018 and 2019 respectively because of they were trapped in roof netting. Table 2.1 gives an overview of the tracking data of all the individuals for the whole year and during only the breeding seasons of 2016-2019.

2.3 Gull handling

2.3.1 Catching and tagging

In May 2016, five lesser black-backed gulls were caught and tagged with GPS devices on the ASSL. The roof was accessible through one of the plant rooms. The roof consisted of a safe working area enclosed by high railings. Most of the gulls were nesting in the corners of the roof and

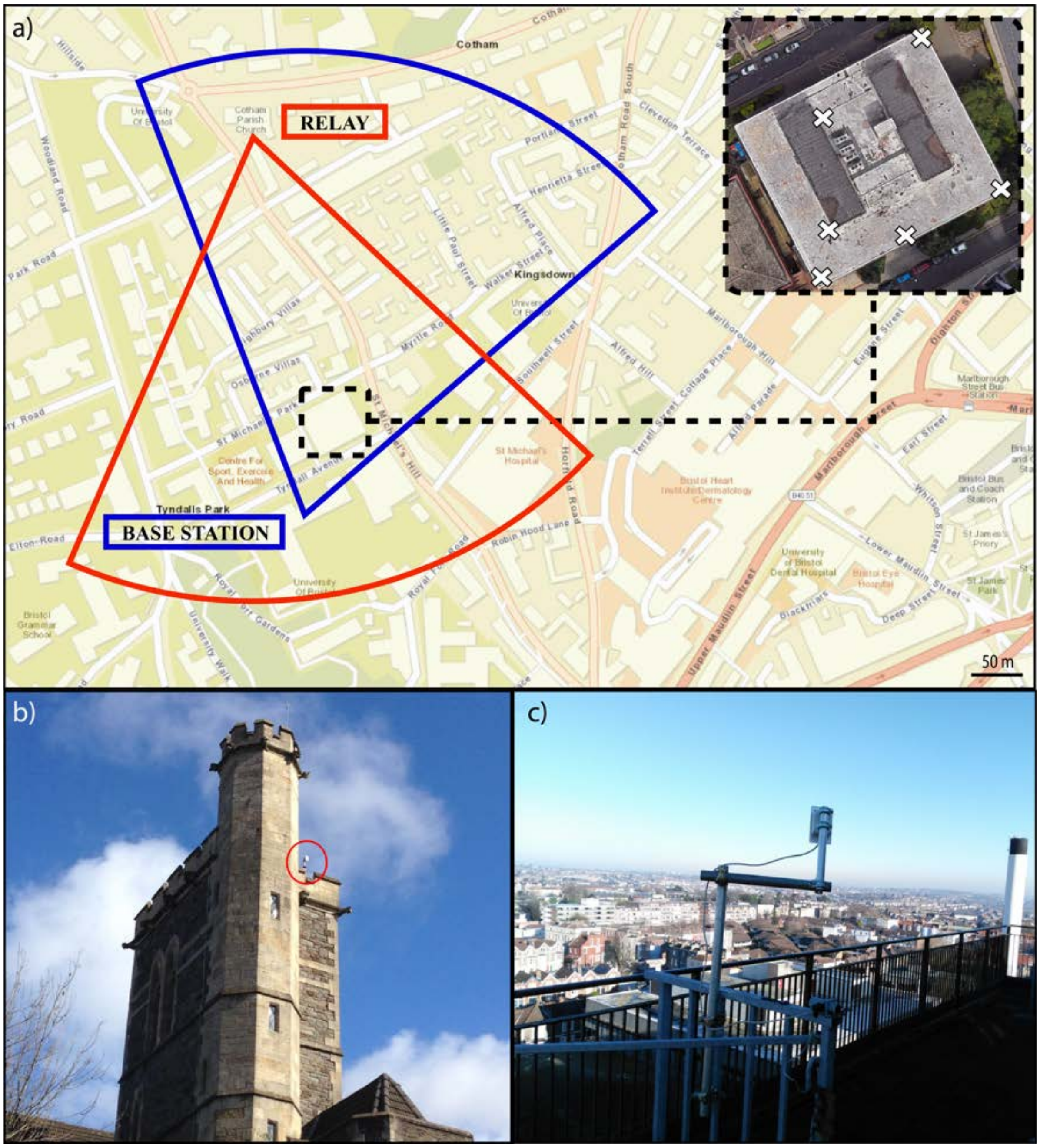

Figure 2.5: The set-up of the equipment for gulls nesting on the Arts and Social Science (ASSL) building. a) The base-station was placed on top of the Physics building which is in close proximity of ASSL (blue) and the relay antenna was placed on top of the Cotham Parish church on the opposite side of ASSL (red). The dotted square represents a close up of the top view of the ASSL roof with the two plant rooms on top and the locations of the studied nests (white crosses). The radius and range of the antennae are for illustrative purposes and not true to reality. b) The relay antenna placed on top of the Cotham Parish church. The red circle indicates where the relay antenna is located on the roof of the church. c) The base-station antenna situated on top of the Physics building. © Anouk Spelt and Cara Williamson. Base map sources: Esri, DeLorme, HERE, USGS, Intermap, iPC, NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Thailand), MapmyIndia, Tomtom.

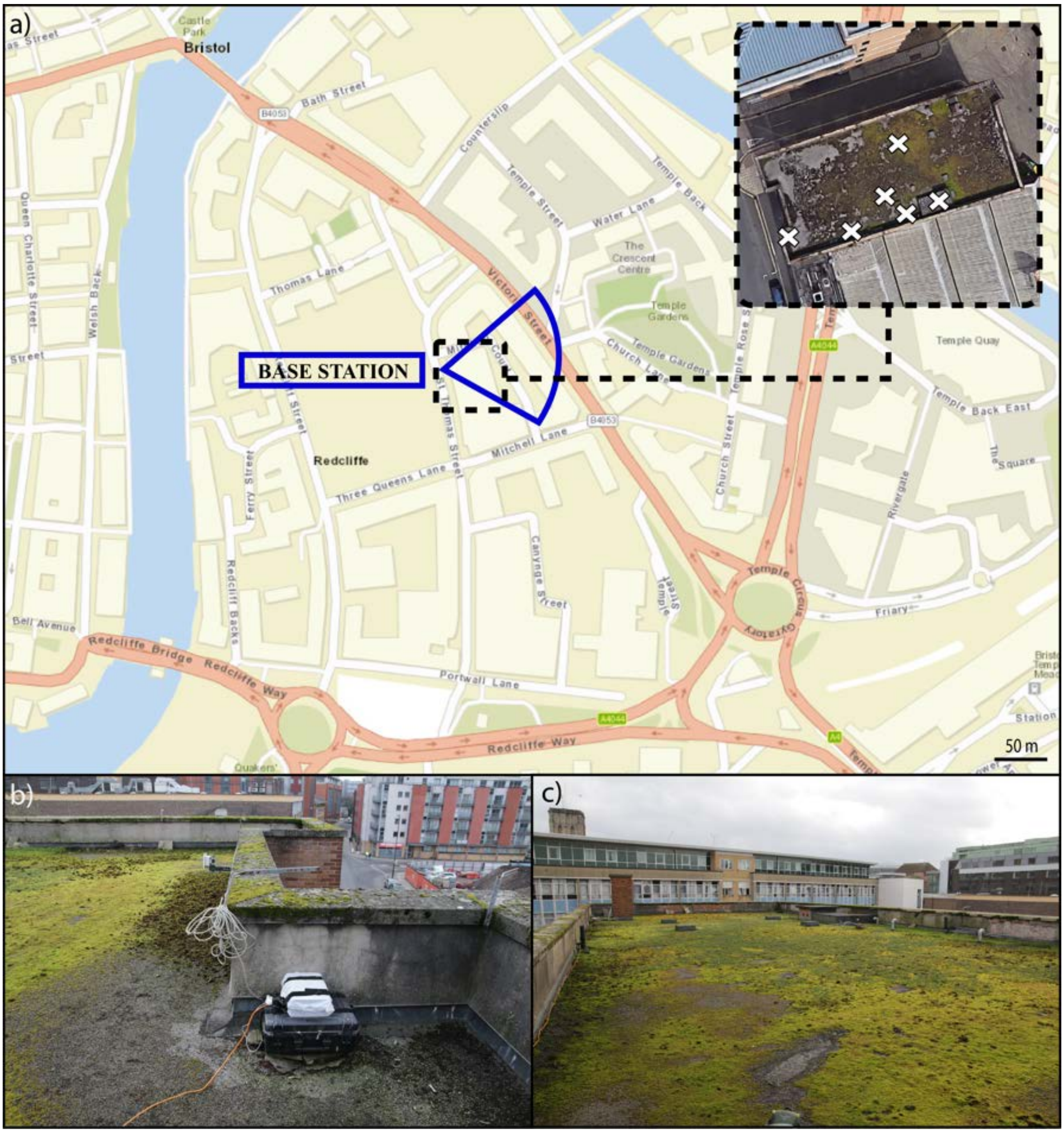

Figure 2.6: The set-up of the equipment for the gulls nesting on the dBs Music building. a) The base-station situated on top of dBs Music roof. The dotted square represents a close up of the top view of the dBs Music roof with the locations of the studied nests (white crosses). The radius and range of the base-station antenna are for illustrative purposes and not true to reality. b) The base-station antenna with the laptop in a waterproof box on the roof. c) A view from the base-station antenna covering the whole roof. © Anouk Spelt and Cara Williamson. Base map sources: Esri, DeLorme, HERE, USGS, Intermap, iPC, NRCAN, Esri Japan, METI, Esri China (Hong Kong), Esri (Thailand), MapmyIndia, Tomtom.

Table 2.1: Overview of the GPS tracking data of the 12 individual gulls followed during four breeding seasons (2016-2019) in Bristol, UK. Five individuals were tagged in 2016 and another seven individuals in 2017. Individual 1 did not collect any data after one week of tracking and was therefore excluded from the dataset. The birds were nesting on two different roofs; Art and Social Sciences Library (ASSL) and dBs music Centre (dBs). Days, fixes and fixes per day (fix/day) are given for the whole year and for when birds were breeding (including fixes at the nest).

ID	Roof	Start date	End date	Whole year			Breeding only		
				Days	Fixes	Fix/day	Days	Fixes	Fix/day
1	ASSL	05/05/2016	11/05/2016						
2	ASSL	04/05/2016	09/08/2019	986	242,421	246	219	132,958	607
3	ASSL	04/05/2016	28/07/2019	798	513,088	643	324	408,773	1,262
4	ASSL	05/05/2016	05/08/2019	297	96,706	326	80	24,169	302
5	ASSL	09/06/2016	02/07/2018	754	149,259	198	19	17,257	908
6	ASSL	18/05/2017	15/08/2018	454	266,679	587	57	88,398	1,551
7	dBs	08/05/2017	20/05/2018	373	241,027	646	73	174,687	2,393
8	dBs	08/05/2017	10/04/2019	703	303,665	432	156	216,610	1,389
9	dBs	08/05/2017	02/07/2018	421	291,665	693	46	86,907	1,889
10	dBs	10/05/2017	10/08/2019	820	362,257	442	212	260,871	1,231
11	dBs	12/05/2017	11/08/2019	821	451,102	549	96	172,579	1,798
12	dBs	19/05/2017	10/08/2019	788	326,893	415	236	260,818	1,105
			Mean	**656**	**294,978**	**471**	**138**	**167,638**	**1,312**
			Min	**297**	**96,706**	**198**	**19**	**17,257**	**302**
			Max	**986**	**513,088**	**693**	**324**	**408,773**	**2,393**

therefore catching them included a high risk of falling of the roof. A belay-system with ropes was constructed to keep the person safe who placed the trap and retrieved the bird. In 2017, an additional seven individuals were caught and tagged, of which six at dBs and one at ASSL. This resulted in a total of 12 individuals over two study locations. In both years, nests with eggs and individuals, that had incubated the eggs for one to two weeks, were selected to ensure the gulls were committed to returning to the nest after placement of the trap. Only one individual per nest was tagged with a GPS device to avoid negative effects on the breeding output of the pair.

The individuals were trapped by placing a cage over the nest which would trap the individual inside. Two different cages were used: (1) a metal trap-door cage consisting of a door which was triggered to close when the bird was sitting on the nest and (2) a walk-in chicken wire cage which made sure the individual could enter but not leave the cage (Figure 2.7). The eggs of the individuals were replaced with fake eggs to prevent damage and overheating. Each individual was weighed and biometrics were measured following standard protocols (see section 2.3.2). Additionally, the individuals were ringed with a metal ring on their left leg and a colour ring on their right leg. Afterwards, the GPS device was attached and handling time was minimised to prevent high stress levels and irreversible changes in behaviour.

Several methods have been proposed to attach GPS devices to birds, but for lesser black-backed gulls the wing harness method was found to be the best method (Thaxter et al., 2014b). The wing harness used in this study was made from tubular Teflon^{TM} ribbon (Bally Ribbon Mills 8476-.25") and was going around the wings and the neck of the individual (Figure 2.8). The combined weight of the GPS device and harness was 18 gram, which was on average 2.4% (range: 2.1-2.7%) of the bird's body mass, which is below the 3% margin generally accepted for tracking animals (Barron et al., 2010). All work was approved by the University of Bristol Animal Welfare and Ethical

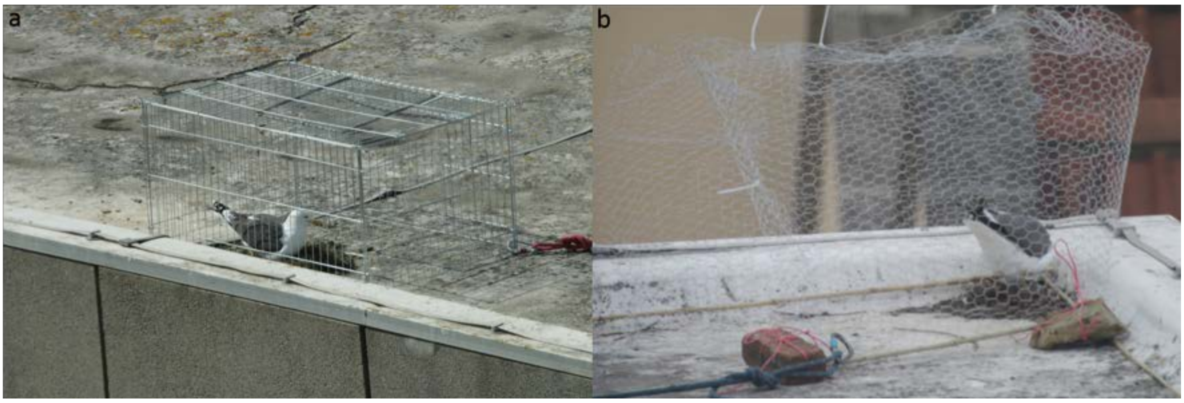

Figure 2.7: The two different cages used in this study to catch the gulls on the roof: a) a metal trap-door cage and b) a walk-in chicken wire cage. © Anouk Spelt and Cara Williamson

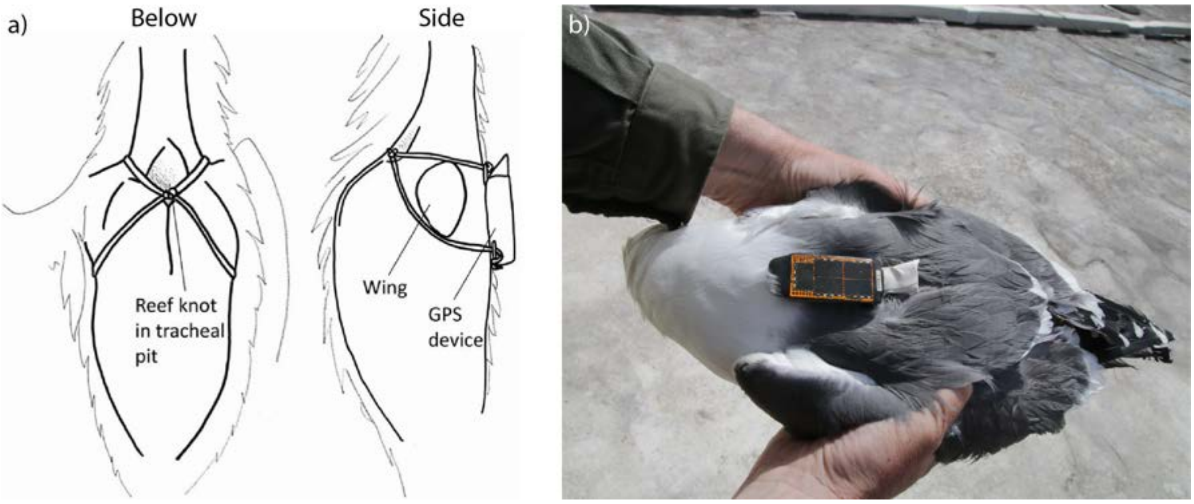

Figure 2.8: Overview of the attachment and position of the wing harness on the gulls. a) View from below and from the side, showing the position of the wing straps and the GPS device placed on the bird's back with straps going around the wings. Modified from Thaxter et al. (2014b). b) Photo of GPS device attached to an individual gull just before releasing. © Anouk Spelt and Cara Williamson

Review Body (UIN UB/15/069). Bird handling, tagging and temporary egg removal was conducted under BTO permit A/2831. All work was carried out in accordance with the relevant guidelines and regulations.

2.3.2 Bird biometrics

Several biometrics were measured for each individual including mass, wing length and total head length (i.e. head and bill), and bill depth at gonys (Table 2.3). The mass was determined by weighing the individual in a bag attached to an electronic scale (1 gr calibration). The head length and bill depth were measured with a Mitutoyu dial caliper (0.05 mm precision). Wing length was measured with a standard ruler (0.1 mm precision). The sex was determined by comparing the head length and depth of the bill to wing length (Rock & Vaughan, 2013) and observations of their sexual behaviour at the nest. All five individuals caught in 2016 were females and from the seven birds caught in 2017, only two were males. Gulls are known to show bi-parental care where both the male and female partner invest equally in their offspring, therefore differences in the movement behaviour of the different sexes can probably not be attributed to the differences in parental care. Lastly, the length and width of the eggs of each nest were measured to calculate egg volume following Harris (1964):

$$V = l * w^2 * (k/1000) \tag{2.1}$$

where V = volume (mm^3), l = length (mm), w = width (mm), k = constant of 0.476. Total clutch volume was then calculated by summing the volume of the eggs of one clutch.

2.4 Observations

2.4.1 Nest observations

Nest observations were conducted to identify breeding status and reproductive success. Monitoring started weekly in February/March to identify the nests and the individuals with GPS devices. Monitoring was performed twice a week when birds started to build nests and incubate their eggs (April/May) until most of the chicks had left the nests (end July). Afterwards, monitoring was performed weekly again until the majority of the gulls had left the roofs and the equipment was taken down. With a telescope (Swarovski STX 30-70 x95) the date and the amount of non-hatched eggs, hatched eggs and chicks were recorded. With this data breeding status and reproductive parameters could be estimated (Table 2.2).

Table 2.2: Overview of the breeding data of the 12 individual gulls followed during four breeding seasons (2016-2019) in Bristol, UK. Laying dates (lay) and hatching dates (hatch) are given for each individual for each year. Breeding output gives information about the reproductive output at the end of each breeding season: individual was not breeding (no nest), individual was breeding at another colony (other), individual has died (X), unknown where nest of individual was (unknown), none of the chicks hatched (eggs), all the chicks died during the breeding season (died) or at least one of the chicks fledged at the end of the season (fledged).

ID	**Roof**	**2016**		**2017**		**2018**		**2019**		**Breeding output**			
		Lay	**Hatch**	**Lay**	**Hatch**	**Lay**	**Hatch**	**Lay**	**Hatch**	**2016**	**2017**	**2018**	**2019**
1	ASSL	01-May	30-May							Fledged	Unknown	Unknown	Unknown
2	ASSL	04-May	27-May	22-May	13-Jun	22-May	11-Jun	16-May	07-Jun	Fledged	Died	Died	Died
3	ASSL	15-Apr	20-May	30-Apr	25-May	05-May	28-May	26-Apr	24-May	Fledged	Fledged	Fledged	Fledged
4	ASSL	04-May	07-Jun					28-Apr	18-May	Died	No nest	Other	Fledged
5	ASSL	02-Jun	22-Jun							Died	No nest	Unknown	Unknown
6	ASSL			10-May		22-May	13-Jun				Eggs	Died	No nest
7	dBs			27-Apr	24-May	06-May					Fledged	Eggs	X
8	dBs			30-Apr	24-May	30-Apr	28-May				Fledged	Fledged	X
9	dBs			30-Apr	26-May						Died	Unknown	No nest
10	dBs			27-Apr	25-May	16-May	07-Jun	30-Apr	28-May		Died	Fledged	Fledged
11	dBs			26-Apr		30-Apr	29-May	NA	NA		Eggs	Fledged	Fledged
12	dBs			09-May	31-May	15-May	05-Jun	01-May	27-May		Fledged	Fledged	Fledged
	Mean	**05-May**	**02-Jun**	**03-May**	**28-May**	**10-May**	**04-Jun**	**02-May**	**27-May**				
	Min	**15-Apr**	**20-May**	**26-Apr**	**24-May**	**30-Apr**	**28-May**	**26-Apr**	**18-May**				
	Max	**02-Jun**	**22-Jun**	**22-May**	**13-Jun**	**22-May**	**13-Jun**	**16-May**	**07-Jun**				

Table 2.3: Overview of the biometrics of the 12 individual gulls followed during four breeding seasons (2016-2019) in Bristol, UK. Sex is either female (F) or male (M). Mass is shown in grams, length and depth measurements in mm, and clutch volume in mm^3.

ID	**Roof**	**Sex**	**Mass**	**Wing length**	**Head length**	**Gonys depth**	**Number of eggs**	**Clutch volume**
1	ASSL	F	658	404	106.5	17.4	3	184
2	ASSL	F	790	416	109.7	18.1	2	145
3	ASSL	F	760	414	113.0	18.4	3	208
4	ASSL	F	665	411	108.8	19.5	3	150
5	ASSL	F	758	422	112.7	18.4	2	142
6	ASSL	F	810	411	110.3	16.5	3	199
7	dBs	F	710	395	109.5	16.8	3	221
8	dBs	M	765	450	115.8	17.5	3	215
9	dBs	F	720	413	109.4	16.9	3	216
10	dBs	F	710	407	109.4	15.4	3	180
11	dBs	M	870	407	119.0	18.2	3	235
12	dBs	F	690	410	107.2	12.0	1	62

Besides monitoring the individuals which were carrying GPS devices, nests in close proximity at both locations were monitored to be able to use these nests as controls when estimating the effect of GPS tracking on reproductive success. Although attaching GPS devices can have negative effects on behaviour and survival of animals (Barron et al., 2010), previous studies on lesser black-backed gulls did not observe short- or long-term effects using the same wing harness method and GPS device (Camphuysen, 2011; Thaxter et al., 2016; Kavelaars et al., 2018). In the current study, due to the low sample size the Fisher's exact test (FET) was used to check for differences in breeding success between control and tagged birds. No difference was found in the number of chicks hatched between control and tagged gulls in 2016 (control, n = 19, mean+SE = 1.95+0.27, tagged: n = 5, mean+SE = 2+0.45, FET: p = 0.648), in 2017 (control, n = 25, mean+SE = 1.85+0.25, tagged: n = 11, mean+SE = 1.66+0.41, FET: p = 0.852), and in 2018 (control, n = 35, mean+SE = 1.89+0.25, tagged: n = 11, mean+SE = 2.11+0.35, FET: p = 0.998). Additionally, no difference was found in the number of chicks fledged in 2016 (control, n = 19, mean+SE = 1.6+0.29, tagged: n = 5, mean+SE = 1.6+0.29, FET: p = 0.649), in 2017 (control, n = 25, mean+SE = 0.44+0.18, tagged: n = 11, mean+SE = 1+0.49, FET: p = 0.280), and in 2018 (control, n = 35, mean+SE = 0.46+0.21, tagged: n = 11, mean+SE = 1.13+0.30, FET: p = 0.098).

2.4.2 Field observations

Field observations were conducted during the breeding seasons of 2016 and 2017. Frequently visited sites were identified by visualising the GPS data in Google Earth. Consequently, these sites were then visited for two reasons: (1) to understand what the gulls were doing at these

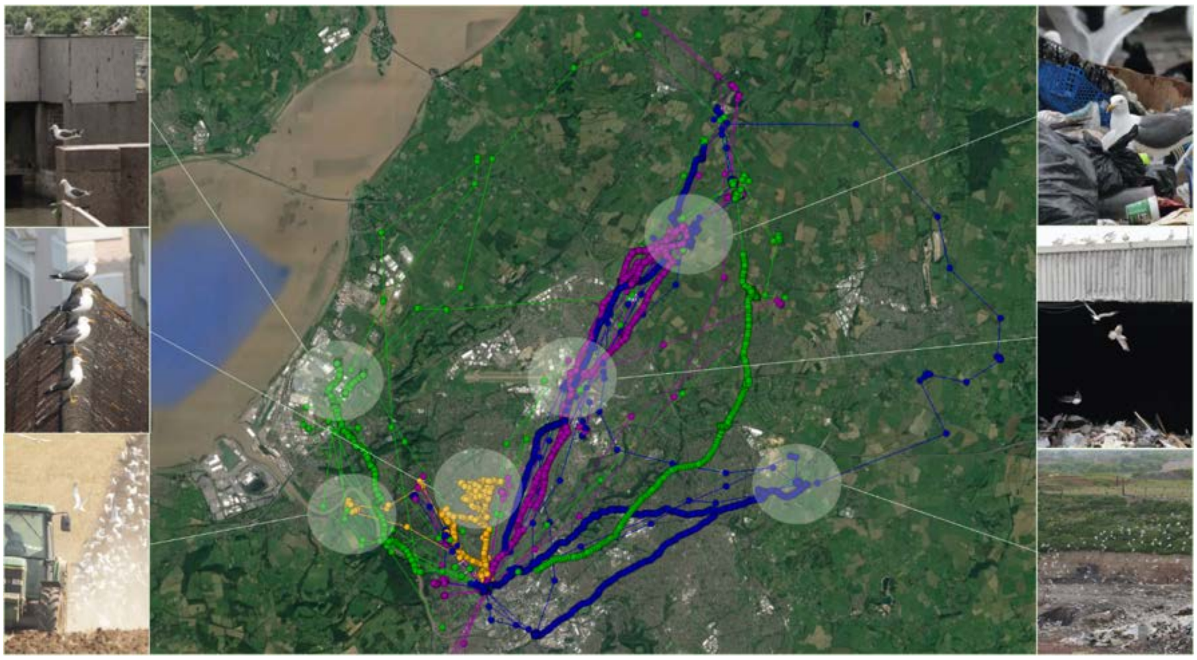

Figure 2.9: GPS tracking data of four individuals in the Bristol area with six randomly selected foraging areas highlighted. The trips of the four different gulls (colours) to these areas over two days are shown, each circle indicates a GPS location. The high-resolution paths indicate a location at every four seconds, the low-resolution paths show locations every five minutes. Examples of these foraging areas are the Bristol Sewage Works, suburban buildings, farms, landfills and waste transfer station. © Cara Williamson and Anouk Spelt

locations and why they would go there, and (2) to assess if the basic habitat map identified the locations correctly (see section 2.6). Areas that were visited included several farms, waste centres (including landfills and the Bristol Sewage Works), parks, the Avonmouth Docks, sport fields, golf clubs, lakes, schools and suburban gardens. By talking to managers, owners and inhabitants of the visited areas knowledge about the behaviour of the gulls and the habitat type was acquired. Based on this knowledge, areas that were not included in the basic habitat map, were added. Additionally, the observations of the bird behaviours were noted down but were not systematic as they were conducted to provide a context of their behaviour in each habitat. Figure 2.9 provides an example of six foraging areas based on a small sub-sample of the GPS tracking data linked with photos of bird behaviours observed at these different locations. During the breeding season of 2018, three specific feeding grounds were selected to conduct observations: a park, a school and a waste centre. For these sites, the observations were systematic counts over the course of a day to identify temporal patterns in presence of gulls, people, human-related activity and food availability. Chapter 4 will discuss the methods used during these observations in more detail.

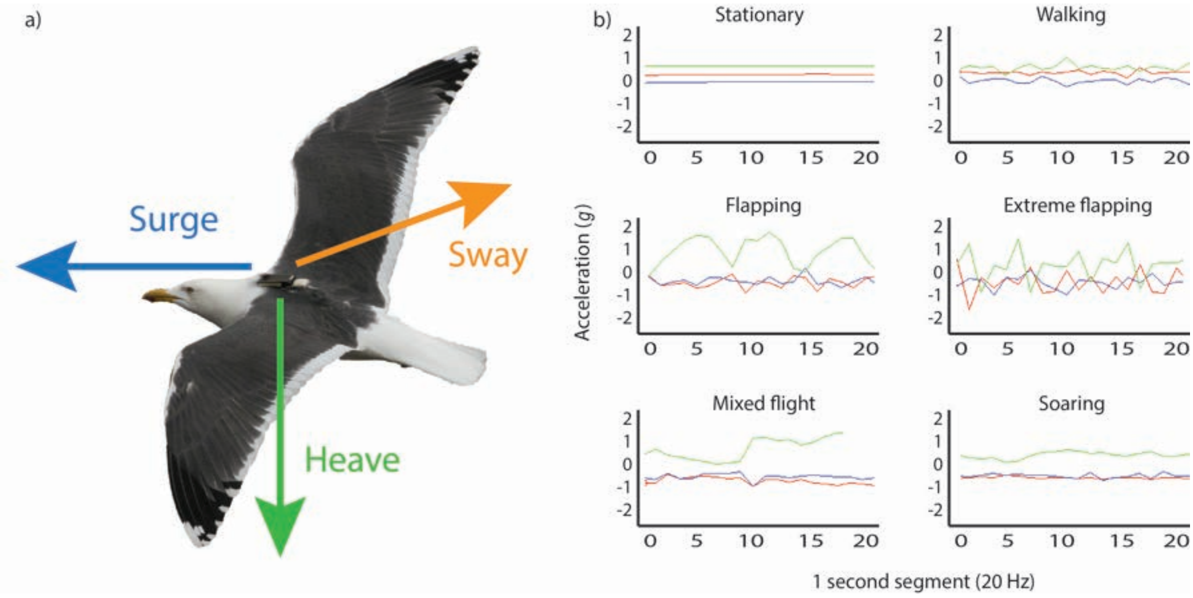

Figure 2.10: Overview of the tri-axial accelerometer showing the three directions and the signals related to different behaviours. a) The three axes projected on the GPS device on the gull are surge (X), sway (Y) and heave (Z). b) The different acceleration signals of the three axes (in *g*) related to six distinct behaviours based on a segment of 1 second of 20 Hz tri-axial data.

2.5 Behavioural data

The GPS devices contain a tri-axial accelerometer which measures the total acceleration in three directions: X - surge, Y - sway and Z - heave (Figure 2.10a). Total acceleration consists of a static component (gravity) and a dynamic component (change in velocity). This means when the GPS device is at rest in a horizontal position, it will only show the static component in the upward direction (Z) due to the Earth's gravity of 1 *g* (~9.81 m/s). Changing the position of the GPS device will change the signal in the static component regardless of the change in velocity. The accelerometers in the GPS device measure the values in mV instead of *g*, therefore these values were transformed by using calibration values estimated by the device manufacturers.

Acceleration data with these devices can be collected continuously or with intervals. In this study, the acceleration data was collected at a frequency of 20 Hz for 1 or 2 seconds directly after the GPS location was taken. This setting provided that the acceleration signal could be coupled to that particular GPS location. The accelerometer measurements were then used to quantify the behaviour of the individuals (Figure 2.10b) and to determine the dynamic body acceleration (DBA) which can be used as a proxy for energy expenditure (see chapter 5).

Table 2.4: Definition of the ten activity classes of lesser black-backed gulls classified from the tri-axial acceleration data and the results from the validation of the training dataset (precision). These activity classes were combined to create seven final activity classes: soaring, flapping, extreme flapping (exflap), mixed flight (mixed), stationary, walking and other. Prec = precision. Modified from Shamoun-Baranes et al. (2016)

General activity	**Final class**	**Activity class**	**Prec**	**Description**
Flight	Flight	Soaring	0.95	Flight with no wing beats
	Flight	Flapping	0.96	Flight with regular wing beats
	Flight	ExFlap	0.43	Irregular and intense wing beats
	Flight	Mixed	0.68	Mixed flapping and soaring signals
Stationary	Stationary	Stationary	0.96	Sitting or standing on land or sea structure
	Stationary	Boat	0.75	Sitting or standing on a boat
Terrestrial locomotion	Walking	Walking	0.92	Walking
	Walking	Pecking	0.46	Walking and pecking
Float	Other	Float	0.97	Floating with the currents at sea
Other	Other	Other	0.35	Signal that does not fit in the above classes

2.5.1 Annotation and classification of behaviours

Behaviours were quantified using a machine learning classifier created by Shamoun-Baranes et al. (2016) with the same GPS devices and the same gull species. In that study, acceleration data was annotated with different behaviours based on simultaneous collected video data and expert knowledge. Of each of the 14 individuals in that study, 28 days were randomly selected and segments were annotated resulting in 3,505 segments of 1 second. From the gulls in the current study, 1,000 segments of 1 or 2 seconds from all individuals were annotated and this was added to the training dataset. From the tracking data, the same set of predictive features from Shamoun-Baranes et al. (2016) were selected to predict the different behaviours. With these features, a random forest classifier was built by supervised machine learning with WEKA datamining software. The class that obtains the most votes will be the final prediction of the model. The classifier was trained with 50 random trees on 60% of the training (annotated) data and validated on the remaining 40% of the training data (validation results can be found in Table 2.4). The model was then applied to all the unclassified data. The classification resulted in ten activity classes: "soaring", "flapping", "extreme flapping", "mixed flight", "walking", "pecking", "float", "boat", "stationary", and "other" (Table 2.4). The "pecking" activity class was combined with the "walking" activity class because these classes were very similar and difficult to distinguish. This was also the case for the "boat" activity class and "stationary" activity class and thus were combined. The activity class "float" was reclassified as "other" due to the low sample size of this behaviour in the current study.

2.6 Habitat data

To quantify the habitat use of urban-nesting gulls, a habitat map of Bristol and surrounding areas was created. This habitat map was based on the Corine Land Cover European seamless vector database version 18.5 (dated 02/2016) provided by National Teams within the I&CLC2000, CARDS, CLC2006 and CLC2012 project (European Commission, 2016). From this vector database, a raster with 2 m resolution was created in ArcGIS (ESRI, 2017). This raster file contained 31 habitat types with basic information of the land use (Table 2.5). To improve this map we added four layers of publicly available datasets: a landfill database (Environment Agency, 2019), an allotment database (Bristol City Council, 2017), a green spaces database (Bristol City Council, 2019a), and a waterbodies database (Jochen & Christoph, 2019). Lastly, we added layers of areas which were frequenly visited by gulls (including the individuals in this study) which were not (or partly) specified in the Corine Land Cover database. The resulting 47 different habitat types were then combined to create seven main habitat types: (1) nesting area, (2) rural green areas, (3) water areas, (4) built-up areas, (5) city green areas, (6) industrial areas and (7) waste processing areas (Table 2.5). Rural green areas were mainly empty land with a few buildings and a low human population density (less than 30 % of the land surface is covered by impermeable features like buildings, roads and artificially surfaced areas) such as agricultural land, forests and meadows. Water areas included both salt and freshwater bodies such as the sea, intertidal zones, estuaries, lakes and rivers. Built-up areas, city green areas, industrial areas and waste processing areas are collectively referred to as suburban and urban areas in the rest of this thesis. Built-up areas were both continuous and discontinuous urban areas characterised by a mid (30-80 % of the land surface) to high (more than 80 % of land surface) density of buildings and human population. City green areas were defined as green urban areas such as parks and allotments plus sports and leisure facilities such as golf courses. Industrial areas included port areas, airports, rail networks, construction sites and commercial units. Lastly, waste processing areas were characterised by landfills, dump sites, transfer waste centres, mineral extraction sites and sewage works. Each GPS location was then linked to a habitat type. The GPS latitude and longitude (downloaded from the GPS device) were transformed into British National Grid UTM locations with the National Grid OSTN02 transformation in ArcGIS (ESRI, 2017) as this was the most accurate transformation available (accuracy < 1 metres).

2.7 Elevation data

To understand the heterogeneous landscape that the urban-nesting gulls are encountering, Digital Elevation Models based on LiDAR data at 2 m spatial resolution were obtained from the Environmental Agency, UK. Raster files of both Digital Surface Models (DSM) and Digital Terrain Models (DTM) were acquired for the whole of the UK. DSM models contain all the objects present on the surface, including buildings, trees, and bridges amongst others. DTM models

Table 2.5: Overview of habitat types quantified in this study. The 47 layers were reclassified into seven main habitat categories for the final habitat map: built-up areas, industrial areas, waste processing areas, city green areas, rural green areas and water areas. CLC = Corine Land Cover database. Databases = publicly available databases. Extra layers = frequently visited areas.

Nr	CLC	Databases	Extra layers	Main habitat categories
1	Continuous urban fabric			Built-up areas
2	Discontinuous urban fabric			Built-up areas
3	Industrial or commercial units			Industrial areas
4	Road and rail networks			Industrial areas
5	Port areas			Industrial areas
6	Airports			Industrial areas
7	Mineral extraction sites			Waste processing areas
8	Dump sites			Waste processing areas
9	Construction sites			Industrial areas
10	Green urban areas			City green areas
11	Sport and leisure facilities			City green areas
12	Non-irrigated arable land			Rural green areas
13	Fruit trees/berry plantations			Rural green areas
14	Pastures			Rural green areas
15	Complex cultivation patterns			Rural green areas
16	Land occupied by agriculture			Rural green areas
17	Broad-leaved forest			Rural green areas
18	Coniferous forest			Rural green areas
19	Mixed forest			Rural green areas
20	Natural grasslands			Rural green areas
21	Moors and heathland			Rural green areas
22	Transitional woodland-shrub			Rural green areas
23	Beaches, dunes, sands			Rural green areas
24	Inland marshes			Rural green areas
25	Peat bogs			Rural green areas
26	Salt marshes			Water areas
27	Intertidal flats			Water areas
28	Water courses			Water areas
29	Water bodies			Water areas
30	Estuaries			Water areas
31	Sea and ocean			Water areas
32		Landfills		Waste processing areas
33		Green Spaces		City green areas
34		Allotment		City green areas
35		Rivers Bristol		Water areas
36			Estuary	Water areas
37			Shortwood	Waste processing areas
38			Northway	Waste processing areas
39			Sewage Works	Waste processing areas
40			Lower Compton	Waste processing areas
41			Waste company	Waste processing areas
42			Other landfills	Waste processing areas
43			Sport fields	City green areas
44			Golf courses	City green areas
45			Avon River	Water areas
46			Nest dBs	Built-up areas
47			Nest ASSL	Built-up areas

contain a "clean" version of the earth surface removing any structures resulting in a model with only natural features. The height of the structures was then calculated by subtracting the DTM model from the DSM model in ArcGIS (ESRI, 2017). Additionally, the aspect and slope of each grid was extracted. Each GPS location was then linked to a grid and for each location the different elevation values were extracted (DTM, DSM, structure height, slope, and aspect).

2.8 Weather data

Weather data was collected from two weather stations which were placed on roofs within Bristol to collect local weather data. One was placed in the city centre on a University of Bristol building close to the nests on the ASSL building (NEST) and the other was placed in the north-east of Bristol on a building from the University of West England (UWE). The weather stations were put up from June 2016 until the end of the project in August 2019 collecting data during almost the whole study period. The weather stations continuously collected data, but the data was averaged over 10 minutes (except for precipitation rate which was averaged over an hour). This was then broadcast to a server from which the weather data could be downloaded and used for analysis. A sub-sample of the data (every hour) was compared between the two weather stations over a time period of 14 days and showed high correlations between the different weather variables (Figure 2.11). In general, the variables at both weather stations followed the same pattern, but for the variable pressure it seemed that the UWE weather station showed lower amplitudes. To create one weather dataset, the data from both weather stations were averaged and each GPS location was then linked to the closest 10-minute data (or 1-hour data for precipitation).

The weather stations contained the following sensors:

- Cup anemometer that measures wind speed in metres per second (m/s)
- Wind vane that measures the wind direction in degrees from North (°)
- Ultra Violet (UV) sensor that measures solar radiation in watt per square metre (W/m^2)
- Rain gauge that measures the rainfall in millimetres per hour (mm/h)
- Temperature gauge that measures the air temperature in degrees centigrade (°C)
- Pressure sensor that measures the atmospheric pressure in Pascals (Pa)

2.9 Database

All the data collected and prepared during this study was combined and stored in a MySQL database to increase efficiency of data analysis and accessibility for future studies. The database

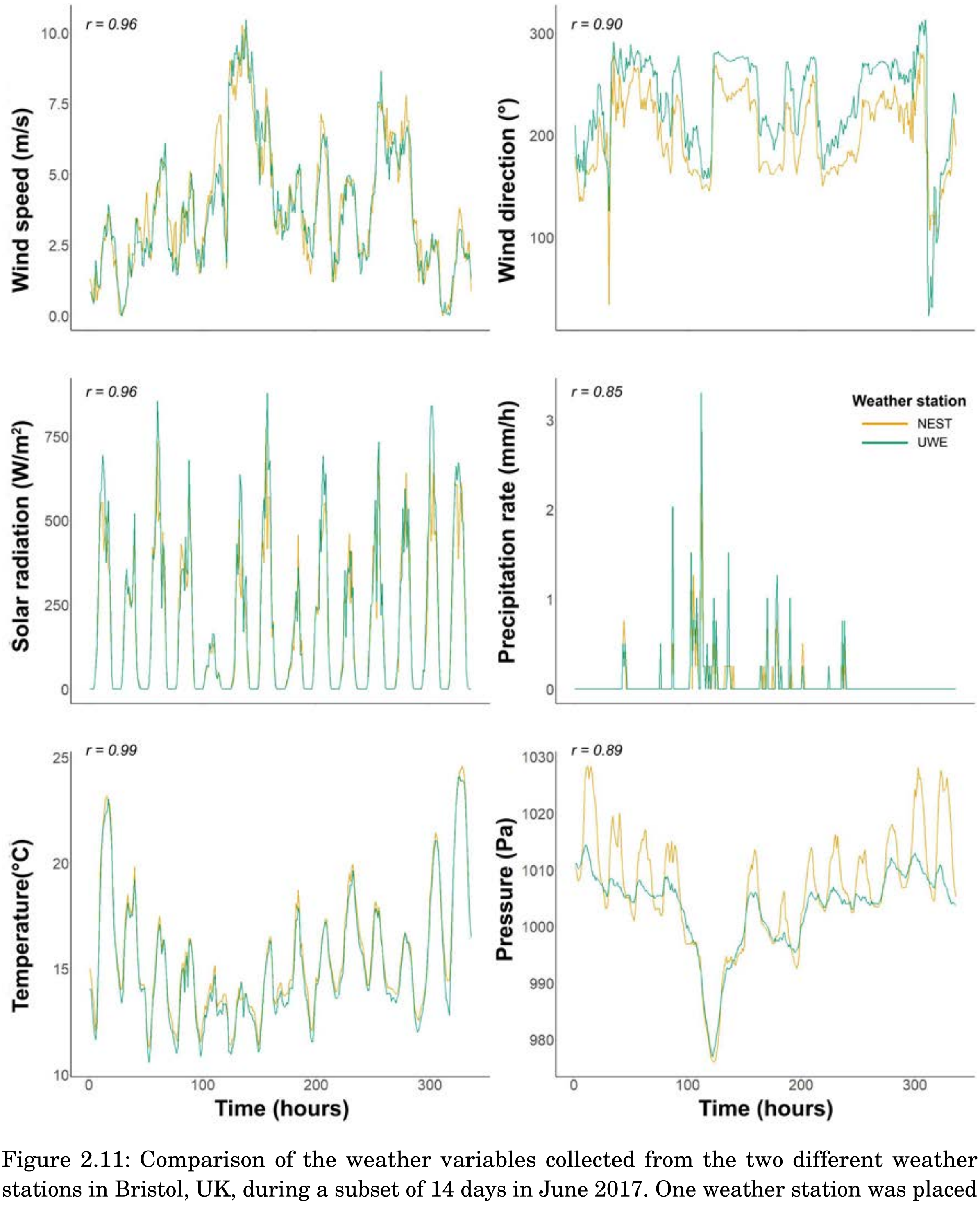

Figure 2.11: Comparison of the weather variables collected from the two different weather stations in Bristol, UK, during a subset of 14 days in June 2017. One weather station was placed close to the nesting area on ASSL in the centre of Bristol (NEST) and the other at the University of West England (UWE). The Pearson's correlation coefficient (r) is shown for each weather variable comparison; wind speed (m/s), wind direction (°), solar radiation (W/m^2), precipitation rate (mm/h), temperature (°C) and pressure (Pa).

consists of the following data tables (Figure 2.12): (1) Individual bird data, (2) Nest data, (3) GPS device data, (4) Sensor data, (5) Behavioural data, (6) Geographical data, (7) Weather data, and (8) Additional data. Database tables 1-3 are linked based on the gull's unique metal ring ID, whereas database tables 4-8 are linked based on the unique ID of the GPS location. Both set of tables are then linked by the ID of the GPS device. The sensor data was filtered and checked after downloaded from the UvA-BiTS system database before adding to the MySQL database. Any other data that was linked to the GPS locations were added to the dataset "Additional data". This included the breeding stage (see section 2.4.1), time of the day (night, dawn, day, dusk), and several trip characteristics (see Chapter 5).

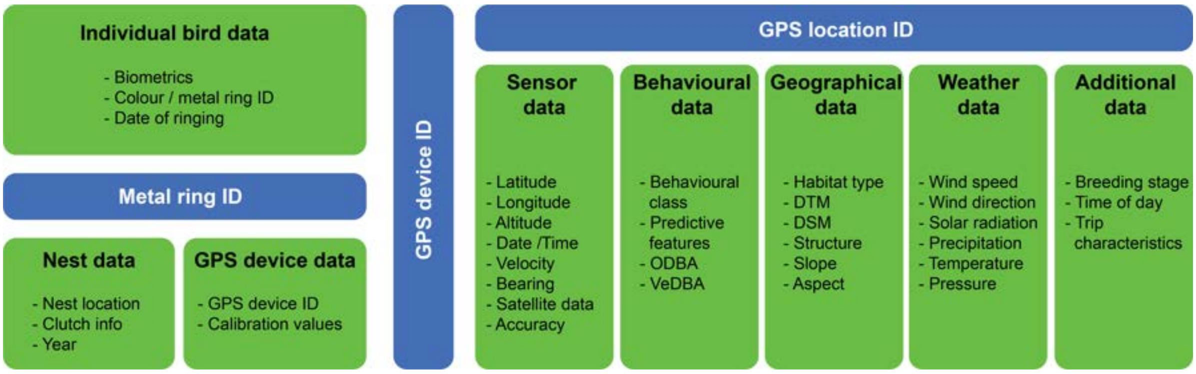

Figure 2.12: Overview of the different dataset tables in the SQL database (green) and how they are linked with each other (blue). The different datasets are described in the sections above and include: individual bird data, nest data, GPS device data, sensor data, behavioural data, geographical data, weather data, and additional data. ODBA = overall dynamic body acceleration, VeDBA = vectorial dynamic body acceleration, DTM = digital terrain model, DSM = digital surface model.

2.10 Outside breeding season

This study only focussed on the movement behaviour of gulls during the breeding season, however, the GPS devices did record their movement outside the breeding season. A summary of the behaviour of these gulls outside the breeding season is provided based on visualisations of the tracking data in Google Earth. Out of the 11 working GPS devices, six individuals performed long-distance migrations to the south, whereas five individuals stayed in the UK. The six individuals migrating to the south either went to Morocco (ID 8 and ID 10), Portugal (ID 4 and ID 7), Spain (ID 5) and France (ID 9). The five individuals staying in the UK either spent the majority of the winter period in the Cotswolds area (ID 2 and ID 12), moving north to Liverpool and Birmingham (ID 3 and ID 11) or to the south-west in Cornwall (ID 6). Some of these UK birds have been visiting their nesting grounds during the winter but not spending much time there.

CHAPTER 3

HABITAT USE AND TIME-ACTIVITY BUDGETS DURING THE BREEDING SEASON

This is the first data chapter of this thesis looking to answer the question: *"To what extent do urban-nesting gulls use urban environments and does this change with the breeding stage?"*. This chapter aimed to provide a first understanding of the general movement of gulls in the city of Bristol and which habitats and therefore food sources they utilise during the breeding season. This chapter has been published in Scientific Reports (Spelt et al., 2019) with the title "Habitat use of urban-nesting lesser black-backed gulls during the breeding season" in collaboration with the following authors: Cara Williamson, Judy Shamoun-Baranes, Emily Shepard, Peter Rock and Shane Windsor. I conceived and planned the research together with C.W., J.S., E.S., P.R., and S.W. I carried out the main part of the fieldwork together with C.W., P.R., and S.W. I performed the analysis and took lead in writing the manuscript for publication. All authors provided critical feedback and helped shape the research, analysis and manuscript.

3.1 Summary

Increasing urbanisation is detrimental for some animal species and potentially advantageous for others. Urban-nesting populations of gulls have undergone rapid population increases worldwide, which have resulted in an increase in human-gull conflicts. In order to inform management and conservation decisions in relation to these populations, more information is needed about the behaviour of these birds in urban settings and how they utilise their environment. This study combined Global Positioning System (GPS) tracking data of 12 urban-nesting lesser black-backed gulls, *Larus fuscus*, with habitat data, breeding stage and behaviour data over three breeding

seasons (2016-2018). Despite the proximity of marine areas (~10 km), the birds only made significant use of terrestrial environments, spending two-thirds of their time away from the nest in suburban and urban areas, and one-third in rural green areas. The gulls utilised suburban and urban areas more as their chicks grew and appeared to use diverse foraging strategies to suit different habitats. These results indicate that the range of potential foraging areas available needs to be considered in management decisions and that urban bird populations may not use the resources they are expected to.

3.2 Introduction

Urbanisation of the landscape affects animal populations worldwide and often results in lower species diversity and richness (Marzluff, 2001). However, some animals can take advantage of urban environments, including various species of gulls, which can use suburban and urban areas for nesting sites and foraging (Monaghan & Coulson, 1977). Gulls traditionally exploit islands or coastal areas for breeding, but across Europe a number of gull species such as lesser black-backed gulls, *Larus fuscus*, herring gulls, *Larus argentatus*, yellow-legged gulls, *Larus michahellis*, and black-legged kittiwakes, *Rissa tridactyla*, now have substantial urban-nesting populations (Coulson, 1963; Rock, 2005; Kubetzki & Garthe, 2007). In the United Kingdom (UK), urban gull populations have seen a rapid increase from the mid-1980's onwards, while non-urban populations have experienced declines over the same period (Balmer et al., 2013; Eaton et al., 2015). However, national population trends differ per colony with both increasing and decreasing trends in UK colonies of three gull species; herring gulls, lesser black-backed gulls and greater black-backed gulls, *Larus marinus* (Nager & O'Hanlon, 2016). A number of possible advantages of nesting in the urban environment have been put forward in relation to the increase in numbers nationally, including warmer temperatures, ample nesting sites, lower predation rates and access to reliable food resources (Rock, 2005).

Cities are landscapes made up of different habitat types (e.g. buildings, gardens, streets, waste centres) and associated resources within them. Little is known about how gulls nesting in these urban areas utilise these habitats, or indeed if they only use urban areas for nesting. Bird-mounted GPS based tracking units are an ideal method for measuring movement patterns in detail and have been used to study gulls across Europe (Camphuysen et al., 2015; Garthe et al., 2016; Gyimesi et al., 2016; Isaksson et al., 2016; Stienen et al., 2016). However, to date these studies have mainly focused on gulls nesting outside the urban environment and only two published studies (to our knowledge) tracked urban-nesting gulls with GPS devices. A short-term tracking study (<48 h) of ring-billed gulls, *Larus delawarensis*, nesting on the ground on a small island within the city of Montreal, found that the birds preferred to forage in agricultural lands (Caron-Beaudoin et al., 2013). A one-year study of four herring gulls nesting on roofs in the small coastal town of St. Ives, UK found that the gulls had highly variable individual home-range sizes and activity patterns, and that the birds spent a considerable amount of time away from suburban and urban areas, visiting both marine and agricultural habitats (Rock et al., 2016). As such, long-term detailed studies of habitat use by urban-nesting gulls in any substantial urban environment are currently limited.

The increase of urban gull populations is linked to an increase in conflicts with people, resulting in perceived problems such as aggression, mess, noise, damage to property, transmission of diseases and hazards to aircrafts (Belant, 1997; Rock, 2005). A range of different non-lethal and lethal control measures have been proposed to control urban gull populations such as removal of access to food resources, frightening devices, netting over roof tops, removing nests and egg oiling (Belant, 1997; Rock, 2005). Although some of them are effective locally and temporarily, they are not on the larger scale (Belant, 1997). Indeed, the potential effectiveness of large-scale control measures such as removal of access to food resources is difficult to estimate as little is known about the behaviour and habitat use of urban-nesting gulls. Therefore, there is a need to understand the behaviour of these birds in urban settings and how they make use of their environment in order to inform management and conservation decisions in relation to increasing urban gull populations.

The aim of this study was to quantify in detail how urban-nesting gulls utilise their environment and if this changes with breeding stage. This was addressed by specific assessment of: (1) the effect of breeding stage on the habitat use of urban-nesting gulls and (2) the effect of habitat and breeding stage on their time-activity budgets. Based on previous studies (Kubetzki & Garthe, 2003; Schwemmer & Garthe, 2005; Camphuysen et al., 2015), we hypothesised that the urban-nesting gulls in Bristol would mostly use terrestrial resources, noting however that due to the proximity of the sea (~10 km), the marine environment could still be utilised. We also expected systematic changes in habitat use and time-activity budgets relating to the breeding stage of the gulls based on dietary and foraging behavioural changes observed in previous studies (Annett & Pierotti, 1989; Noordhuis & Spaans, 1992; Raven, 1997; Belant et al., 1998; Camphuysen et al., 2015). Our study focused on urban-nesting lesser black-backed gulls in the city of Bristol, UK. This species is amber listed in the UK and their overall population in the UK decreased by 48% from approximately 91,300 to 43,824 Apparently Occupied Nests (AON) between 2000 and 2013 (Eaton et al., 2015; Nager & O'Hanlon, 2016). We fitted twelve individuals with long term GPS tracking devices (Bouten et al., 2013) and collected high-resolution positional and acceleration data over three breeding seasons (2016-2018). The tracking data were then combined with behavioural data, breeding status and habitat data to quantify the habitat use and time-activity budgets of these urban-nesting gulls.

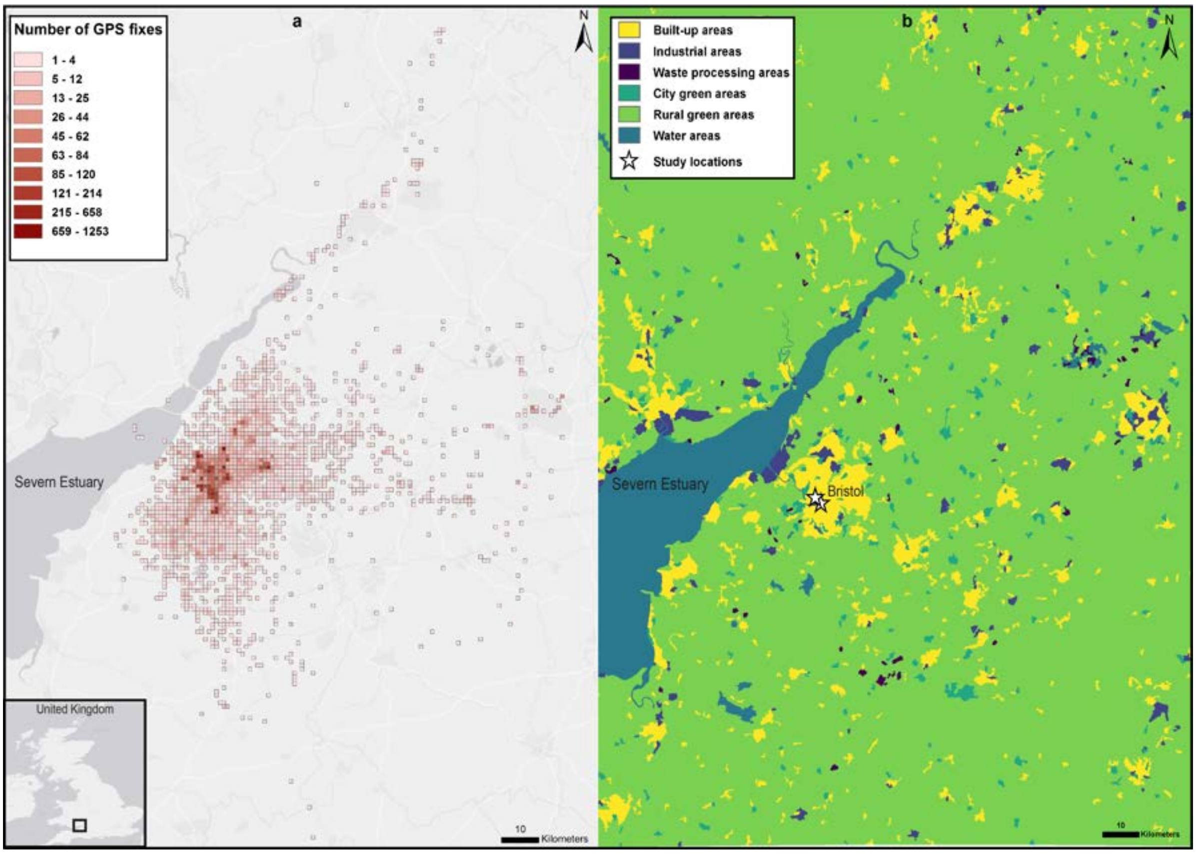

Figure 3.1: Maps of the density of GPS locations in relation to habitat type. a) The number of GPS locations (filtered to 30 mins) of all individuals during three breeding seasons (2016-2018). Grid cell size was set to 1,000 m. Base map sources: Esri, DeLorme, HERE Technologies, MapmyIndia. b) Map of Bristol in the UK coloured by habitat type (Table 2.5). The locations of the two study locations used in this study are marked with a white star (coordinates in decimal degrees for Arts and Social Sciences Library (ASSL): 51.459600, -2.601648 and for dBs music centre (dBs): 51.451582, -2.588388).

3.3 Methods

3.3.1 Study area and species

This study was carried out in the city of Bristol, UK (Figure 3.1b). The city covers an area of approximately 110 km^2 with a human population of 463,400 (Bristol City Council, 2019b). The Severn Estuary and the open sea are located ~10 km from the city centre. Lesser black-backed gulls nesting on two buildings in the city centre were tagged in this study (Figure 3.1b – white stars); the Arts and Social Science Library (ASSL) at the University of Bristol and the dBs Music building in the centre of Bristol. The two study locations are situated approximately 1.5 km from each other (see chapter 2 for more details about the study area and species).

3.3.2 GPS devices and attachment

Breeding adults were caught at their nest during the first or second week of incubation with either a walk-in chicken wire cage or metal trap-door cage. Eggs were replaced with fake eggs to prevent damage and overheating during warm days. The handling time was minimized (mean: 28 min, range: 16-50 min) to prevent high stress levels and irreversible changes in behaviour. In 2016, five birds were caught and tagged with UvA-BiTS GPS devices (Bouten et al., 2013) at ASSL. In 2017, an additional seven birds were caught and tagged, one at ASSL and six at dBS which resulted in a total of 12 individuals. Unfortunately, one GPS device (Individual 1) stopped working after a week therefore this individual has been excluded from this study.

The GPS devices were attached using a wing harness made from tubular Teflon^{TM} ribbon (Bally Ribbon Mills 8476-.25"). The wing harness method has been found to be the best method of attaching a GPS device for gulls (Thaxter et al., 2014b). The mass of both unit and harness was 18 gram, which was < 3% of the birds' body mass (mean: 2.4%, range: 2.1-2.7%). Mass of the birds was quantified by weighing the individuals in a bag attached to an electronic scale (1 gram precision) and sex was determined by comparing the head length and bill depth to wing length (Rock & Vaughan, 2013). The five individuals caught in 2016 were all females and from the seven birds caught in 2017, two were males. All individuals were colour ringed. Table 2.3 provides detailed information about each individual gull. The UvA-BiTS GPS devices are lightweight, solar powered units with rechargeable batteries, and have tri-axial accelerometers and temperature sensors. They log on-board and the data can then be accessed remotely via a Zigbee two-way radio transceiver. The tri-axial accelerometer measures linear acceleration in three directions; X (surge), Y (sway) and Z (heave). Data was downloaded to a field laptop regularly via the radio transceivers placed at the study locations.

3.3.3 Monitoring breeding stage and device effects

Monitoring of the nests were conducted with a telescope (Swarovski STX 30-70 x95) from overlooking buildings to determine breeding stage with laying, hatching and fledging dates being recorded where possible (for an overview of breeding parameters see Table 2.2). Monitoring was performed weekly in March and August (pre-egg laying and after fledging) and twice a week from April until fledging of the chicks (end July). Monitoring continued until a majority of the nests had been checked. The incubation period was defined as from when the first egg was laid until the first egg had hatched (generally four weeks), and the chick rearing period was defined as from when the first egg had hatched until eight weeks later (generally the fledging age of chicks) or until the chicks had died. These breeding periods were determined separately per individual per year. The GPS data was assigned to specific breeding stages which were defined in two-week intervals for more detailed analysis.

Attaching GPS devices and other transmitters to free-living birds can have negative effects on their behaviour and survival (Barron et al., 2010). Previous studies using the same GPS device and harness as in the current study have observed no short- or long-term effects on lesser black-backed gulls (Camphuysen, 2011; Thaxter et al., 2016; Kavelaars et al., 2018). To test for tag effects on breeding output, we compared the breeding success of our tagged individuals with control gulls nesting on the same roof or adjacent roofs in order to identify possible tag effects. For all three years, no difference was found between number of chicks hatched (χ^2_1 = 0.002, p = 0.961) and number of chicks fledged (χ^2_1 = 2.4, p = 0.124). All work was approved by the University of Bristol Animal Welfare and Ethical Review Body (UIN UB/15/069). Bird handling, tagging and temporary egg removal was conducted under BTO permit A/2831. All work was carried out in accordance with the relevant guidelines and regulations.

3.3.4 Habitat map

A habitat map was created to assign each GPS location to a habitat type in ArcGIS (ESRI, 2017). This map was based on the 2 m resolution Corine Land Cover European seamless vector database (European Commission, 2016). Several layers with similar spatial resolution were added to the map to improve local habitat types. These layers include data from a landfill database (Environment Agency, 2019), an allotment database (Bristol City Council, 2017), a green spaces database (Bristol City Council, 2019a), and a waterbodies database (Jochen & Christoph, 2019). Additionally, we added an extra layer of habitat types which included sites that were frequently visited by the gulls and the nesting areas. This resulted in a dataset of 47 different habitat types which were combined to create a dataset with seven main habitat types: (1) nesting area, (2) rural green areas, (3) water areas, (4) built-up areas, (5) city green areas, (6) industrial areas and (7) waste processing areas (Table 2.5). In this study, the latter four types are collectively referred to as suburban and urban areas. Rural green areas were mainly characterised by agricultural land, forests and meadows. Water areas include rivers, lakes, intertidal areas and the sea.

During the breeding seasons of 2016 and 2017 we inspected sites which were frequently visited by the birds as shown by the GPS tracks in order to create the extra layer of habitat types. These sites included agricultural lands, waste processing centres in and outside of Bristol, and areas such as city parks, sports fields, suburban gardens and schools. These observations were used to assess if the basic habitat map (CLC) identified these locations correctly. If this was not the case, they were added to the layer. During these visits we also noted bird behaviours at specific feeding sites to provide some ecological and behavioural context. These observations were not systematic and are referred to as personal observations.

3.3.5 Data processing

Data preparation

This study focussed only on actively breeding birds, therefore part of the data for three gulls was excluded as they did not breed in the subsequent year (Table 2.2). Additionally, only data within the breeding period was included in this study, e.g. when a nest failed the data collected after this point was removed. This resulted in different number of fixes contributing to each individual's dataset, however this assured that the habitat use was linked to breeding behaviour and not to behaviour of failed or non-breeders. Additionally, the GPS devices recorded at intervals between 4 and 1800 seconds during the breeding season and between 1800 and 3600 seconds outside the breeding season. Data was filtered to a 30-min rate for habitat use analysis to create equal sampling rates during the breeding season.

Habitat use

To demonstrate the distribution of urban-nesting gulls in Bristol, we conducted a point pattern analysis on the filtered 30-min data set of all individuals during the three breeding seasons (2016-2018). Data within the nesting areas were excluded from this analysis based on a cut-off radius of 50 m per nest (Figure 2.4), resulting in a total of 21,143 GPS fixes used for this analysis. A uniform grid was created with a cell size of 1,000 m and the same extent of the GPS fixes. For each grid cell the number of GPS fixes within this grid cell was calculated giving the total number of points per grid cell.

In order to assess how urban-nesting gulls use their surrounding environmen,t we included GPS fixes collected both in flight and on the ground. As we were interested in both general habitat use and foraging behaviour, excluding flight behaviour from the analysis would not be justified. Also, gulls are opportunistic foragers and therefore searching flight cannot definitively be distinguished from commuting flight based on the data collected. Data within the nesting areas were included in this analysis. The filtered 30-min data was used to quantify the habitat use and the effect of breeding stage on habitat use. The response factor was habitat use and was defined as the proportion of time spent in each habitat during a specific breeding stage. The breeding stages were defined per individual per year and set at zero on hatching day. Breeding stage was classified using two-week intervals: before egg laying, pre-hatch 4-2 weeks, pre-hatch 2-0 weeks, 0-2 weeks after hatching, 2-4 weeks, 4-6 weeks, 6-8 weeks and after fledging (8-10 weeks).

Time-activity budgets

Acceleration data was collected after each GPS location at a frequency of 20 Hz for 1 or 2 seconds which meant that the acceleration data was coupled to a particular GPS location for that individual. The acceleration data was then used to quantify the behaviours of the gulls using a machine learning classifier created by Shamoun-Baranes et al. (2016). That study annotated behaviour of lesser black-backed gulls nesting on an island in the Netherlands based on video data, simultaneous acceleration data and expert knowledge. This annotated dataset plus a set of 14 selected features were used to create a random forest classifier which predicted behaviour. This same classifier was used in this study resulting in the same ten activity classes: "soaring", "flapping", "extreme flapping", "mixed flight", "walking", "pecking", "float", "boat", "stationary", and "other". Table 2.4 explains these activity classes in more detail. For this study, we were mainly interested in three major activity classes: "flying", "walking" and "stationary". Therefore, the activity classes "soaring", "flapping", "extreme flapping" and mixed flight were combined as "flying". The "pecking" activity class was found to be similar to "walking", therefore these activity classes were combined as "walking". Additionally, the activity classes "boat" and "stationery" were similar and reclassified as "stationary". Lastly, the activity class "float" was reclassified as "other" due to the low sample size of this behaviour. The behavioural data was combined with the GPS locations and the habitat map to compare time-activity budgets between habitats using the proportion of time spent performing each behaviour in each habitat. Data within the nesting areas were included in this analysis.

Analysis

To analyse the birds' habitat use and time activity budgets, two generalised linear mixed models (GLMMs) with poisson distribution and logit link were fitted with the lme4 package (Bates et al., 2015) in R version 3.5.3 (R Core Team, 2019). To analyse the bird's habitat use away from the nesting area, the proportion of time spent in each habitat was modelled by adding time spent in each habitat as a response variable and an offset of log(total time spent). Additionally, habitat and an interaction between habitat and breeding phase were included as fixed factors, and a random slope for individual was included to control for within-subject effects (Table 3.1 – model 1). To analyse time-activity budgets in the different habitats and the effect of the breeding stage on these time-activity budgets, the proportion of time spent on each behaviour was modelled by adding time spent on each behaviour as response variable and an offset of log(total time spent). Additionally, a random slope for individual was included. The following fixed factors were included in the model: a) behaviour, b) an interaction term between habitat and behaviour, c) an interaction term between breeding phase and behaviour, and d) a three-way interaction term between breeding phase, habitat and behaviour (Table 3.1 – model 2).

Following Zuur et al. (2009) we conducted a multiple step process to select the "best-fit" model. The optimal structure was defined by comparing several information criteria, including the Akaike's information criterion (AIC), corrected Akaike's information criterion for small sample sizes (AICc) and Bayesian information criterion (BIC). Additionally, likelihood ratio tests were performed to assess if variables significantly improved the model. The final models can be found in Table 3.1. Model validation was done by looking for patterns in residual plots and checking heteroscedasticity, uniformity, zero-inflation and overdispersion with the DHARMa package (Hartig, 2017). Overdispersion was assessed by comparing the ratio of actual to expected variance. The significance level was set at $\alpha = 0.05$ and for results mean and standard error are reported unless stated otherwise.

3.4 Results

3.4.1 Breeding activity

On average the gulls were tracked for 128 ± 26 days (range: 19-299) during the three breeding seasons (2016-2018), with five birds being tagged at the beginning of the 2016 breeding season and then an additional seven birds in 2017 (Table 2.1). Mean first egg laying date was 5^{th} May in 2016 (range: 15/04-02/06), 3^{th} May in 2017 (range: 26/04-22/05) and 10^{th} May in 2018 (range: 30/04-22/05). Mean hatching date of the first egg was 2^{rd} June in 2016 (range: 20/05-22/06), 28^{th} May in 2017 (range: 24/05-13/06) and 4^{rd} June in 2018 (range: 28/5-13/6). During the breeding season of 2016 all five individuals produced chicks, with three individuals successfully fledging chicks (Table 2.2). In 2017, nine individuals produced eggs, chicks hatched in seven nests and four individuals had one or two chicks successfully fledged. In 2018, eight individuals produced eggs of which chicks hatched in six nests and five individuals had one or two chicks successfully fledged.

3.4.2 Habitat use

Our point pattern analysis showed that out of 21,143 GPS locations away from the nesting area only five were in the marine environment (Figure 3.1a). These GPS locations corresponded to one individual performing one short trip to the Severn Estuary during the breeding season in 2018. The overwhelming majority of GPS locations were situated on land and were concentrated around the Bristol City area, with up to 1,253 GPS locations per km^2, and locations being taken every 30 minutes. Over the course of the breeding season the gulls spent $29.8 \pm 2.3\%$ of their time away from the nesting area (Figure 3.2a) which was defined as a buffer of 50 m around each nest (Figure 2.4). The birds spent the greatest proportion of this time away from the nesting area in suburban and urban areas ($23.2 \pm 0.4\%$), which included the main habitat categories: built-up areas (buildings, roads and artificially surfaced areas), city green areas, industrial areas and waste processing areas (Figure 3.2b). The gulls also spent a substantial proportion of their time in rural green areas ($7.1 \pm 0.6\%$), with this main habitat category being largely made up of visits to agricultural fields.

Table 3.1: Model selection of the two models based on likelihood ratio tests. First the random terms were selected keeping fixed terms the same, and secondly the fixed terms were defined with the best selection of random terms. The model highlighted in bold is the final 'best' fit model for that analysis (1e and 2g respectively). Both models resulted in a GLMM model with a random slope. H = habitat, B = behaviour, S = breeding stage, ID = individual ID, AIC = Akaike information criterion, AICc = second order information criterion, BIC = Bayesian information criterion, logLik = log-likelihood ratio statistic, Dev = deviance, Chisq = Chi-square statistic, df = degrees of freedom. The significance level was set at $\alpha = 0.05$.

Model		**Fixed terms**	**Random terms**	**Test**	**AIC**	**AICc**	**BIC**	**logLik**	**Dev**	**Chisq**	**df**	**p**
1	1a	H + H*P			8,465	8,473	8,726	-4,176	8,353			
	1b	H + H*P	H / ID	1a vs 1b	5,738	5,759	6,130	-2,785	5,570	2,782	28	<0.001 ***
	1c		H / ID		7,851	7,854	7,987	-3,897	7,793			
	1d	H	H / ID	1c vs 1d	7,769	7,799	7,959	-3,863	7,726	67	6	<0.001 ***
	1e	**H + H*P**	**H / ID**	**1d vs 1e**	**5,738**	**5,759**	**6,130**	**-2,785**	**5,570**	**2,156**	**49**	**<0.001 *****
2	2a	B*H + B*P + B*P*H			12,745	12,772	13,706	-6,205	12,409			
	2b	B*H + B*P + B*P*H	B / ID	2a vs 2b	12,498	12,527	13,493	-6,075	12,150	259	6	<0.001 ***
	2c		B / ID		81,124	81,083	81,164	-40,555	81,110			
	2d	B	B / ID		81,083	81,124	81,134	-40,532	81,065	46	2	<0.001 ***
	23	B*H	B / ID	2c vs 2d	80,272	80,273	80,444	-40,106	80,212	852	21	<0.001 ***
	2f	B*H + B*P	B / ID	2d vs 2e	14,439	14,441	14,713	-7,172	14,343	65,869	18	<0.001 ***
	2g	**B*H + B*P + B*P*H**	**B / ID**	**2e vs 2f**	**12,498**	**12,527**	**13,493**	**-6,075**	**12,150**	**2,193**	**126**	**<0.001 *****

*** p <0.001, ** p <0.01, * p <0.05, . p <0.1

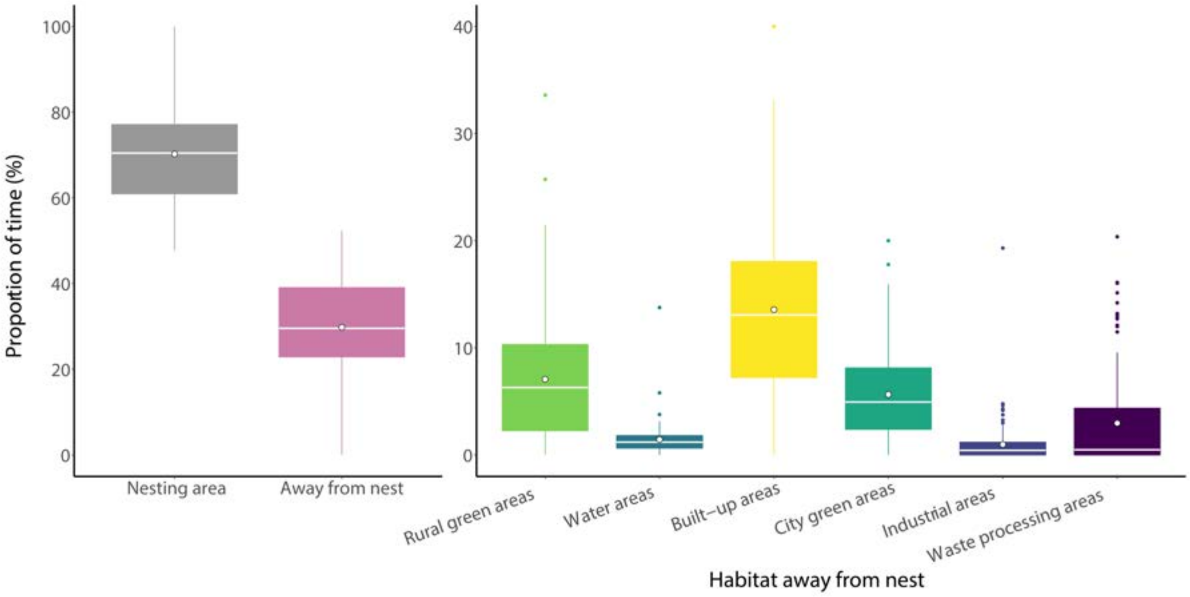

Figure 3.2: The proportion of time spent during the breeding season. a) Time in the nesting area and time spent away from the nesting area. b) Time in the six different habitat types when away from the nesting area. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR. White dots represent the mean proportion of time.

The proportion of the total time (including at the nest) spent in specific habitats varied substantially with the stage of the breeding season (Figure 3.3). As the breeding season progressed, birds spent less time on the nest and more time overall and proportionally in suburban and urban areas, with the proportion of time spent in suburban and urban areas increasing from incubation (14.5 ± 0.7%) to early chick rearing (26.1 ± 0.8%) to late chick rearing (32.6 ± 1.3%). This increase could mainly be attributed to an increase in the amount of time spent in the main habitat categories built-up areas (incubation: 8.2 ± 1.1%, early chick rearing: 15.4 ± 1.1%, and late chick rearing: 19.3 ± 1.3%) and waste processing areas (incubation: 1.6 ± 0.6%, early chick rearing: 3.0 ± 0.9%, and late chick rearing: 5.5 ± 2.2%). Over the same period the proportion of time spent in rural green areas (mainly agricultural fields) remained relatively constant from incubation (6.6 ± 1.3%) to early chick rearing (7.0 ± 1.1%), to late chick rearing (5.9 ± 1.1%). The best model predicting the proportion of time spent included habitat (χ^2_6 = 67, p<0.001), the interaction term habitat*breeding stage (χ^2_{49} = 2,156, p < 0.001) and random slope of individual (χ^2_{28} = 2,782, p<0.001). Therefore, habitat type and breeding stage were important drivers for the proportion of time spent in the habitats, but this proportion differed between individuals (Figure A.1).

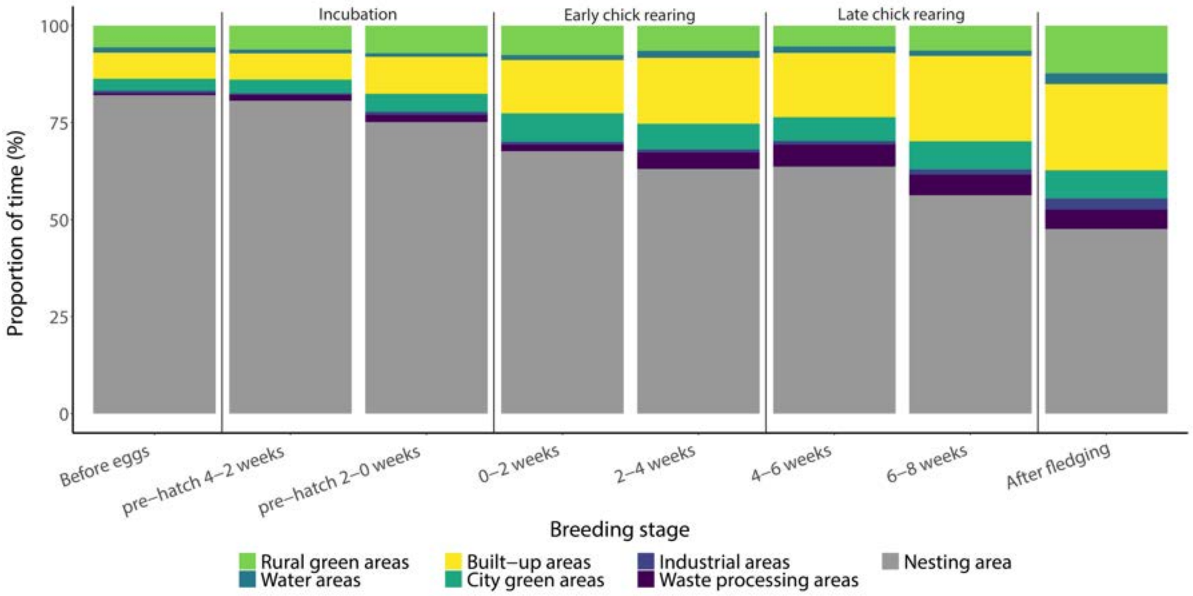

Figure 3.3: Mean proportion of time spent in the seven different habitat types depending on breeding stage. Time periods of incubation, early chick rearing, and late chick rearing are indicated at the top of the graph.

3.4.3 Time-activity budgets

The accelerometer-based time-activity budgets showed that the gulls spent in general 14.4 ± 1.1% of time in flight, 10.4 ± 3.0% walking and 75 ± 1.6% stationary, although time-activity budgets differed between individuals (Figure A.2). This proportion of time spent performing different behaviours varied with habitat (Figure 3.4). The time-activity budgets in built-up areas and the nesting area were different from any of the other main habitat types, whereas similar behavioural patterns were seen between rural green and city green areas, and between waste processing and industrial areas. In order to compare the behavioural patterns and the different foraging strategies of gulls, we have highlighted four examples of the time-activity budgets in four specific feeding grounds within the different main habitats (Figure 3.5); (1) Bristol city centre (within main habitat built-up areas), (2) Agricultural lands (within main habitat rural green areas), (3) Landfills (within the main habitat waste processing areas), and (4) Bristol Sewage Works (within the main habitat waste processing areas). Time-activity budgets in Bristol city centre and at the Bristol Sewage Works seemed to be quite similar, with high proportions of time spent in flight or stationary, and a low proportion of time spent walking. By contrast, on agricultural lands, time-activity budgets showed that gulls spent the largest proportion of their time walking, while in landfills the majority of the gulls' time was spent sitting or standing.

The proportion of time spent on different behaviours also varied with breeding stage, resulting in proportionally more time spent stationary and less time spent in flight at the beginning

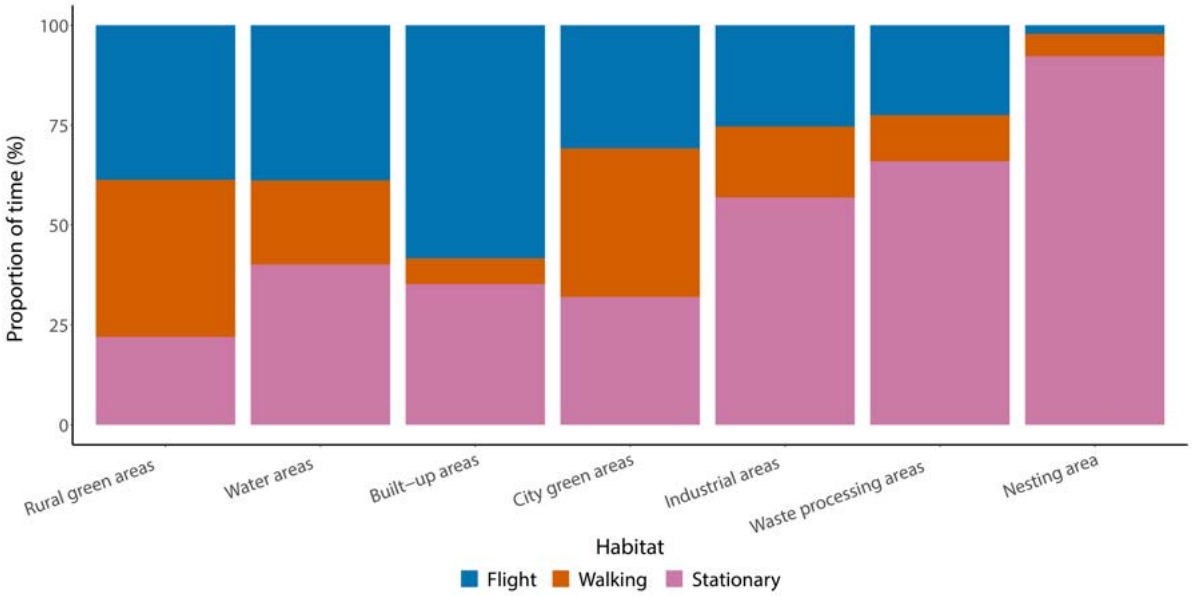

Figure 3.4: Mean proportion of time spent on each of the three behaviour types in the seven different main habitats. Behaviour classification is based on accelerometer data.

and end of the breeding season (Figure 3.6). Meanwhile, the proportion of time spent walking remained similar over the breeding season. The time-activity budgets showed different behaviour patterns in each habitat as the breeding season progressed, but all except waste processing areas showed an increase in stationary behaviour at the end of the breeding season (Figure A.3). The best model predicting the proportion of time spent on a behaviour (time-activity budgets) included the interaction behaviour (χ^2_2 = 46, p<0.001), the interaction behaviour*breeding phase (χ^2_{21} = 852, p<0.001), behaviour*habitat (χ^2_{18} = 65,869, p<0.001), the three-way interaction behaviour*habitat*breeding phase (χ^2_{126} = 2,193, p<0.001), and random slope of individual (χ^2_6 = 259, p<0.001). This indicates that time-activity budgets varied per breeding stage, per habitat and that the different habitats had distinct changes in activity patterns as the breeding season progressed.

3.5 Discussion

Our study showed that despite the close proximity to the coast (~10 km), the gulls tracked in this study did not make use of the marine environment during the breeding season, except for a single trip by one gull. The degree to which gull colonies use the marine environment is likely to reflect a balance between costs and benefits of different foraging strategies. The birds' ability to fly the distance to the coast does not appear to be a limiting factor, as the maximum distance away from the colony during the breeding season was 87 km. Other tracking studies with the same species breeding in non-urban areas found maximum foraging ranges from 80 (Garthe et al., 2016) up to 359 km (Camphuysen, 2011) during the breeding season, with mean foraging

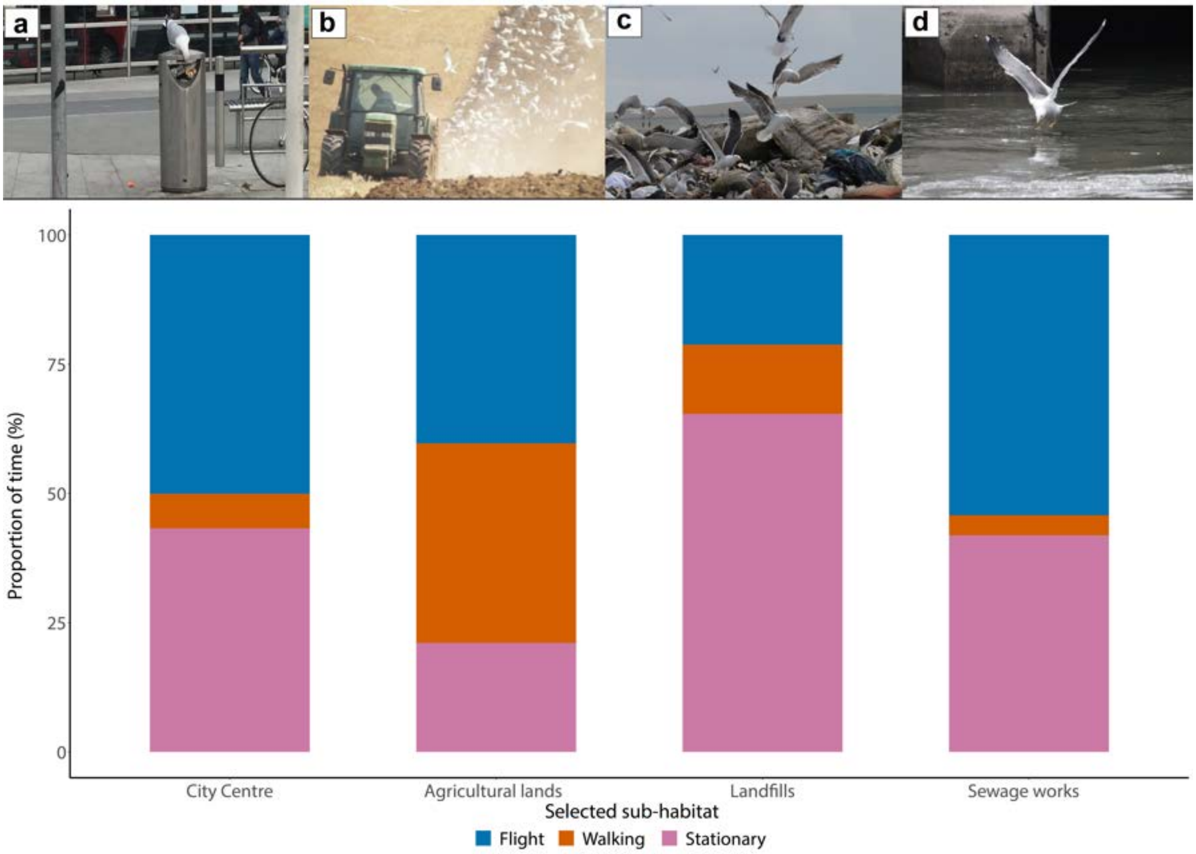

Figure 3.5: Photographs of gull behaviour taken during observations at four specific feeding grounds within the main habitats and the mean proportion of time spent on each behaviour in those habitats based on accelerometer data. a) City centre. b) Agricultural lands. c) Landfills in and around Bristol. d) Bristol Sewage Works. These specific feeding grounds were selected from the main habitat types: built-up areas (a), rural green areas (b) and waste processing areas (c/d).

ranges of 20-30 km. Gulls nesting on two islands in the Bristol Channel (Steep Holm and Flat Holm), both within foraging range of Bristol (~40 km), have been observed to feed their chicks with marine invertebrates (Mudge & Ferns, 1982) indicating that the marine area close to Bristol does offer potential food sources. In addition, some of the birds in this study visited the marine areas close to Bristol both before and after the breeding season, indicating that they were aware of this resource but did not make use of it during the breeding season. Although studies with seabirds have shown that a shift to marine resources can be very beneficial during chick-rearing due to high nutrimental value of these resources (Spaans, 1971; Annett & Pierotti, 1989), the gulls in Bristol were selecting to use terrestrial foraging sites over marine foraging areas during the whole breeding season. This suggests that the net energy gain of foraging in the available terrestrial environment seemed to be higher than for the local marine environment for these urban-nesting birds and this might reflect the state of the resource availability and foraging costs in the surrounding ecosystem.

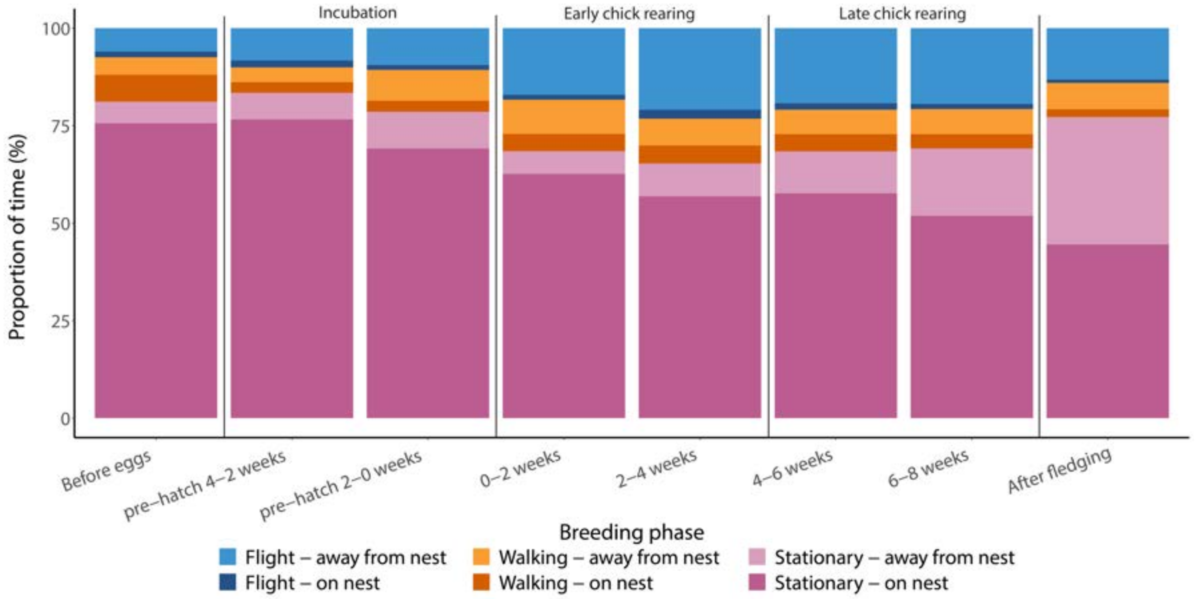

Figure 3.6: Mean proportion of time spent on each of the three behaviour types either on the nest (darker shades) or when away from the nest (lighter shades) depending on breeding stage. Behaviour classification is based on accelerometer data.

The birds in this study appear to forage both in suburban and urban environments, as well as in the rural green areas (mainly agricultural lands) around the city of Bristol. When away from their nest the birds spent on average two-thirds of their time in the suburban and urban areas and one-third of their time in rural green areas such as agricultural fields. When in the suburban and urban areas, it appears likely that many of the gulls in this study would have obtained a substantial amount of food for themselves and their chicks from anthropogenic waste based on the locations they visited, and the behaviours seen in those locations. Indeed, dietary studies have shown that anthropogenic waste can be a large part of the diet of urban-nesting gulls (Raven, 1997; Coulson & Coulson, 2008). Interestingly, on average the birds spent nearly one third of their time away from their nests in the rural green areas around the city. Presumably the gulls were using these areas for foraging as they are often rich in earthworms and insects and these are easier to find in short vegetation or after fields have been disturbed by activities such as ploughing (Buckley & McCarthy, 1994; Coulson & Coulson, 2008). Our personal observations confirmed that gulls were often present when farmers were working on fields and our movement data showed gulls returning to specific fields in the days after they were ploughed. Other studies with large gulls have shown that individuals forage and feed at agricultural lands (Coulson & Coulson, 2008; Caron-Beaudoin et al., 2013; Gyimesi et al., 2016) with one study showing the most common items of food in pellets were coming from this habitat (Garthe et al., 2016).

We observed a clear decreasing pattern in the proportion of time spent at the nest as the breeding season progressed, with the proportion of time spent in suburban and urban areas (especially built-up and waste processing areas) increasing from incubation to early and late chick rearing. The trend of decreasing time at the nest was expected based on similar patterns in nest attendance observed in non-urban colonies of the same species (Camphuysen et al., 2015). The increase in time in suburban and urban areas suggests that resources in these areas, such as human food waste, provide important resources for chick rearing. This is supported by other studies of large gulls showing increased use of suburban areas, city parks (Huig et al., 2016) and landfills (Belant et al., 1998) from incubation through post fledging. However, results of studies on dietary switching in gulls are mixed as to changes in the proportion of anthropogenic food intake over the breeding season. One study with herring gulls in the UK found a decrease in the proportion of agricultural food and an increase in proportion of anthropogenic waste food (Raven, 1997), but other large gull studies showed no change in dietary proportions (Hunt, 1972; Nogales et al., 1995; Bertellotti & Yorio, 1999), while still others found a decrease in the proportion of anthropogenic food (Annett & Pierotti, 1989; Noordhuis & Spaans, 1992). However, trends in dietary studies are difficult to compare with patterns in habitat use measured in GPS tracking studies due to the different limitations of the methods. Diet analysis methods do not provide information about where the food has been obtained by the individual and often underestimate the amount of soft and fully digestible food, such as bread (Weiser & Powell, 2011). GPS tracking studies are able to indicate where the food has been obtained but cannot provide information as to the type and amount of food obtained in the areas visited.

We propose three – not mutually exclusive – hypotheses to explain the increase in the proportion of time spent in suburban and urban areas from incubation to chick rearing as the chicks' food demand increases. (1) Suburban and urban food resources are readily available and more predictable in space and time than rural food sources (Marzluff, 2001; Shochat, 2004). Human activities, such as daily feeding of birds in gardens, weekly waste collection from the streets and daily operating waste processing centres, are providing gulls with a predictable and widely available food resource. On the other hand food resources from rural green areas, such as earthworms and insects, are present when the soil is disturbed by ploughing on the land, which takes place at irregular times, and when local weather conditions increase arthropod availability, e.g. damp or wet ground (Sibly & McCleery, 1983a; Buckley & McCarthy, 1994; Coulson & Coulson, 2008). (2) Suburban and urban food resources have a higher energetic value than rural food resources. The energetic content of waste has been calculated to be 2.2 calories/gram, whereas for earthworms this is only 0.71 calories/gram (Hunt, 1972). With observed ingestion coefficients (rate of increase of mass) of herring gulls (Sibly & McCleery, 1983b), the net rate of energy intake would be higher during feeding on waste (28 calories/hour) than on earthworms (23 calories/hour). (3) Suburban and urban food resources are closer to the nesting area. A shorter distance from the nest would imply less commuting time and therefore possibly shorter, more frequent, and more efficient foraging trips with a higher net energy intake. For example, a study on lesser black-backed gulls in a traditional island colony showed that the foraging trip duration was shorter during chick rearing in comparison to during incubation when parents only have to feed themselves (Camphuysen et al., 2015). Currently, data are not available to test all three hypotheses, therefore this study is not able to differentiate between them, with the possibility that all three play a role.

The gulls had distinct time-activity budgets associated with each habitat type, which appeared to reflect the use of different foraging strategies in four specific feeding grounds (Figure 3.5). At waste processing areas, such as landfills, the main behaviour observed was "stationary" behaviour. Together with our personal observations this suggests a "sit-and-wait" strategy, where the birds would wait until new waste was unloaded before flying in and feeding. A particularly characteristic behaviour was observed at the Bristol Sewage Works, where gulls would wait lined up along the wall of the sewage flow and then fly down to snatch food waste from the sewage water that flowed past. This behaviour was confirmed by the time-activity budget (Figure 3.5d) where the proportion of time spent in flight was larger than in landfills. On agricultural lands, time-activity budgets showed that gulls spent the largest proportion of their time walking. This strategy is frequently used by gulls to feed on both invertebrates and insects in fields (Mudge & Ferns, 1982). Lastly, in built-up areas, such as the city centre, besides the "sit-and-wait" approach, the main strategy seems to be flying and actively searching for feeding opportunities from the air. Overall, these different time-activity budgets related to habitat type probably reflect the availability of resources and the foraging strategies needed to acquire them in each of the habitat types, with different costs and intake resulting in differing profitability for each habitat.

The change in the birds' time-activity budgets over the breeding season suggests that they shift some of their resting behaviour to their foraging grounds. The overall proportion of stationary behaviour decreased from incubation - when the vast majority of stationary behaviour occurs at the nest - to chick rearing. However, during chick rearing, while the overall time spent stationary stays relatively constant, a progressively greater proportion of stationary behaviour occurs away from the nest. This shift in stationary behaviour to other habitats away from the nest may allow them to forage more efficiently. Nest attendance is assumed to be important during incubation and early chick rearing stages when either the clutch or chicks need to be protected (Cadiou, 1999). During later chick rearing stages returning to the nest to rest and protect the chicks may become less important, as the chicks are now better able to fend for themselves. Indeed, gulls have been observed resting away from the colony during the breeding season (Schwemmer & Garthe, 2005; Shamoun-baranes et al., 2011) and resting at feeding grounds might be energetically more efficient than flying back to the nest. Moreover, an increase in stationary behaviour away from the nest could indicate an increase of the "sit-and-wait" foraging strategy which may be less energetically demanding as flying and actively searching for food. At the end of the breeding season (~8 weeks), the time spent stationary increased again, which could be related to the fledging chicks being able to leave the nest. Chicks have been seen leaving the nest with their parents and being fed by them at different feeding grounds (pers. obs). These results suggest that these birds may shift their time-activity budgets during the breeding season to be able to rest at the foraging grounds and therefore gain energy more efficiently.

In the UK, several gull species are amber listed, with varying rates of population decline (Eaton et al., 2015). Gull populations in cities, however, are increasing which is resulting in higher numbers of human-gull conflicts. With respect to these trends in urban gull populations, a range of lethal and non-lethal control measures are currently being implemented (Monaghan & Coulson, 1977; Rock, 2005). When considering these measures for urban-nesting gulls it would appear that although suburban and urban areas may provide the majority of foraging opportunities during the breeding season, that the birds are also foraging outside of these areas and are capable of utilising a wide range of food sources. This needs to be taken into account when applying control measures, such as the removal of access to waste processing centres, as the birds may easily shift their foraging efforts to other food sources. This shifting of foraging effort with changes in the availability of point food sources has been documented in gulls (Rock, 2004a; Zorrozua et al., 2018) and other bird species (Steenhof & Kochert, 1985; Sample et al., 1993; Donázar et al., 2010). In addition, it is clear from this study that the birds ranged over a large proportion of the suburban and urban environment and that the individuals seen in a particular location could be nesting in a distant part of the city. Other studies with gulls show that non-urban nesting individuals may also forage in urban areas well away from their colony (Rock, 2005; Bouten et al., 2013; Huig et al., 2016). Together this indicates that local control measures for nesting birds may not have an effect on the number of birds in that area. Human-wildlife conflicts are not only observed in gulls, with other species that thrive in urban environments being reported to cause problems with damage to properties, disease transmission, and aggression (Soulsbury & White, 2016). Understanding the behaviour and habitat use of urban-living animals is therefore crucial when trying to control and/or mitigate conflicts between people and wildlife in cities.

Overall, these results show that these urban-nesting gulls spent the majority of their time in suburban and urban areas during the breeding season, while also utilising rural areas surrounding the city to a reasonable extent. The birds however did not make any use of the marine areas close to the city and this is likely to be due to the availability of terrestrial environments offering more efficient foraging opportunities. They appeared to use different foraging strategies to suit different habitats. When considering conservation measures for gull species as a whole, this study supports the view that gulls are generalist opportunistic foragers, taking advantage of a wide variety of food sources (Mitchell et al., 2004; Schwemmer et al., 2008; Camphuysen et al., 2015; Garthe et al., 2016). The birds utilised suburban and urban areas more as their chicks grew and their time-activity budgets were variable over time and between habitats. Temporal variability in behaviour and habitat use during the breeding season is also observed in other bird species (Pütz, 2002; Anderson et al., 2003). Overall, this raises the possibility that bird species and populations which might be considered as urban living (Marzluff, 2001; Shochat et al., 2006), may make use of resources from outside urban areas and that their behaviour and habitat use may change over the course of the breeding season. This potentially needs to be considered when designing control and conservation measures for any urban species.

CHAPTER 4

TEMPORAL PATTERNS IN FORAGING BEHAVIOUR LINKED TO HUMAN ACTIVITY

This is the second data chapter of this thesis looking to answer the question: *"Are there temporal patterns in the foraging behaviour of urban-nesting gulls and how are these linked to human-related activity and food availability?"*. Based on the findings of the previous chapter that gulls spent their majority of their time in suburban and urban areas, this chapter aimed to understand if urban-nesting gulls can adjust to artificial temporal cycles in food availability related to human activity in different urban feeding grounds. The ability to adapt to temporal patterns in predictable food sources might be another reason for the success of gulls in cities. This chapter has been submitted in an adjusted form as a manuscript to a Scientific Journal with the title "Urban gulls adapt foraging timing to human-activity patterns" in collaboration with the following authors: Oliver Soutar, Cara Williamson, Jane Memmott, Judy Shamoun-Baranes, Peter Rock, and Shane Windsor. I conceived and planned the research together with AS, OS, CW, JM, PR, and SW. I carried out the main part of the fieldwork together with OS. I performed the analysis and took the lead in writing the manuscript for publication. All authors provided critical feedback and helped shape the research, analysis and manuscript.

4.1 Summary

Numerous animals are able to adapt to temporal patterns in natural food availability, but whether species living in relatively novel environments such as cities can adapt to artificial activity cycles is less well understood. We aimed to assess the extent to which urban gulls have adapted their foraging schedule to temporal fluctuations in anthropogenic food sources related to human

activity by combining field observations at three distinct urban feeding grounds (park, school and waste centre) with global positioning system (GPS) tracking data of gulls visiting similar types of feeding grounds throughout the same city. We found that the birds' foraging patterns closely matched the timing of school breaks and showed different temporal patterns during the week compared to weekends. The gulls also matched their foraging schedule to the opening and closing times of the waste centre and the proportion of gulls foraging on food waste was negatively related to activity on the waste pile. On the other hand in the park, the gull activity appeared to correspond with the availability of natural food sources instead of human-related activity or food availability. Overall, this suggests that gulls may have the behavioural flexibility to adapt their foraging behaviour to human time schedules when beneficial and that this trait could potentially enable them to thrive in cities.

4.2 Introduction

Optimal foraging theory predicts that animals should adopt a foraging strategy that provides the greatest reward compared to cost, maximizing net energy gain and eventually fitness (Stephens & Krebs, 1986). While searching for food, animals have to respond to both spatial and temporal variations in food availability. Some animals are able to adapt to temporal fluctuations in natural resources, many of which vary in predictable ways based on environmental cycles, such as circadian, tidal, and seasonal rhythms (Cox et al., 2013; Lin et al., 2013). In comparison to natural environments, urban environments are novel for animals on an evolutionary time-scale and present a wide array of potential food sources. However, in urban environments, food availability often fluctuates temporally according to artificial activity patterns, such as weekday/weekend cycles. Currently, little is known about how urban animals cope with these fluctuations in anthropogenic food availability.

Readily available food in urban environments is believed to be one of the reasons why numerous animal species are thriving in cities around the world (Shochat, 2004). These include insect pollinators (Baldock et al., 2015), birds (Blair, 2001; Marzluff, 2001) and carnivorous mammals such as foxes, bears and hyaenas (Bateman & Fleming, 2012). This increase in urban animals has resulted in complex human-wildlife interactions (Ditchkoff et al., 2006) with people either being attractants (a signal that food might be available) or deterrents (causing disturbance). Gulls are an example of a species thriving in cities worldwide (Monaghan & Coulson, 1977; Balmer et al., 2013), but the exact reasons for their success are uncertain and could be a result of several factors such as warmer temperatures, fewer predators, ample nesting sites and predictable food conditions (Rock, 2005). Gulls exploit numerous anthropogenic food sources, such as food waste and fishery discards (Washburn et al., 2013; Tyson et al., 2015). They have also been observed to following fishing vessels during weekdays (Tyson et al., 2015) and visit urban feeding grounds at specific times of the day, which is suggested to be related to human activities (Yoda et al., 2012). Additionally, the foraging behaviour of gulls has been linked to natural patterns in food availability, such as feeding on pasture fields around sunrise or in the intertidal zone depending on the tidal cycle (Sibly & McCleery, 1983b; Irons, 1998). Using gulls as study species can provide insights into the potential ability of urban animals to adapt their foraging schedules to artificial temporal patterns in food availability.

This study aimed to quantify temporal patterns in gulls' use of urban feeding grounds and to assess the extent to which gulls have adapted their foraging schedules to human activities. From the GPS tracking data we selected three urban feeding grounds frequently visited by the gulls to conduct observations. Given previous observations of the timing of gulls' use of urban feeding grounds (Sibly & McCleery, 1983b; Yoda et al., 2012), we expected the gulls to match their foraging schedule to the times when human activity and/or food availability was highest. Additionally, we predicted that the foraging schedule would vary at each feeding ground, reflecting differences in the temporal characteristics of the food sources.

4.3 Methods

4.3.1 Study area and species

This study was conducted during the gull breeding season between 18 June and 16 July 2018 in Bristol, UK. Based on the collected GPS tracking data and field observations conducted in Chapter 3, we selected three urban feeding grounds for observations: a park, a school, and a waste centre (Figure 4.1). These locations were selected because they were frequently used by the GPS-tracked gulls and were on average 2.9, 6.7 and 7.1 km respectively from the two nesting areas (~1.5 km apart). All species of gulls present at these sites were recorded and counted, but no distinction was made between the species. These included lesser black-backed gulls, *Larus fuscus*, herring gulls, *Larus argentatus*, and black-headed gulls, *Chroicocephalus ridibundus*.

4.3.2 Feeding ground observations

Each of the three feeding grounds was observed for seven days. This included two weekend days in order to capture the difference between weekdays and weekends. At each site we conducted counts every 15 minutes for up to 12 hours between 04:00-16:00 (the park), 07:00-17:00 (the school), and 06:00-18:00 (the waste centre). We used the GPS tracking data to identify these locations and the time periods for observation to ensure that the observations included the majority of the time that the gulls were present at these feeding grounds. For each count at the park and the school, the following variables were recorded: (1) number of gulls, (2) number of people, (3) anthropogenic food presence and (4) day of the week. Food was considered to be present when people were observed consuming food. For the park, gulls present within the park boundary were included in the counts, but gulls flying over the park at high altitudes were excluded. For

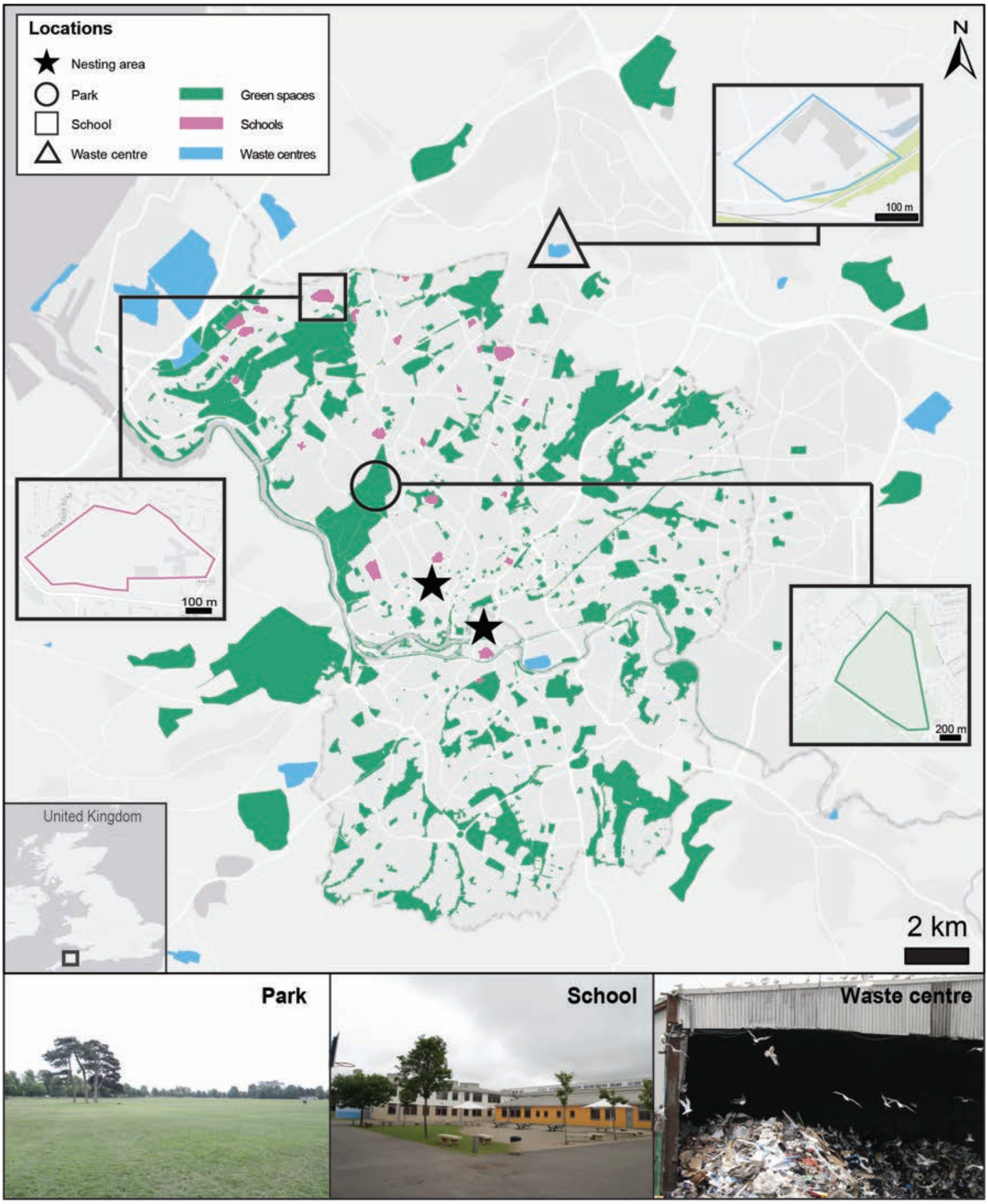

Figure 4.1: Habitat map of the study area in Bristol, United Kingdom, indicating the different habitat types (green spaces, schools and waste centres), the location of the nesting areas (stars) and the specific feeding grounds: the park (circle), the school (square) and the waste centre (triangle). These feeding grounds are located on average at 2.9, 6.7 and 7.1 km respectively from the two nesting areas (~1.5 km apart). Insets of each specific feeding ground show the area where counts were conducted. Base map sources: ESRI, DeLorme, HERE Technologies, MapmyIndia.

Table 4.1: Classification of activity level (AL) for counts at the waste centre.

AL	Definition
0	Nothing happened at the time of the count
1	Activity occurring off the waste pile at the time of the count, e.g. people walking past
2	Single activity occurring on the waste pile at the time of the count, e.g. truck unloading food waste
3	>1 activity occurring on the waste pile at the time of the count

the school, we counted the gulls present at the school playgrounds, on the surrounding school buildings and the adjacent sports fields because these areas were all used by people during the day.

The waste centre is a transfer station where 35,000 tonnes of commercial mixed waste, including food waste, is processed annually. At the waste centre, besides the total number of gulls, we recorded both the number of gulls on the roofs of the surrounding buildings, as well as gulls on the food waste pile, the distinction being that birds on the food waste pile were actively searching for food, whilst those on the roofs were not. We also recorded the time of any waste-related activity which was any activity happening on or around the food waste pile, e.g. such as unloading food waste. This was then used to calculate the time since waste unload and a waste-related activity level for each count (Table 4.1). This resulted in the following variables for the waste centre: (1) total number of gulls, (2) percentage of gulls on the waste pile, (3) waste-related activity level, (4) time since waste unload and (5) day of the week. For all sites, gull counts were excluded when the gulls were disturbed by birds of prey.

For statistical analysis, we modelled the number of gulls (at the time of each count) in the park and at the school in relation to the following predictors: time of day (continuous - 15 min), number of people (continuous), anthropogenic food presence (categorical - Yes, No) and day of the week (categorical - Weekday: Monday-Friday, Weekend: Saturday-Sunday). At the waste centre, we modelled the number of gulls (at the time of each count) in relation to the following predictors: time of day, day of the week and waste-related activity level (categorical - 4 levels). We used generalised additive mixed models (GAMMs) in order to account for the non-linear relationship between time of day and the number of gulls. Lastly, for the waste centre, we also modelled the percentage of gulls on the waste pile (at the time of each count) in relation to the following predictors: activity level, day of the week and time since waste unload (categorical - 7 levels). We used a generalised linear mixed model (GLMM) because the time of day was not included as we expected time of day to have no effect on the percentage of gulls on the waste pile. Interaction terms of predictor variables were included when this seemed appropriate during data exploration. Models were created with a negative binomial distribution due to overdispersion. GAMMs were modelled using the mgcv package (Wood, 2011) and the GLMM was modelled using lme4 package (Bates et al., 2015) in R version 3.6.0 (R Core Team, 2019). For the GAM, diagnostics were checked via gam.check and the number of knots were set at the default (K=10). We conducted a forward-step selection procedure to select the "best-fit" model based on chi-square tests (appropriate for negative binomial distributions) following Zuur et al. (2009). Additionally, we checked the AICc values of the fitted models to provide verification of the significance of the terms and these can be found in Table A.1. Model residuals were normally distributed and showed homogeneity of variance, and predictor variables did not show collinearity. The significance level was set at $\alpha = 0.05$ and results are reported as the mean and standard deviation.

4.3.3 GPS tracking data

GPS tracking data were examined in this study to calculate the percentage of total time spent in the different feeding grounds at specific times of the day, for the same period as the feeding ground observations. For full details of the GPS tracking methods, see Chapter 2. In brief, 12 lesser black-backed gulls in Bristol were tagged with UvA-BiTS GPS devices (Bouten et al., 2013) in 2016 and 2017. The weight of both device and harness was 18 gram, which was < 3% of the birds' body mass (mean: 2.4%, range: 2.1-2.7%). These devices recorded location at different intervals during the breeding season (from 4 to 600 seconds), therefore data were sub-sampled to a 15-minute rate to create equal time resolutions and match the feeding ground observation times. Data from nine individuals was available for inclusion in this study which had either active or non-active nests. To identify the different feeding grounds in Bristol, a habitat map was created in ArcGIS Desktop 10.5.1 (Figure 4.1). Data was extracted from several datasets: Corine Land Cover European seamless vector database (European Commission, 2016), a landfill database (Environment Agency, 2019), an allotment database (Bristol City Council, 2017) and a schools of Bristol dataset (Deepspace Web Services, 2019). The final map consisted of three habitat types: (1) green spaces (including parks, allotment sites and sports fields), (2) schools, and (3) waste centres. GPS locations were selected during 18 June and 16 July 2018 between the same times as the feeding ground observations and resulted in a total of 18,305 GPS locations. Firstly, we identified the percentage of total time spent in the three specific feeding grounds (park, school and waste centre) by dividing the amount of GPS locations in a specific feeding ground by the total number of GPS locations. From the GPS dataset, 18 GPS points were in the park, 44 at the school and 399 at the waste centre. Secondly, we identified the percentage of total time spent in the three habitat types of interest. From the GPS dataset, 918 GPS points were located in green spaces (~150 locations), 185 in schools (25 locations) and 680 in waste centres (49 locations). In terms of the use of the specific feeding grounds, four individuals used the park (1 fix, 3 fixes, 5 fixes, 9 fixes), two individuals used the school (4 fixes and 40 fixes) and 6 individuals used the waste centre (1 fix, 1 fix, 13 fixes, 28 fixes, 54 fixes, 302 fixes). With respect to multiple feeding grounds of these habitat types, all gulls used all three habitat types over the 4-week period. All work was approved by the University of Bristol Animal Welfare and Ethical Review Body (UIN UB/15/069) and access permissions were obtained from all properties visited.

Table 4.2: Summary of the significance of terms included in both GAMM and GLMM analyses of the different feeding grounds. s(Time) = time of day (15 min) as a smooth term, s(Time:week) = time of day on weekdays as a smooth term, s(Time:weekend) = time of day on weekend days as a smooth term, df = degrees of freedom, EDF = estimated degrees of freedom, chisq = Chi-square test. Estimates (β-coefficients) are given for the terms in the final best-fit model except for the categorical variables with more than two levels which can be found in Table A.2.

Model	**Response**	**Explanatory**	**df**	**chisq**	**p**	**β-coefficient / edf**
Park	Number of gulls (at time of count)	Number of people (continuous)	1	13.9	<0.001 ***	-0.135
		s(Time)	6.51	46.94	<0.001 ***	5.41
School	Number of gulls (at time of count)	Number of people (continuous)	1	11.84	<0.001 ***	0.0055
		Food (factor)	1	7.84	0.005 **	0.34
		Number of people : Day of the week	1	4.76	0.029 *	-0.057
		s(Time)	7.08	120	<0.001 ***	5.915
Waste centre	Number of gulls (at time of count)	Day of the week (factor)	1	241.5	<0.001 ***	-0.917
		s(Time)	5.55	31.768	<0.001 ***	4.715
		s(Time:weekday)	4.85	15.695	0.023 *	4.086
		s(Time:weekend)	11.92	1.799	0.509	1.468
Waste centre	Percentage on pile (at time of count)	Day of the week (factor)	1	14.745	<0.001 ***	0.323
		Waste-related activity level (factor)	3	1601	<0.001 ***	see Table A.2
		Time since waste unload (factor)	6	241.58	<0.001 ***	see Table A.2

*** p <0.001, ** p <0.01, * p <0.05, . p <0.1

4.4 Results

Based on the feeding ground observations in the park, gulls were mainly present during the early morning when people were not (Figure 4.2, Table 4.2). The number of gulls present was not related to anthropogenic food availability (χ^2_1 = 0, p = 0.999, Figure 4.3) nor was there a difference in the number of gulls present between weekdays and weekends (χ^2_1 = 0.444, p = 0.657, Figure 4.2).

The number of gulls present at the school showed a small peak at 8:45 (12 ± 5.3) and was highest at 11:15 and 12:45 local time (25 ± 10.5 and 38 ± 21.5 gulls, respectively), which coincided with an increase in the number of people present due to the students having breaks from 11:00-11:20 and 12:20-13:00 (Figure 4.2, Table 4.2). Additionally, on average significantly more gulls were present when food was present (33 ± 17.4) than when food was not present (9 ± 7.8, Table 4.2, Figure 4.3). Although there were more gulls present during the week (week: 13 ± 10.2 vs weekend: 8 ± 5.6) this was not statistically significant (χ^2_1 = 0.09, p = 0.767, Figure 4.2), neither was the interaction between time and day of the week (χ^2_1 = 0.01, p = 0.999). The interaction effect between the day of the week and number of people present was significant, with an increase in the number of people resulting in increased gull numbers during the week, but decreased gull numbers during the weekend (Table 4.2, Figure 4.2). This decrease in gull numbers during the weekend could be related to the organised sports events which occurred at the school's sports fields in the afternoon during the weekend.

The waste centre was open from 7:30 until 16:30 on weekdays but was closed over the weekend. During weekdays at the waste centre, the number of gulls was higher (134 ± 59.7) but the percentage of gulls on the waste pile was lower (32 ± 25%) compared to during the weekend (73 ± 38.31 and 52 ± 26% respectively, Table 4.2, Figures 4.2 and 4.4). During the week the number of gulls increased in the morning and decreased in the afternoon (Table 4.2, Figure 4.2), but during the weekend fewer gulls were present and the numbers slowly declined (Figure 4.2). The waste-related activity level did not affect the number of gulls present (χ^2_3 = 2.40, p = 0.495, Fig. S3); however, higher waste-related activity levels resulted in lower percentages of gulls on the pile (Table 4.2, Figure 4.5). Finally, the percentage of gulls on the pile decreased as the time that had elapsed since a waste unload increased (Table 4.2, Figure 4.6).

The percentage of time spent by the GPS tracked lesser black-backed gulls at the three feeding grounds changed over the course of the day (Figure 4.7), following similar patterns during the week to those observed in the feeding ground observations (Figure 4.2). However, during the weekend our birds did not visit the three feeding grounds as frequently, resulting in very low percentages of time in these locations. Additionally, the percentage of time spent at multiple green spaces (including parks), schools and waste centres in Bristol showed that these patterns were not only specific to the three feeding grounds, where the field observations were made, but were similar for all feeding grounds of these types (Figure 4.7 – green line). However, we do note that the temporal pattern at multiple waste centres showed a high peak at the beginning of the day and the temporal pattern at multiple green spaces showed the presence of gulls at later times during the day.

4.5 Discussion

This study found that temporal patterns in gulls' use of urban feeding grounds were linked to human activity and food availability. This was mainly evident at the school and the waste centre where gulls matched their foraging timing to the times of the school breaks (e.g. a high number of people and presence of food) and times when the waste centre was open (e.g. during the week and when waste was unloaded). These results match those of a study with herring gulls where the number of individuals at a refuse tip in Walney, UK, increased when the tip was open and was highest when new waste was unloaded (Sibly & McCleery, 1983b). We also found that the percentage of gulls at the waste pile was highest just after the waste was unloaded, suggesting a possible trade-off between feeding on the waste pile during an activity, which might be dangerous due to the possibility of injury, and maximising food intake by foraging when food availability is probably highest.

The negative relationship between people and gull presence in the park could have been a result of disturbance as observed in other birds (Fernández-Juricic & Tellería, 2000). However, gulls that were present in the morning were predominantly observed walking and pecking for food within the short vegetation (pers. obs.). Therefore, it seems possible that the presence of earthworms – known to be abundant during early hours of the day (Sibly & McCleery, 1983b) – or other arthropods, offers an explanation for the presence of gulls in the morning. This is in agreement with previous studies on foraging behaviour in gulls where numbers in pasture fields were highest around dawn (Sibly & McCleery, 1983b) and terrestrial foraging trips were more frequent than marine trips around sunrise (Isaksson et al., 2016).

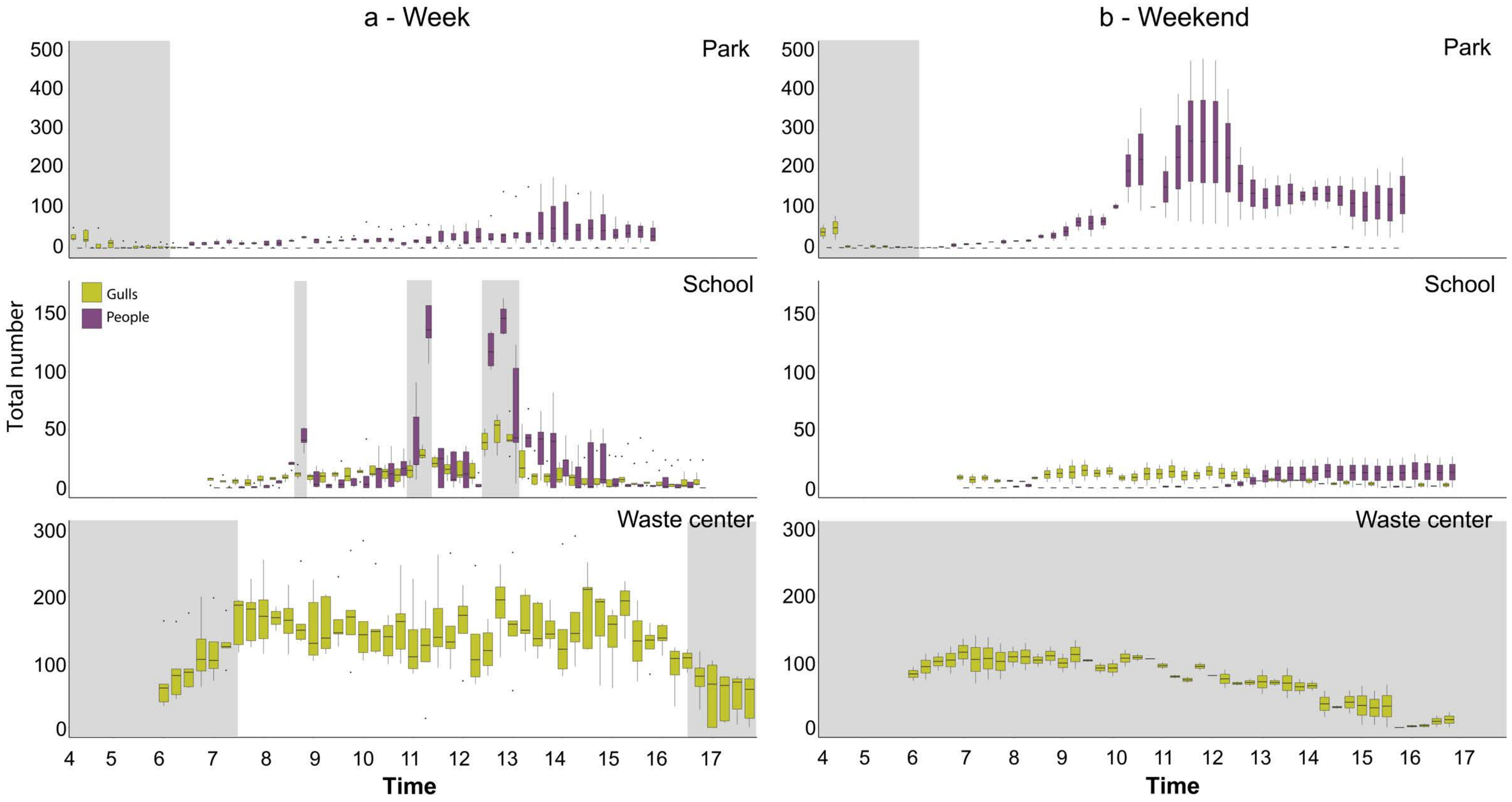

Figure 4.2: The number of gulls (yellow) and people (purple) based on the feeding ground observations during the week (a) and weekend (b) at the three specific feeding grounds: park, school, and waste centre. At the waste centre, the number of people was not counted, but instead waste-related activity level (not shown here, Figure 4.5). Grey areas represent the period till sunrise (park), break times (school) and times of closure (waste centre). The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR.

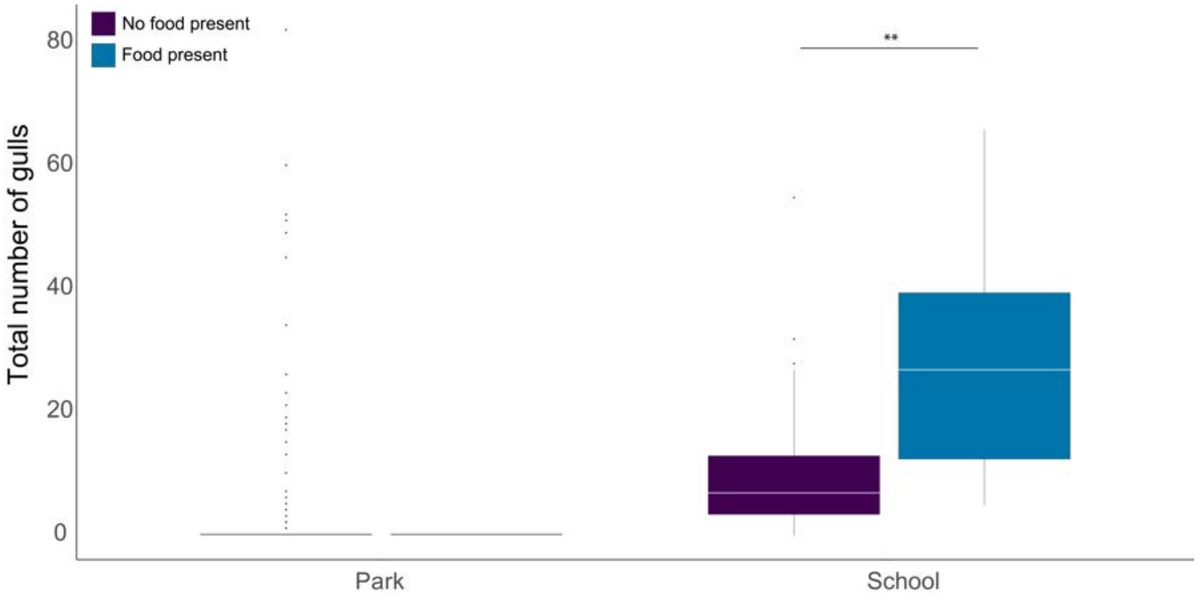

Figure 4.3: The total number of gulls when food is not present (purple) and when food is present (blue) at the park and the school. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR. Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

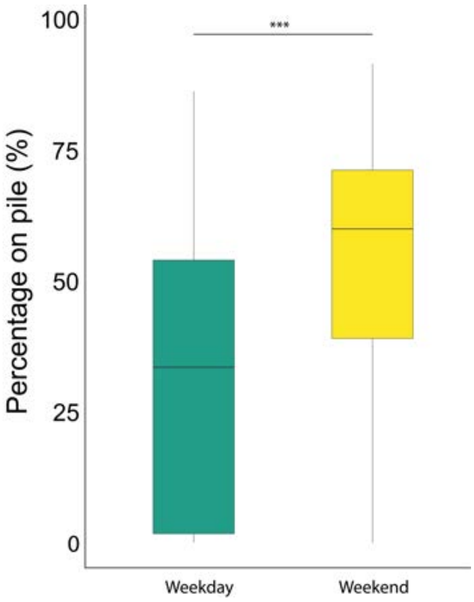

Figure 4.4: The difference in percentage of gulls on the waste pile between week and weekend. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR. Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

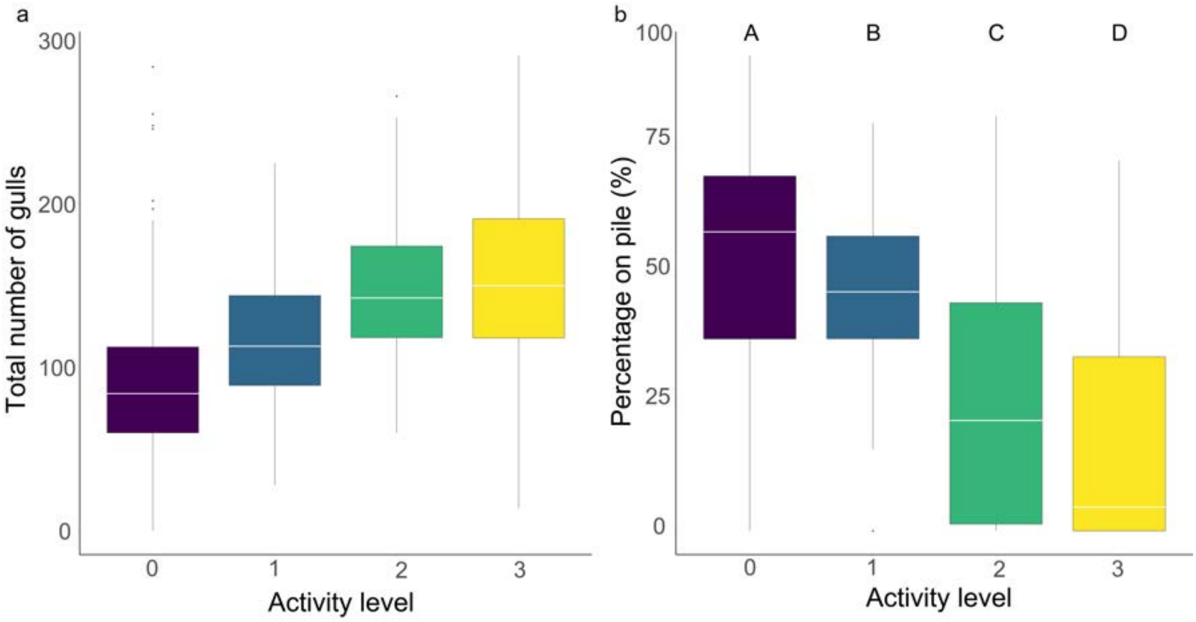

Figure 4.5: The total number of gulls (a) and percentage of gulls on the waste pile (b) compared to the activity level at the waste centre. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR. Different letters represent significantly different groups.

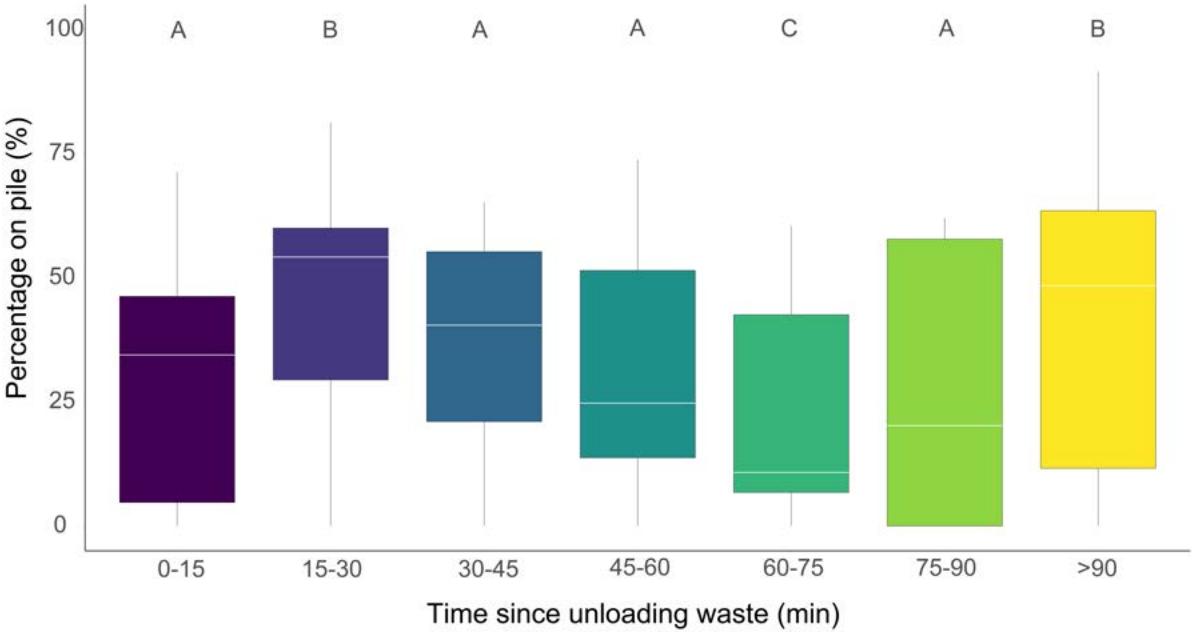

Figure 4.6: The percentage of gulls on the pile (%) compared to the time since unloading waste at the waste centre. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR. Different letters represent significantly different groups.

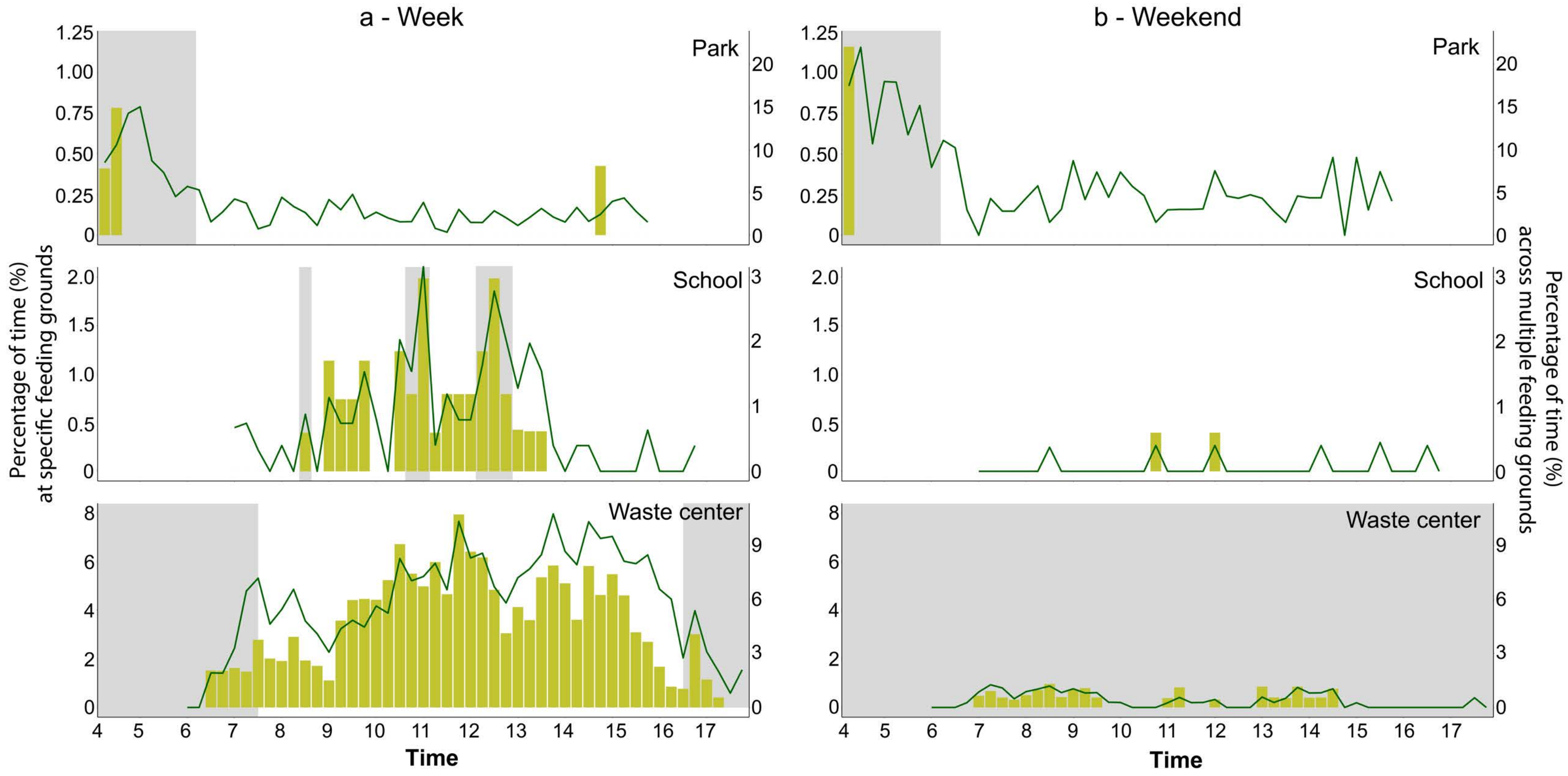

Figure 4.7: The percentage of total time spent (%) during the week (a) and weekend (b) based on the GPS tracking data. Yellow bars show the percentage of total time at the three specific feeding grounds: park, school, and waste centre. Green lines represent the percentage of time spent across multiple feeding grounds of the same type in Bristol, United Kingdom: ~150 green spaces, 25 schools and 49 waste centres. Grey areas represent the period till sunrise (park), break times (school) and times of closure (waste centre).

The number of gulls and the number of people at the school were positively related during weekdays, but negatively related during the weekend, indicating that people acted as both attractants (during weekdays) and deterrents (during the weekend). Indeed, at the weekend the sports fields were used by community groups from midday at which point the gulls, who were present in the morning, were disturbed (pers. obs.). However, we must note that these contrasting relationships might be specific to this particular school. At the waste centre, the temporal pattern of the number of gulls present was different during the week compared at the weekend. During the week, waste was unloaded regularly (up to 10 times a day) during the opening times of the centre, however, at the weekend no new waste was unloaded due to the centre being closed. This could explain the decrease in the number of gulls with time and the generally lower numbers present at the weekend.

The percentage of time spent at the three specific feeding grounds based on GPS tracking data supported our field observations, showing that the individuals we tracked exhibited similar foraging schedules to the gulls observed during counts being present in the morning in parks, following school break times during the week and opening times of the waste centre. Although we only conducted observations at three specific feeding grounds (one site per habitat type), our GPS tracking data demonstrated that the temporal patterns of gull numbers at schools and waste centres are similar across other sites in Bristol of the same habitat type despite the possibility that the exact timing of the gulls' presence might vary due to different school break times and opening times of the waste centres. Although the GPS tracking data for multiple green spaces showed a similar peak in the morning as found in the observed park, gulls were also visiting green spaces later in the day possibly attracted by food consumed by people. The observed park is one of the largest parks in Bristol and more used as a recreational space than a space to consume food, therefore this could be a reason that the GPS tracked gulls did not visit the observed park later in the day frequently.

At both the school and the waste centre, gulls were observed waiting on the surrounding rooftops before school breaks and before waste was unloaded, implying that they were waiting there specifically for food to become available. The temporal predictability of the food sources at these sites appears to have resulted in the birds adopting a "sit-and-wait" foraging strategy instead of actively searching for food (Schoener, 1971). This approach may allow them to minimise the time and energy spent searching for food. Similar behaviour has been observed in other bird species. For example, suburban Florida scrub-jays, *Aphelocoma coerulescens*, which had access to predictable human-provided food spent less time foraging and were more efficient foragers than rural scrub-jays (Fleischer et al., 2003). This suggests that the ability to predict the availability of anthropogenic food sources can maximise net energy gain and fitness which could eventually be reflected in population growth changes (Stephens & Krebs, 1986; Oro et al., 2013). It seems that in the current study the availability of food sources might be separated in time (park - early morning, school - break times, and waste centre - during the day) raising the question of whether the birds are able to optimise their use of resources by tracking their availabilities in a single day. More detailed analysis of the GPS tracking data is required to analyse this behaviour and the effects of predicting availability on the birds' net energy gains.

Numerous animals are able to adapt to natural temporal fluctuations in food availability (Cox et al., 2013; Lin et al., 2013) but whether animals are able to cope with artificial temporal rhythms in anthropogenic food availability is relatively unknown. Seabirds have been shown to adjust their foraging strategies to match daily and weekly rhythms in fishery activity (Bartumeus et al., 2010; Tyson et al., 2015) and red-winged starlings, *Onychognathus morio*, were able to deal with the fluctuations in food availability between weekday and weekends as a result of student absence at an University campus during the weekends (Stofberg et al., 2019). Although based on a small sample size, we showed that gulls in urban environments have the behavioural flexibility to adapt their foraging behaviour to human time schedules by making use of different anthropogenic resources depending on the timings of their availability. These human time schedules differ from natural circadian or seasonal rhythms as they either happen over shorter time-scales (within a day: school break times) or have irregular patterns (weekday vs weekend: waste centre opening times). This suggests that one of the traits enabling gulls to live so successfully in cities may be their ability to adapt their foraging timing to human-activity patterns and that this could potentially be a common trait in other successful urban-dwelling species.

CHAPTER 5

TIME INVESTMENT AND ENERGY COSTS IN RELATION TO WEATHER CONDITIONS

This is the third and final data chapter of this thesis is looking to answer the question: *"How do weather conditions affect both time investment and energy costs of urban-nesting gulls in the urban environment"*. Because gulls spent the majority of their time in the urban environment (Chapter 3), this chapter aimed to understand how urban-nesting gulls deal with the range of diverse and complex weather conditions present in the city during the breeding season. The ability to adapt to favourable conditions and minimise their time and energy costs might be another reason for the success of gulls in cities.

5.1 Summary

Optimising energy expenditure is important in an animal's life especially during a challenging period such as the breeding season. Energy costs can be affected by extrinsic factors such as weather conditions. For example, birds can save energy by using lift created when air is deflected upwards by structures (orographic lift) or when columns of hot air rise upwards due to unequal heating of the Earth's surface (thermals). Other weather conditions, such as precipitation can also affect flight behaviour and costs. Gulls are an example of facultative soaring birds which can adapt their flight style (flapping versus soaring) to different weather conditions. Cities consist of complex wind flows and a higher probability of thermals due to the UHI-effect, therefore these gulls could use these conditions to minimise their time investment and energy costs during the breeding season. This study aimed to analyse how weather conditions affect both time investment and energy costs of gulls nesting in an urban environment. By combining GPS tracking data with behavioural data, weather data and time-energy budgets, we found that precipitation did not affect the proportion of time spent in flight but did increase daily time spent away from the nest and the trip duration. In combination with increased time spent in flapping flight with slight precipitation levels, this resulted in a higher total trip energy cost. Additionally, gulls shifted to energetically cheaper flight behaviours (e.g. mixed and/or soaring flight) with increasing levels of solar radiation (a proxy for thermals) and wind speeds (a proxy for orographic updraft). However, this did not minimise their time investment or energy cost as the birds spent proportionally more time in flight. Spending more time in flight at higher wind speeds could provide the opportunity for gulls to encounter new ephemeral food sources during their trip at the same overall cost. Spending more time in flight at higher solar radiation levels in combination with a lower energy cost per unit distance suggested that the gulls could fly to foraging areas further from the nest with more predictable food sources without affecting their energy costs substantially. These opportunities could have increased their energy intake and maximised their net energy gain. The higher possibility of thermal and orographic lift in cities in combination with the gulls' flexibility of their flight behaviour to maintain similar time invesment and energy costs could be a useful trait for successful city life.

5.2 Introduction

Energy expenditure is an important aspect of an animal's life and can affect many life-history traits, such as growth, survival and reproduction (Brown et al., 2004). Optimal foraging theory predicts that animals need to choose a foraging strategy with the highest energy intake at the lowest cost, maximising their net energy gain (Stephens & Krebs, 1986; Bell, 1991). Maximising this net energy gain is especially important when animals are constrained in time, for example during migration or during the breeding season when parents have to take care of both themselves and their offspring (Drent & Daan, 1980). During the breeding season in systems with parental care, parents must balance the time and energy invested in themselves and their offspring (Stephens & Krebs, 1986).

Energetic costs attributed to movement can be affected by the environment animals move through. Energy landscapes have been created to help to understand these costs across different landscape features and atmospheric conditions (Wilson et al., 2012; Shepard et al., 2013). The aerial environment is especially variable in time and space and specific weather conditions (e.g. wind, solar radiation, precipitation) can affect flight behaviour and performance, changing foraging efficiency, timing of breeding and migration in birds (Schreiber & Burger, 2001). However, the effects of weather seem to be dependent on the flight style of the bird which in turn is related to their wing morphology and body mass (Spear & Ainley, 1997).

For example, wind conditions can have different effects on birds that only flap and birds that are able to soar besides flapping. For flapping birds, strong winds have shown to disrupt flight control during landing in cliff-nesting auks (Shepard et al., 2019) or increase the energy expenditure in flight in common murres, *Uria aalge* (Gabrielsen, 1996). However, wind can also be beneficial during flapping flight as supporting winds can increase grounds speeds (Safi et al., 2013) and tailwinds can be of support to cover long distances for example during migration (Liechti, 2006). For birds which can use atmospheric updraft created by vertical wind shear and orographic lift, wind can create opportunities to increase time in soaring flight (Shamoun-Baranes et al., 2016; Gibb et al., 2017; Santos et al., 2017). Orographic lift results from when moving air rises upwards after deflection over physical structures (e.g. cliffs, mountains and buildings, Figure 5.1a). Birds can exploit this rising air mass to soar in flight and save energy. Some species of birds are able to make use of this orographic lift to increase their time spent in flight without increasing and potentially minimising their energy costs (Lanzone et al., 2012; Shamoun-Baranes et al., 2016; Poessel et al., 2018).

Another source of atmospheric updraft which birds can use to save energy is thermal convection (Figure 5.1b). Thermals are columns of hot rising air generated by the uneven heating of the Earth's surface (Hardy & Ottersten, 1969). Thermals or thermal streets (multiple thermals in a row) are not only used by birds but also by human-driven gliders to reduce the power requirements of flight (Pennycuick, 1998). Thermals mostly occur over terrestrial environments (but see Woodcock 1975) and several bird species can use them to minimise their energy during foraging trips (Hernández-Pliego et al., 2015; Shamoun-Baranes et al., 2016) and during migration (Kerlinger & Moore, 1989; Spaar & Bruderer, 1996; Alerstam & Hedenström, 1998; Duerr et al., 2015). The availability and strength of thermals change over the course of a day and are both affected by topography of the landscape and the atmospheric conditions (Young, 1988; Kerlinger & Moore, 1989). This temporal and spatial availability constrains the time and amount of energy a bird can save by using thermals for soaring flight.

Besides wind and thermals, other weather conditions such as precipitation can potentially affect animal flight behaviour and associated costs. Wind tunnel studies showed that precipitation can decrease the aerodynamic efficiency of artificial wings (Thompson et al., 1995) and therefore affect flight performance. However, despite these negative effects, some birds (Ortega-Jimenez & Dudley, 2012) and bats (Voigt et al., 2011) have been seen flying during heavy rain, although their energy costs did increase. Studies looking at bird migration observed an effect of precipitation, either reducing the probability of departure for migration (Schaub et al., 2004) or when precipitation was absent the intensity of migration increased (Erni et al., 2002). During the breeding season, precipitation did not affect foraging or flight behaviour in Northern gannets, *Morus bassanus* (Lane et al., 2019) but increased foraging duration in Cape gannets, *Morus capensis*, which was possibly related to reduced prey visibility (Pistorius et al., 2015).

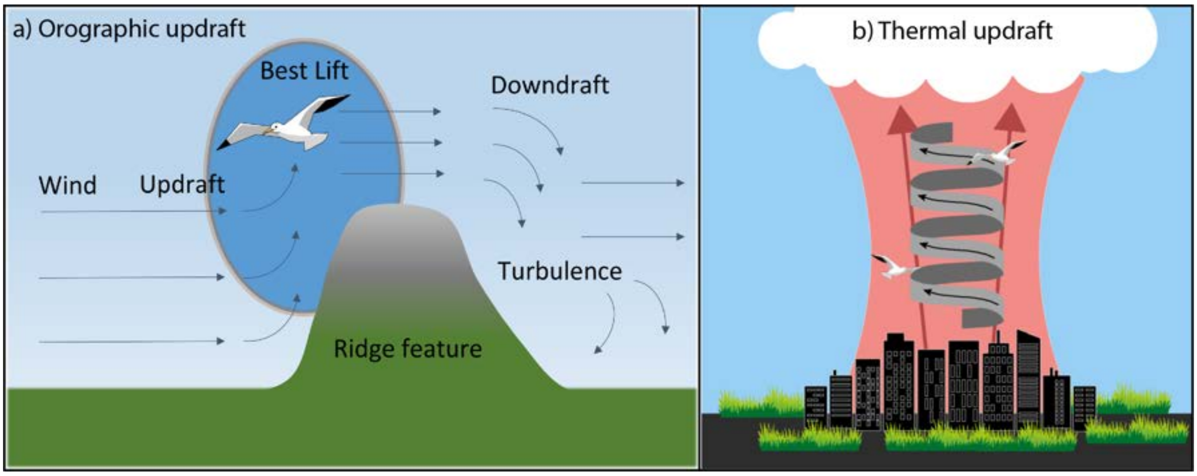

Figure 5.1: Example of two sources of lift for soaring birds. a) Orographic updraft resulting from moving air deflected upwards by physical structures. b) Thermal updraft resulting from columns of hot rising air due to uneven warming of the Earth's surface. Adjusted from Williamson (2020).

Gulls are an example of facultative soaring birds, meaning they can use both flapping and soaring flight. They are known to be able to change their flight behaviour according to different weather conditions, increasing their proportion of soaring flight when orographic or thermal lift is available (Shamoun-Baranes et al., 2016; Sage et al., 2019). Additionally, they can follow specific wind-ways using the orographic updraft generated by buildings along a beach front (Shepard et al., 2016) or along dunes and dykes in a flat landscape (Sage et al., 2019). Gulls are also increasing in numbers in urban areas all over the world which is suggested to be a result of several factors such as warmer temperatures, fewer predators, and predictable food sources (Rock, 2005). However, cities have complex wind flows providing orographic lift from structures such as buildings and trees. Additionally, temperatures in cities are considered warmer than the surrounding environment due to increasing heat of solar radiation on artificial surfaces, also called the 'urban heat island' effect (Manley, 1958; Oke, 1973), increasing the formation of thermals within cities. Therefore, the potential for birds breeding in cities to minimise their time investment and energy costs during foraging to these favourable conditions might be another reason for their success in cities.

Energy expenditure is defined as the amont of energy to carry out physical functions and can be measured by oxygen consumption. One method to assess oxygen consumption is the double-labelled water (DLW) technology (Lifson & McClintock, 1966). Initial studies were performed in the laboratory conducting experiments with rats, mice, birds and humans (Westerterp, 2017), but more recently DLW has been applied to free-living animals in the field (Butler et al., 2004; Shaffer, 2011). An alternative method is the use of heart-rate monitors which have been validated against DLW in different species (Fahlman et al., 2008; Halsey et al., 2009). However, both techniques have their own drawbacks such as costs, invasiveness, impracticality for larger animals and applicability to large sample sizes (Butler et al., 2004). In the last decades, due to advances in bio-logging technology, a new technique based on the acceleration of the body has been developed as metabolism is often correlated to mechanical power (Wilson et al., 2006). Acceleration of the body in three axes (X, Y, Z) is measured with accelerometers attached to the animal's body from which dynamic body acceleration (DBA) can be calculated. DBA has been linked and validated against both DLW and heart-rate monitors in some species and therefore used as a proxy for energy expenditure (Halsey et al., 2008; Green et al., 2009; Elliott et al., 2013; Jeanniard-du Dot et al., 2016). A big advantage of this method is the practicality of measuring body acceleration in both captive and free-living animals. However, this method also has its weaknesses as for each species a validation is required for each activity before converting the body acceleration to metabolic rates as the extent to which the regressions between DBA and metabolic rates for one activity can be used for other activities (especially flight) or species is under dispute (Gómez-Laich et al., 2011; Halsey et al., 2011; Wilson et al., 2020). Additionally, environmental conditions such as wind, which are not linked to active movement, can affect the acceleration measurement (Halsey et al., 2011; Gómez-Laich et al., 2011). Nevertheless, the use of body acceleration seems to be a promising technique but should be used with consideration and needs to be validated. This study did not have the scope to validate DBA with DLW or heart-rate measurements but did compare DBA calculations with energy cost calculations based on metabolic rate estimations from previous studies.

The current study aimed to analyse how weather conditions affect both time investment and energy costs of gulls nesting in an urban environment. These costs were estimated at both daily and trip level. The weather variables wind speed and direction, solar radiation and precipitation rate were considered in this study. Based on previous studies showing that the probability of orographic lift increased with higher wind speeds, it was expected that the birds would increase their orographic soaring flight and decrease their total energy costs both on the trip and daily scale with increasing wind speeds. Also, higher wind speeds have been found to result in higher grounds speeds, thus it was expected that higher wind speeds could result in shorter trip durations and possibly less time spent away from the nest on a daily level. Additionally, increasing solar radiation can be linked to a higher probability of thermal updraft, therefore, we expected that increasing solar radiation would result in higher proportions of soaring flight (similar to wind speeds) and therefore lower both the daily and trip total energy costs. Time investment, however, would not be minimised as using thermals may increase the time spent flying and therefore increase trip duration, possibly showing an increase in time spent away from the nest on a daily level. Lastly, precipitation could hinder flight performance of birds, therefore, it was expected that higher precipitation would result in lower proportions of time in flight but increase both the trip and daily total energy costs. In order to test these expectations, weather data was combined with GPS tracking data (trip characteristics), acceleration data (flight behaviours), and energy costs. Trip characteristics and flight behaviours were quantified in order to be able to explain possible relationships between weather and time investment and/or energy costs. Lastly, two methods to calculate energy costs were compared, DBA calculations and time-energy budgets based on metabolic rate estimations.

5.3 Methods

5.3.1 Study area and species

This study took place between 2016-2019 during the breeding season (April-August) in Bristol, United Kingdom. Lesser black-backed gulls, *Larus fuscus*, from two nesting areas in the city centre were tracked during the breeding season. Their nests were located on the roofs of the Arts and Social Science Library at the University of Bristol and the dBs Music Centre (Figure 5.2). For more detailed information about the study area and species, see Chapter 2.

5.3.2 GPS tracking

The GPS tracking data was examined to quantify individual foraging trips (Figure 5.2). GPS locations were recorded between 4 and 600 seconds during the breeding season, with fixes every 600 seconds within the nesting area and fixes between 4 and 300 seconds outside the nesting areas. For the daily analysis, GPS locations were sub-sampled to 10 minutes to create equal intervals while including the GPS locations at the nest, however for the trip analysis, GPS locations were sub-sampled to five minutes to provide the highest resolution and equal intervals between the locations for all the trips. Days were quantified as 24 hours from midnight to midnight. Foraging trips were quantified by starting with the last point in the nesting area until the next point back in the nesting area. Trips included in the current analysis were at least 60 minutes to count as a foraging trip but not more than 24 hours, and had no gaps more than 30 minutes between two fixes. We calculated the following trip characteristics: duration, travel distance, maximum range, initial direction, directness and mean ground speed in flight during a trip. The trip duration was defined as the time between the first GPS location and the last GPS location of the trip. Travel distance was calculated by summing all the distances between two consecutive GPS locations during a trip. Maximum range was defined as the distance between the nest and the GPS location furthest away from the nest during a trip. Trip initial direction was defined as the direction between the first GPS location of the trip and the first GPS location on the ground outside the nesting area (defined as a GPS location when the bird conducted ground behaviour). Trip directness was calculated by dividing the travel distance by maximum trip range resulting in a value of two if the trip was direct and values higher than two for decreasing directness. The mean ground speed in flight was calculated by averaging the instantaneous ground speeds (measured by the GPS device) of the GPS locations when the birds were in flight.

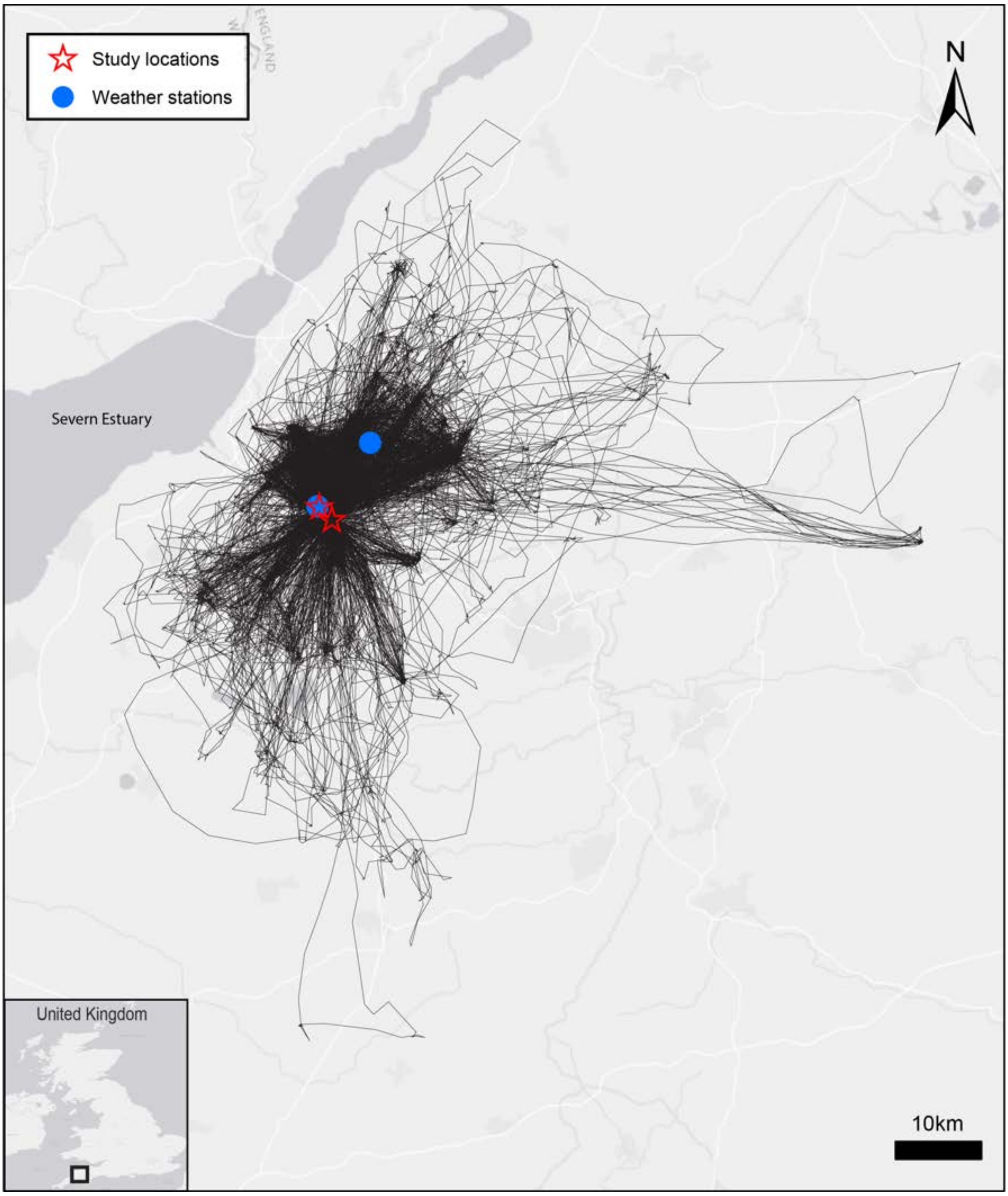

Figure 5.2: Map of Bristol area with the gull foraging trips (black lines) during the breeding seasons of 2016-2019. The study locations are indicated with red stars and the locations of the two weather stations with blue circles. The dark grey area is the Severn Estuary. Base map sources: ESRI, DeLorme, HERE Technologies, MapmyIndia.

5.3.3 Behaviour and breeding stage

A behaviour model was used to classify seven behavioural classes of the birds based on accelerometer data collected alongside the GPS tracking data: "soaring", "flapping", "extreme flapping", "mixed flight", "walking", "stationary", and "other". More information about the classification of these behaviours can be found in Chapter 2. For this study, we focussed on the flight behaviours "soaring", "flapping" and "mixed flight", not using "extreme flapping" due to the low sample size. For each trip at least 80% of the GPS locations were annotated with behavioural information. From the behavioural dataset, several flight characteristics were quantified to be able to explain possible relationships between weather and time investment and/or energy costs. These variables included: the proportion of time spent in flight, and when in flight, the proportion of time spent in flapping flight, in mixed flight, and in soaring flight. Additionally, nest observations were conducted to determine the breeding stage which is also described in more detail in Chapter 2. To analyse the effect of weather on time investment and energy costs, we only included data from the early chick-rearing stage (0-4 weeks). The reason behind this choice was that gulls change their flight and foraging behaviour throughout the breeding season (Chapter 3) and therefore selecting only one stage would be a consistent comparison. The early chick-rearing stage was chosen as this is the period where the parents are constrained to go back to the nest to feed their chicks and therefore the trips away from the nest could be considered to be mainly foraging trips.

5.3.4 Weather data

From two different weather stations within Bristol (Figure 5.3), weather data was extracted either with 10-min resolution (wind speed, wind direction, solar radiation, temperature, pressure) or 1-hour resolution (precipitation rate). The weather data from both stations followed a similar pattern over the course of a sub-sample of 14 days and were highly correlated (Figure 2.11). Consequently, weather variables were averaged across the two weather stations. GPS locations were interpolated in time to the closest value of the final weather dataset. Weather data for the daily analysis were averaged over a whole day, whereas for the trip analysis weather data was averaged over the duration of a trip. Wind direction was averaged using the circular package (Agostinelli & Lund, 2017) in the programme R (R Core Team, 2019) and afterwards combined into northerly, easterly, southerly and westerly winds (factor - 4 levels). The prevailing winds in Bristol are westerly, therefore the sample size is larger for this category on both the daily and trip level (Figure 5.3). On the daily level, precipitation was maintained as a continuous variable, however, on the trip level, the values were combined into three categorical levels based on Met Office guidelines (0 mm/h, 0-1.5 mm/h and 1.5-3 mm/h) due to the low sample size of trips with precipitation (Figure 5.3). Correlations between weather variables were checked and due to the correlation between solar radiation, temperature and pressure, only solar radiation was chosen to retain in the models. The variable solar radiation was used as a proxy for thermal formation as higher solar radiation levels can increase the surface warming and thus also the probability of

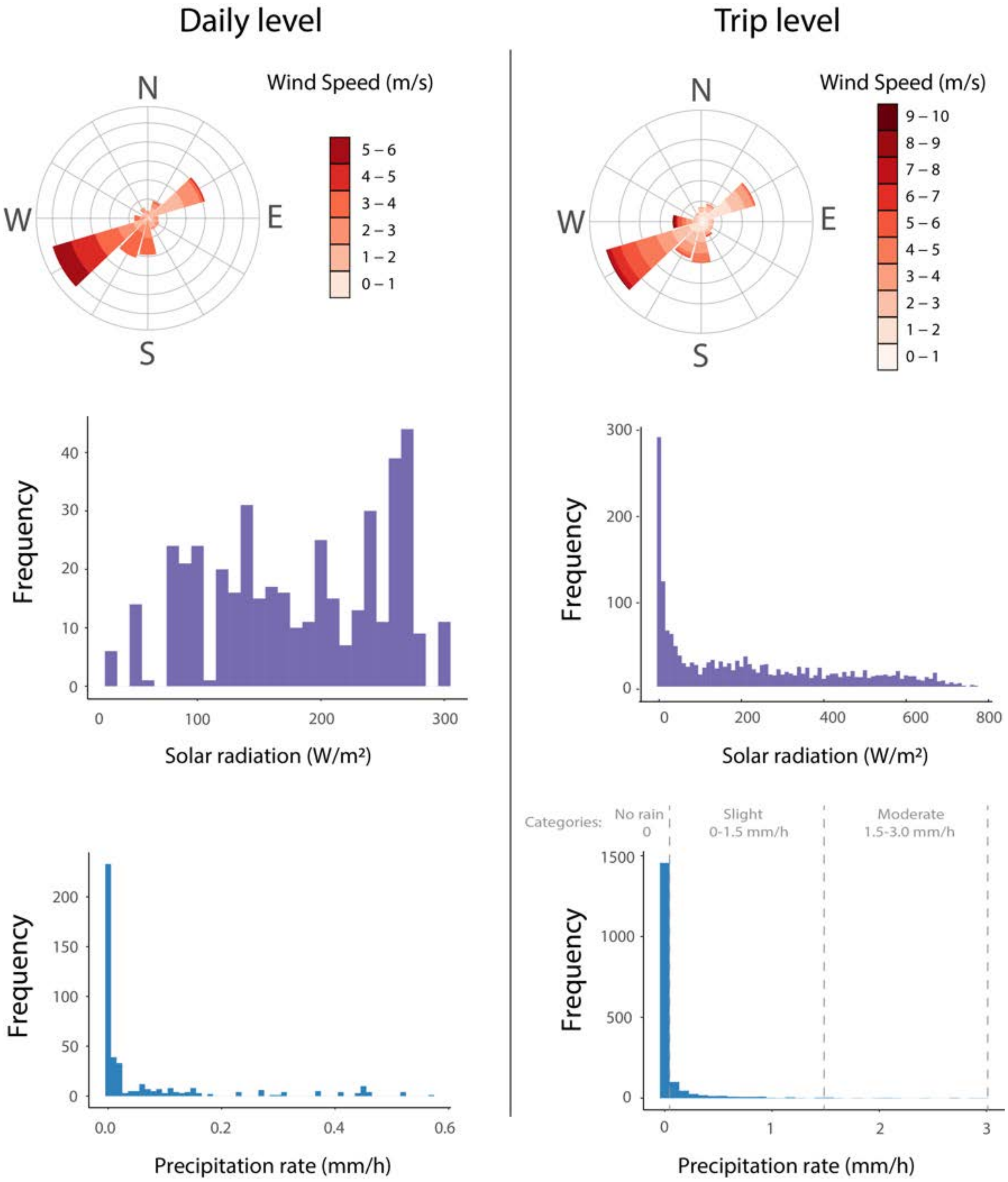

Figure 5.3: Overview of the mean weather variables of the two weather stations in Bristol, UK, during the breeding seasons of 2016-2019 on both the daily and trip level; mean wind speed, mean wind direction, mean solar radiation and mean precipitation rate. Frequency and speed of the wind is shown with each direction that was present. For precipitation at a trip level, the used categories are indicated (grey - dashed line).

thermal formation (Garratt, 1994; Ákos et al., 2010; Hernández-Pliego et al., 2015). The variable wind speed was used as a proxy for providing orographic lift as increasing wind speeds could result in higher possibilities of soaring (Shamoun-Baranes et al., 2016; Santos et al., 2017).

5.3.5 Time investment and energy costs

To quantify the effects on the weather on the time investment and energy costs, several parameters were defined on two different scales: daily and trip level (Figure 5.4). For time investment, we defined the time away from the nest in hours on a daily level, and duration of a trip in minutes for the trip level. For energy costs, we defined the total daily energy cost, and the total trip energy cost. These costs were calculated by two different methods which we compared with each other: (1) time-energy budgets and (2) dynamic body acceleration.

(1) Energy cost calculation based on time-energy budgets

Besides total trip energy cost (kJ), trip energy cost per unit time (kJ/h) and trip energy cost per unit distance (kJ/km) were added as proxies for energy expenditure during a trip because the birds might not change their overall energy costs but minimise energy in terms of time or distance during a trip. Metabolic rates were estimated for the different behaviour types per individual based on the method of van Donk et al. (2019b). In contrast to that study, we used five behaviour classes instead of four, separating mixed flight from soaring, resulting in the following behaviours: (1) flapping flight, mixed flight, soaring flight, terrestrial locomotion, and stationary behaviour. We decided to separate this mixed behaviour because this strategy is quantified as a combination of flapping and soaring flight. Therefore, we assumed this behaviour had lower costs than flapping flight but higher than soaring flight. We validated our assumption by looking at both the ODBA and VeDBA values of each behaviour type and found that mixed flight behaviour had on average an ODBA and VeDBA value in between flapping and soaring flight (Figure 5.5 - only ODBA values are shown). The basic metabolic rate (BMR) in kJ per hour was calculated with the following formula with body mass in gram (Bryant & Furness, 1995):

$$BMR = (2.3 \, * \, (\, body \; mass \; ^{0.774} \;) \, / \, 24 \tag{5.1}$$

The average BMR was 16.09 ± 0.98 (mean ± standard deviation) for all our individuals. The resting metabolic rate in kJ per hour (RMR) was calculated as **1.7 * BMR** (Baudinette & Schmidt-Nielsen, 1974). The average RMR was 27.35 ± 1.66 for all our individuals. We used RMR instead of BMR as a value for metabolic rates when birds were stationary/inactive as this should at least include in some way the energy expenditure due to non-movement behaviours such as thermoregulation and digestion (Furness, 1978). Based on estimations of gull flight in wind tunnels, the energy cost for flapping flight was defined as **7 * RMR** (Tucker, 1972) and for soaring flight as **2 * RMR** (Baudinette & Schmidt-Nielsen, 1974). Following the approach of van Donk

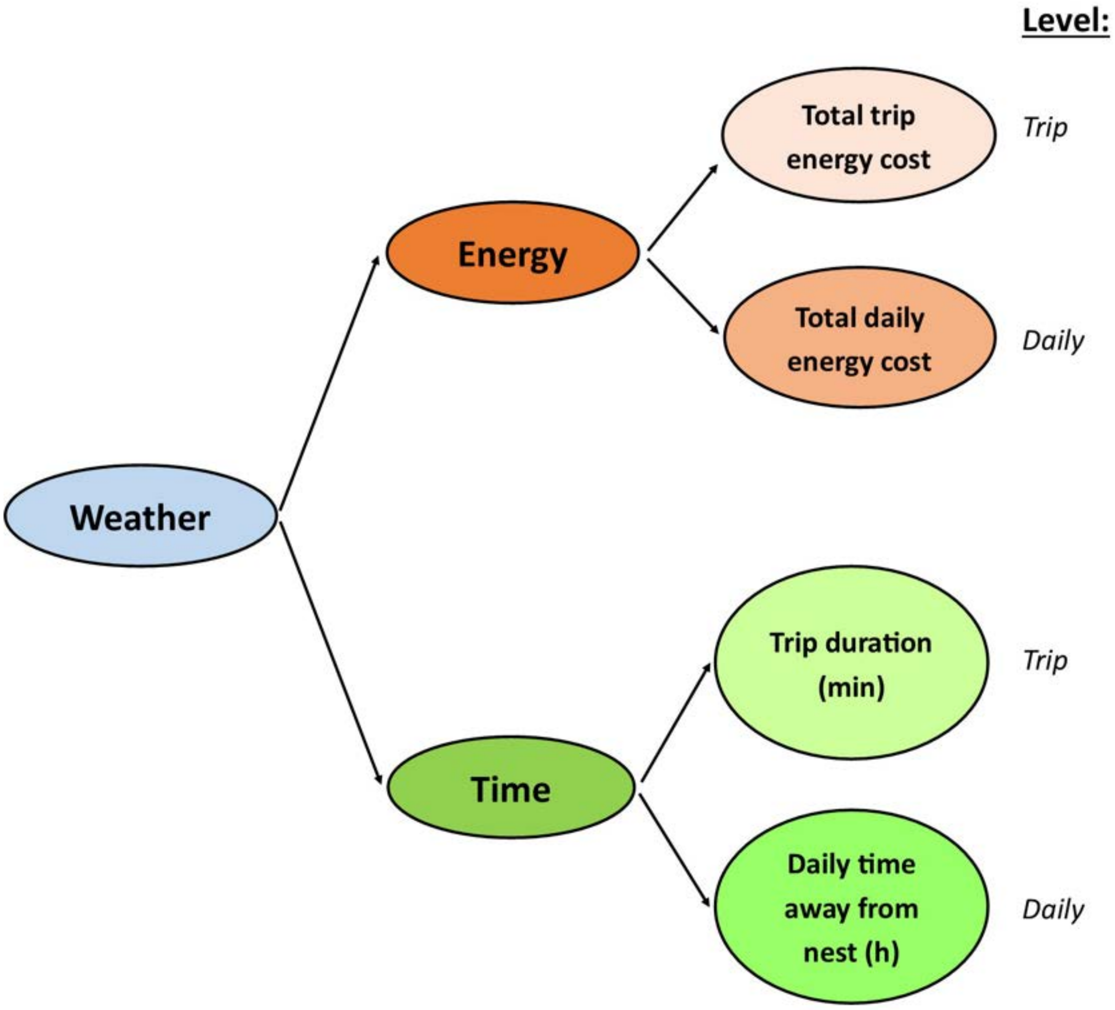

Figure 5.4: Overview of the response variables estimated for time investment and energy costs on both the daily and trip level.

et al. (2019b), the energy costs for terrestrial locomotion was defined as **2 * BMR**. This was based on a formula of energy costs in starlings, *Sturnus vulgaris* (Bautista et al., 1998) and similar costs in Barnacle geese, *Branta leucopsis*, during terrestrial locomotion (Nudds et al., 2010). We estimated the energy cost for mixed flight to be in between the costs for flapping and soaring flight with **4.5 * RMR**. Total energy cost was calculated by multiplying the energy cost per hour (kJ/h) of each behaviour with the duration (h) spent on that behaviour and summing these values either per day or per trip. For trips, trip energy cost per unit time (kJ/h) was calculated by dividing the total energy budget by the trip duration and trip energy cost per unit distance (kJ/km) was calculated by dividing the total energy budget by the trip travel distance.

(2) Energy cost calculation based on dynamic body acceleration

DBA was used as the second proxy for energy expenditure. Body acceleration consists of two components, namely static acceleration which is the result of gravity forces, and dynamic acceleration which is related to the movement of the animal. The dynamic acceleration was obtained from the acceleration data by subtracting the static acceleration from the total acceleration measurement by smoothing the data over 1-2 seconds as a running mean (Shepard et al., 2008). From this, we calculated both overall dynamic body acceleration (ODBA) and vectorial body acceleration (VeDBA) because it seems that both methods are valid, similar, and applied interchangeable (Qasem et al., 2012; Wilson et al., 2020). We calculated ODBA (g) and VeDBA (g) with the following formulas with DA being the dynamic acceleration in either X, Y, or Z direction (Wilson et al., 2006; Qasem et al., 2012):

$$ODBA = |DA_x| + |DA_y| + |DA_z| \tag{5.2}$$

$$VeDBA = \surd(DA_x^2 + DA_y^2 + DA_z^2) \tag{5.3}$$

Each GPS location was annotated with both DBA values (ODBA and VeDBA). Daily energy cost was calculated by taking the sum of the DBA values over the 24 hours which is the same as integrating due to the fact that the time interval between the GPS fixes was the same. For trips, total trip energy cost was calculated as the sum of the DBA values during a trip.

5.3.6 Statistical analysis

At the daily level, time spent away from the nest in hours (time investment) and daily energy cost were modelled in relation to the following weather predictors (Table 5.1): wind speed (continuous), wind direction (categorical - East, North, West, South), solar radiation (continuous) and precipitation rate (continuous). Weather variables were not correlated; wind speed and solar radiation (-0.07), wind speed and precipitation (-0.01), and solar radiation and precipitation (0.45). Variable Inflation Factors (VIF) were also low; daily mean wind speed (1.01), daily mean solar radiation (1.45), daily mean precipitation (1.45) and wind direction (1.7). Besides the time investment and energy costs, the following flight characteristics were modelled in relation to the weather predictors: daily proportion of time spent in flight, in flapping flight, in mixed flight and in soaring flight (Table 5.1). For all the daily models, two random factors were added to account for non-independency of the data: date and bird ID. These were crossed factors because multiple days were sampled from all individuals and days were similar between individuals.

At the trip level, we model trip duration in minutes (time investment), total trip energy cost (kJ), trip energy cost per unit time (kJ/h) and trip energy cost per unit distance (kJ/km) in relation to

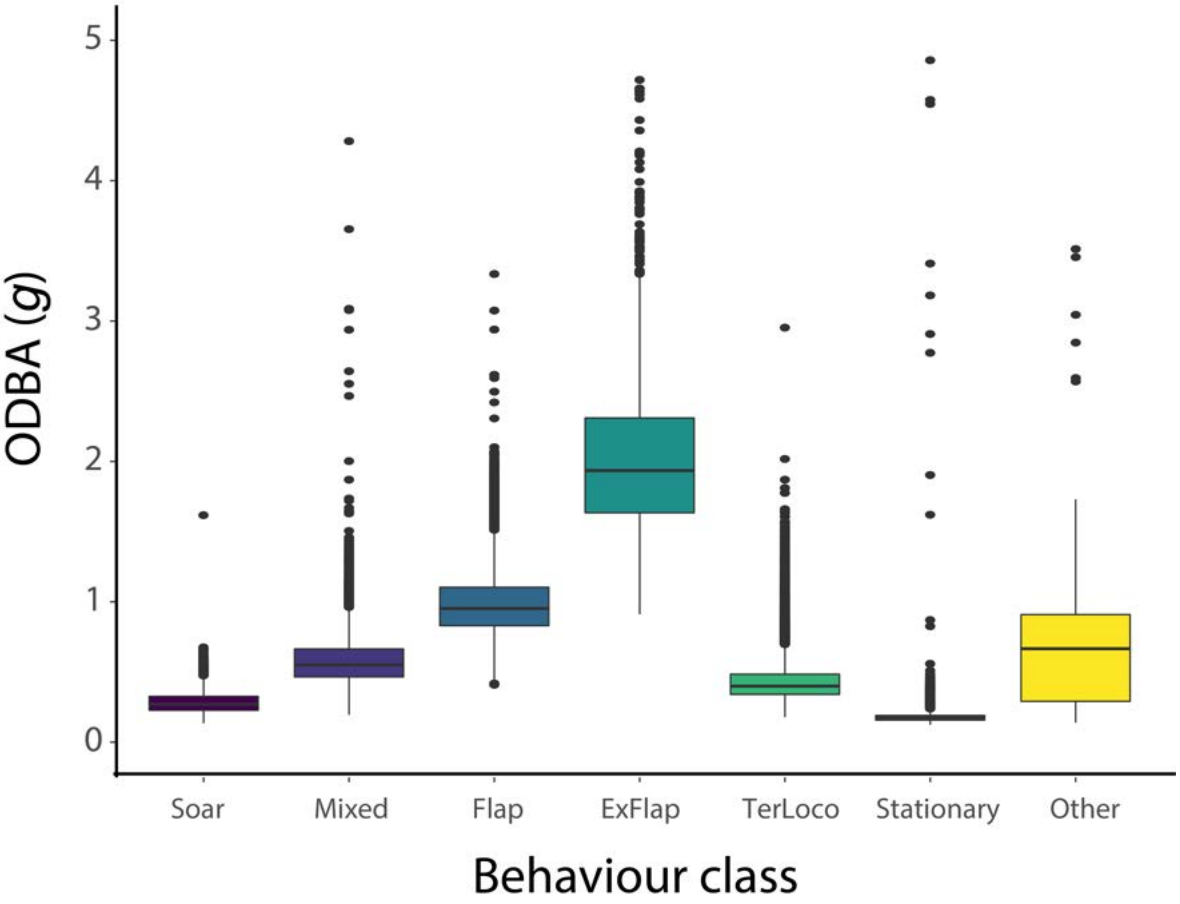

Figure 5.5: ODBA values per behaviour class. Soar = soaring flight, Mixed = mixed flight, Flap = flapping flight, ExFlap = extreme flapping flight, TerLoco = terrestrial locomotion (walking), Stationary (sit and standing behaviour), Other = other behaviour. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the black points are data outside 1.5 * IQR.

the following weather predictors (Table 5.2): wind speed (continuous), wind direction (categorical - East, North, West, South), solar radiation (continuous) and precipitation rate (categorical - 0 mm/h, 0-1.5 mm/h, 1.5-3 mm/h). Wind speed and solar radiation were not correlated (0.17). Variable Inflation Factors (VIF) were also low; mean wind speed (1.4), mean solar radiation (1.1), mean precipitation rate (1.1), and wind direction (1.4). Similar to the daily level, the following flight characteristics were modelled in relation to the weather predictors: proportion of time spent in flight during a trip, in flapping flight, in mixed flight and in soaring flight (Table 5.2). Additionally, the following trip characteristics were modelled in relation to the weather predictors (Table 5.2): travel distance, maximum range, directness and mean ground speed in flight during a trip. For all the trip models, birdyearID (a combination of bird and year) was added as a random factor to account for non-independency of the data, because multiple trips per bird per year were sampled. We included 21 bird-year combinations.

We used (generalised) linear mixed models for each response variable depending on the nature of the variable, the normality and homogeneity of the distribution of the residuals (Table 5.1 and Table 5.2). To account for overdispersion in Poisson count models, either observer random level effects (ORLE) were included or the negative binomial distribution was used (Elston et al., 2001). Zero-inflated models were used when the number of zero's in the dataset was too high for a model with Poisson or negative binomial distribution to deal with. Offsets were included when proportions instead of counts were modelled. The final (G)LMMs for the response variables with their respective distribution, link, offset and r package used can be found in Table 5.1 for the daily models and Table 5.2 for the trip models. We conducted a forward-step selection procedure to select the "best-fit" model based on chi-squared tests following Zuur et al. (2009). The models can be found in Table A.3 and A.4. The significance level was set at α=0.05 and results are reported as the estimated marginal means (EMM) and standard error (SE) unless stated otherwise.

5.4 Results

5.4.1 Comparisons between methods for energy cost calculation

We calculated the daily and trip energy costs by two different methods: time-energy budgets based on BMR estimations and dynamic body acceleration. For the latter method, we extracted two values: overall dynamic body acceleration (ODBA) and vectorial dynamic body acceleration (VeDBA). The different methods were compared with Pearson's correlation tests. At the daily level, total daily energy cost based on BMR was highly correlated to both summed ODBA (PC: n=116, r=0.79, p<0.001) and summed VeDBA (PC: n=116, r=0.79, p<0.001), and both DBA values were highly correlated (PC: n=116, r=0.98, p<0.001, Figure 5.6). For trips, the total trip energy cost was also highly correlated with summed ODBA (PC: n=1752, r=0.93, p<0.001) and summed VeDBA (PC: n=1752, r=0.87, p<0.001) over the trip, and the correlation between the DBA values was also high (PC: n=1752, r=0.96, p<0.001, Figure A.4). We used the time-energy budgets based on BMR estimations as a proxy for energy expenditure in this study as the energetic cost of flight relative to BMR has been measured in wind tunnel studies for gull species (Tucker, 1972; Baudinette & Schmidt-Nielsen, 1974) and DBA has not yet been validated in gulls.

5.4.2 Daily analysis

During the early chick-rearing stage 130 days were sampled in the breeding seasons of 2016, 2017, 2018 and 2019 from 10 individual birds. One individual was removed from the dataset due to abandoned breeding before the chick-rearing stage in one year and unknown in subsequent years. Daily mean wind speed varied from 0.64 m/s to 5.86 m/s, daily mean solar radiation ranged from 29.7 W/m^2 to 298.7 W/m^2, and daily mean precipitation varied from 0 mm/h to 0.57 mm/h. The main wind direction within Bristol is westerly (163 days), followed by easterly (108 days), southerly (120 days) and northerly (50 days).

Table 5.1: Overview of models constructed for the *daily* level with the type of model, distribution, link, random variable, offset and which package used in the statistical programme R. GLMM = generalised linear mixed model, ORLE = observer random level effect

Model	Response	Model	Distribution	Link	Random	Offset	Package
1	Time away from nest	GLMM	Poisson	Log	date & bird		lme4
2	Daily total energy budget	GLMM	Poisson with ORLE	Log	date & bird		lme4
3	% in flight	GLMM	Poisson	Log	date & bird	Hours in a day	lme4
4	% flapping in flight	GLMM	Poisson with ORLE	Log	date & bird	Flight time	lme4
5	% mixed in flight	GLMM	Zero-inflated negative binomial	Log	date & bird	Flight time	glmmTMB
6	% soaring in flight	GLMM	Zero-inflated negative binomial	Log	date & bird	Flight time	glmmTMB

Table 5.2: Overview of models constructed for the *trip* level with the type of model, distribution, link, random variable, offset and which package used in the statistical package r. (G)LMM = (generalised) linear mixed model, ORLE = observer random level effect

Model	Response	Model	Distribution	Link	Random	Offset	Package
1	Trip duration	GLMM	Poisson with ORLE	Log	Birdyear		lme4
2	Trip energy budget	LMM	Log transformed response		Birdyear		lme4
3	Energy budget per hour	GLMM	Negative binomial	Log	Birdyear		lme4
4	Energy budget per distance	GLMM	Negative binomial	Log	Birdyear		lme4
5	% in flight	GLMM	Negative binomial	Log	Birdyear	Trip duration	lme4
6	% flapping in flight	GLMM	Negative binomial	Log	Birdyear	Flight time	lme4
7	% mixed in flight	GLMM	Zero-inflated negative binomial	Log	Birdyear	Flight time	glmmTMB
8	% soaring in flight	GLMM	Zero-inflated negative binomial	Log	Birdyear	Flight time	glmmTMB
9	Travel distance	GLMM	Negative binomial	Log	Birdyear		lme4
10	Maximum range	GLMM	Poisson with ORLE	Log	Birdyear		lme4
11	Mean speed in flight	LMM	Normal distribution		Birdyear		lme4
12	Directness	GLMM	Negative binomial	Log	Birdyear		lme4

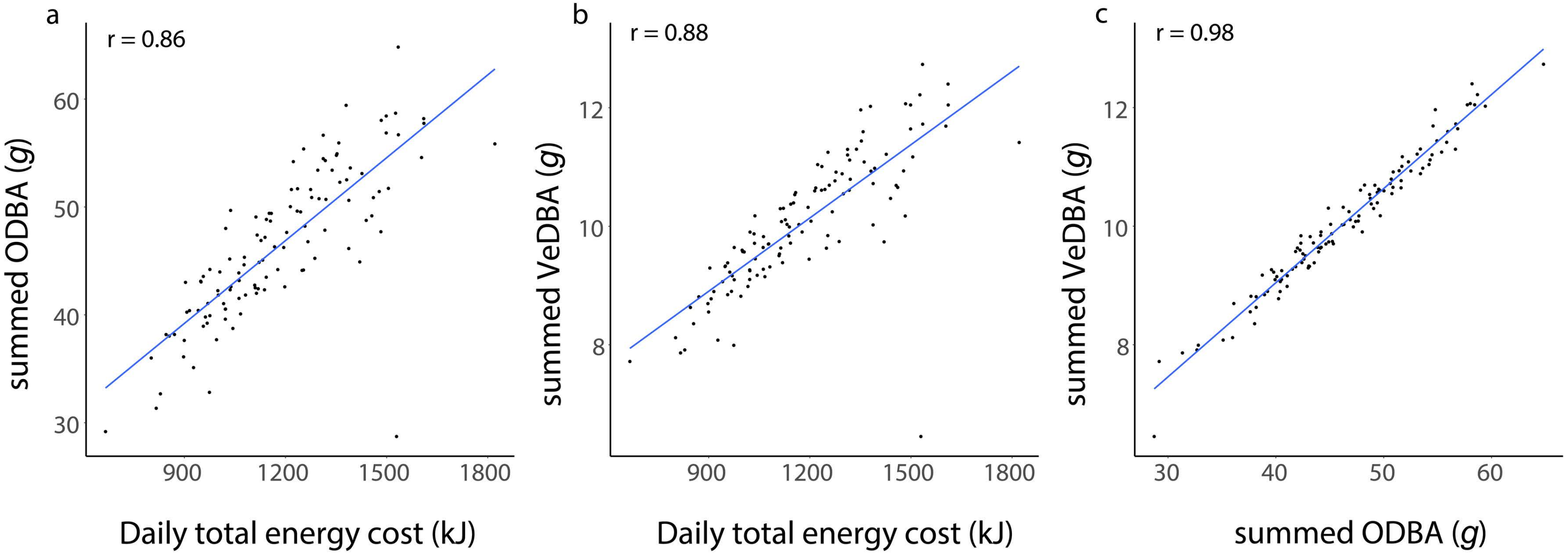

Figure 5.6: Comparison between different methods to calculate total daily energy expenditure: daily summed overall dynamic body acceleration (ODBA), daily summed vectorial dynamic body acceleration (VeDBA) and total daily energy cost based on metabolic rate estimations from previous studies. A linear regression line with confidence interval has been plotted to show the correlation.

Time investment

The daily time investment was examined by the of time spent away from the nest during the day. Both daily mean wind speed (χ_1^2 = 1.90, p = 0.168) and daily mean solar radiation (χ_1^2 = 0.65, p = 0.420) did not affect the daily time spent away from the nest, however, the birds spent more time away from the nest with increasing precipitation (Table 5.3, Figure 5.7). Although wind direction was not significant (χ_3^2 = 7.29, p = 0.063), it seemed that southerly winds resulted in more time spent away from the nest than during easterly winds. Lastly, the interaction with wind speed did not improve the model (χ_4^2 = 5.60, p = 0.231).

Energy costs

Overall, the total daily energy cost was not affected by solar radiation (χ_1 = 0.79, p = 0.374), precipitation rate (χ_1 = 0.95, p = 0.329), wind speed (χ_1 = 2.09, p = 0.149) or wind direction (χ_3 = 7.35, p = 0.062, Figure 5.8). The interaction between wind speed and wind direction does improve the model (Table 5.3), resulting in an increased total daily energy cost with increasing wind speed during northerly winds compared to the other wind directions (Figure A.5).

Flight behaviour

We analysed the effect of wind speed (Figure 5.9), solar radiation (Figure 5.10), wind direction (Figure 5.11) and precipitation rate (Figure 5.12) on the different flight behaviours. The proportion of time spent in *flight* increased with increasing wind speeds (Table 5.3) but was not affected by solar radiation (χ_1^2 = 2.38, p = 0.123) nor by precipitation (χ_1^2 = 0.932, p = 0.334). Wind direction did not improve the model (χ_3^2 = 3.65, p = 0.302) nor did the interaction between wind direction and wind speed (χ_3^2 = 3.83, p = 0.281). Secondly, the proportion of time spent in *flapping* flight decreased with increasing wind speed, with increasing solar radiation, and increased with increasing precipitation (Table 5.3). Wind direction did not affect the proportion of flapping (χ_1^2 = 1.07, p = 0.783) nor did the interaction between wind direction and speed (χ_1^2 = 0.675, p = 0.879). Thirdly, the proportion of time spent in *mixed* flight increased with increasing wind speed and depended on the wind directions (Table 5.3), resulting in higher proportions of mixed flight during winds from the east (17.5±0.15%) than winds from the west (12.7±0.10%). Solar radiation (χ_1^2 = 0.43, p = 0.511) and precipitation (χ_1^2 = 1.07, p = 0.301) did not affect the proportion of mixed flight, nor was the interaction between wind speed and direction significant (χ_1^2 = 4.60, p = 0.203). And lastly, the proportion of time spent in *soaring* flight increased with increasing solar radiation and decreased with increasing precipitation (Table 5.3). Wind speed did not affect the proportion of soaring flight (χ_1^2 = 0.78, p = 0.377) nor did wind direction (χ_3^2 = 1.65, p = 0.647) or the interaction between the two variables (χ_4^2 = 4.54, p = 0.338).

Table 5.3: Overview of the response variables and significant explanatory terms, model output and estimates (β-coefficients) of the different models on a *daily* scale. WD = mean daily wind direction, WS = mean daily wind speed (m/s), SR = mean daily solar radiation (W/m^2), PR = mean daily precipitation rate (mm/h), df = degrees of freedom, chisq = Chi-square test result, p = p-value. For the β-coefficients, the estimates of the categorical levels for wind direction are compared to East (intercept); 1 = North, 2 = South, 3 = West. For the interaction between wind direction and speed, the β-coefficients are 1 = East, 2 = North, 3 = South, 4 = West.

Model	**Response**	**Explanatory**	**df**	**chisq**	**p**	**β-coefficients**			
						1	2	3	4
1	Time away from nest	Intercept				1.92 ± 0.08			
		Mean precipitation	1	4.79	0.029 *	0.03 ± 0.02			
2	Total energy cost	Intercept				7.09 ± 0.04			
		Wind direction * speed	4	13.3	0.009 **	0.04 ± 0.03	0.18 ± 0.05	-0.03 ± 0.03	0.02 ± 0.02
3	% in flight	Intercept				-1.73 ± 0.06			
		Mean wind speed	1	7.98	0.005 **	0.07 ± 0.02			
4	% flap in flight	Intercept				-0.58 ± 0.03			
		Mean wind speed	1	46.5	<0.001 ***	-0.11 ± 0.01			
		Mean solar radiation	1	56.6	<0.001 ***	-0.08 ± 0.01			
		Mean precipitation	1	5.07	0.024 *	0.03 ± 0.01			
5	% mixed in flight	Intercept				-1.75 ± 0.09			
		Mean wind speed	1	67.9	<0.001 ***	0.37 ± 0.03			
		Mean wind direction	3	11.7	0.009 **	-0.15 ± 0.11	-0.20 ± 0.08	-0.32 ± 0.09	
6	% soar in flight	Intercept				-1.37 ± 0.09			
		Mean solar radiation	1	71.1	<0.001 ***	0.18 ± 0.02			
		Mean precipitation	1	6.37	0.012 *	-0.07 ± 0.03			

*** p <0.001, ** p <0.01, * p <0.05, . p <0.1

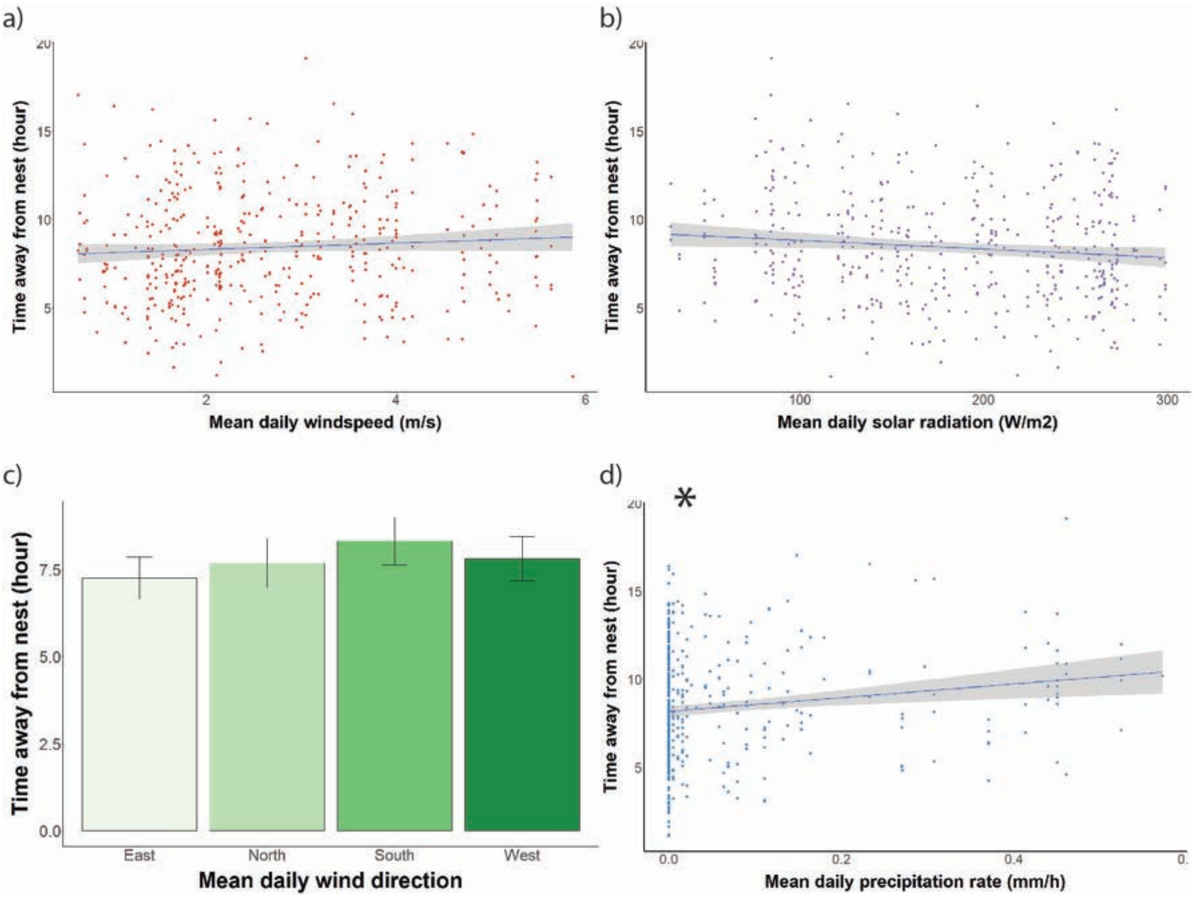

Figure 5.7: Amount of time away spent from the nest (h) during the day with different weather conditions. a) mean daily wind speed (m/s), b) mean daily solar radiation (W/m^2), c) mean daily wind direction, and d) mean daily precipitation rate (mm/h). For wind direction, estimated marginal means ± standard errors are presented. Stars represent significant weather variables (precipitation rate). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

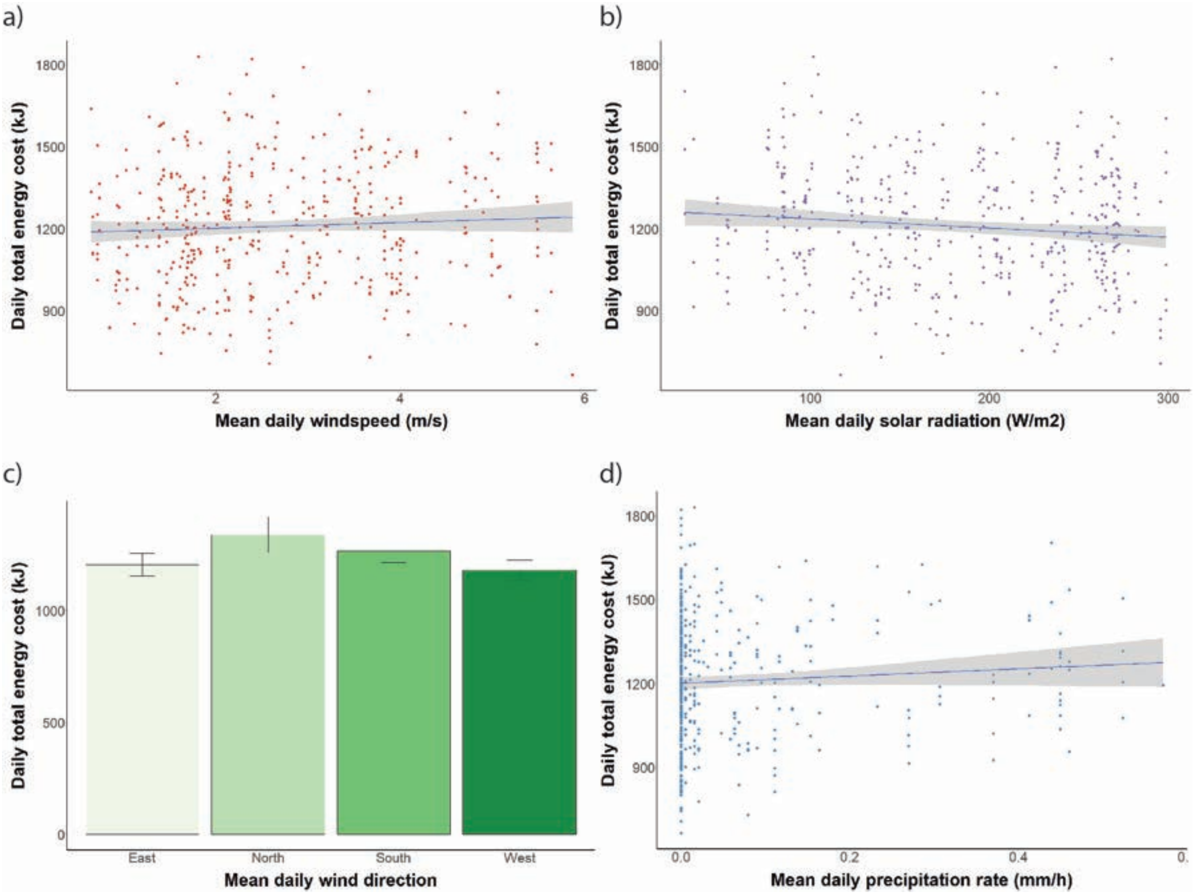

Figure 5.8: Total daily energy cost (kJ) during the day with different weather conditions. a) mean daily wind speed (m/s), b) mean daily solar radiation (W/m^2), c) mean daily wind direction, and d) mean daily precipitation rate (mm/h). For wind direction, estimated marginal means ± standard errors are presented.

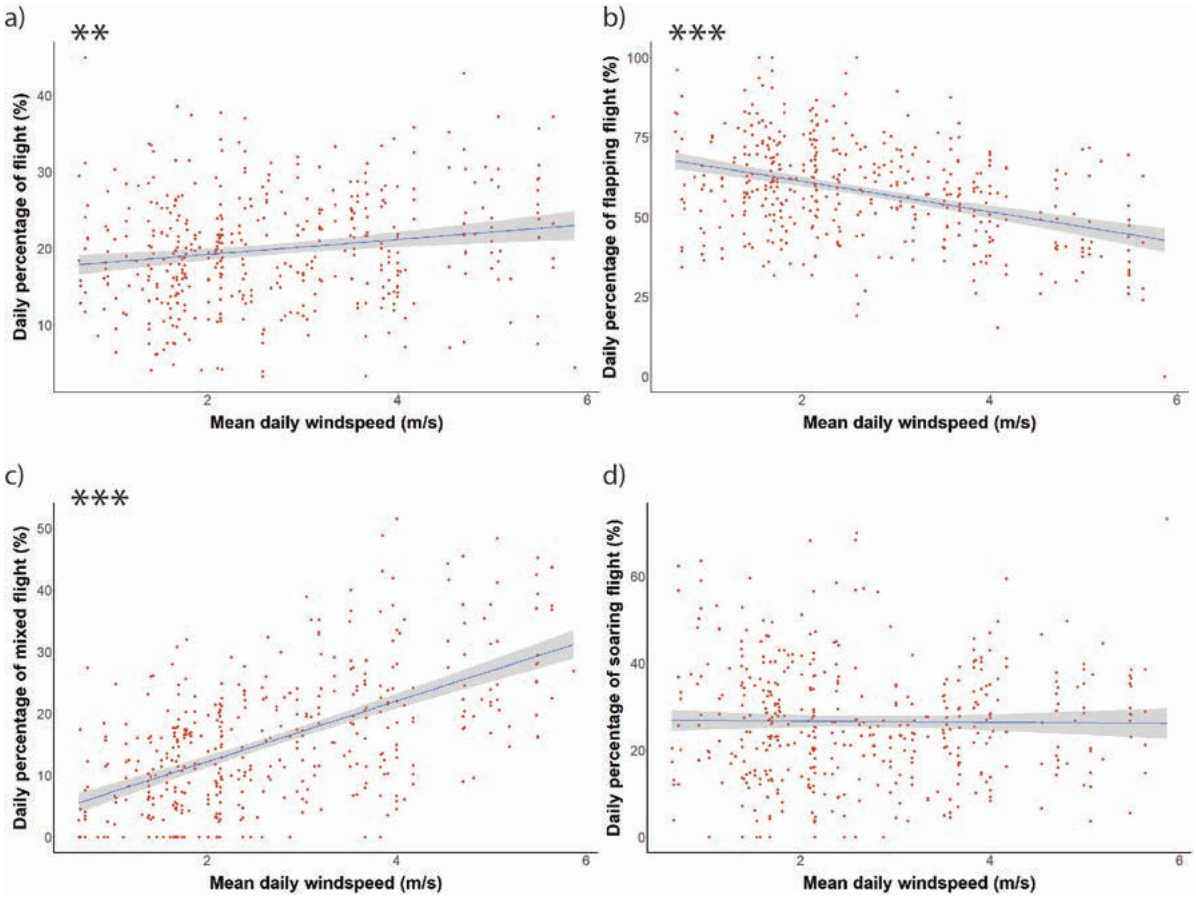

Figure 5.9: The daily flight behaviours of gulls in relation to mean daily wind speed (m/s). a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

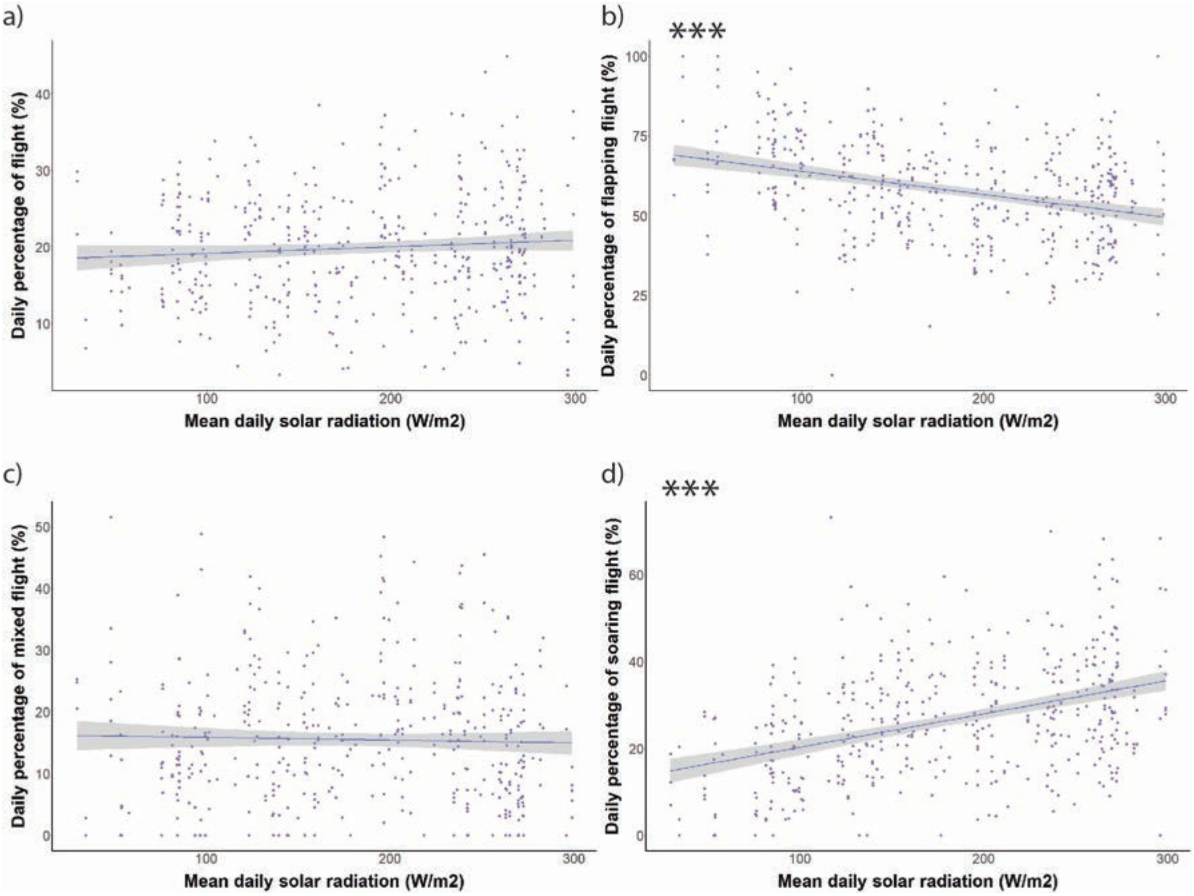

Figure 5.10: The daily flight behaviours of gulls in relation to mean daily solar radiation (W/m^2). a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) d) and percentage soaring in flight (%). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

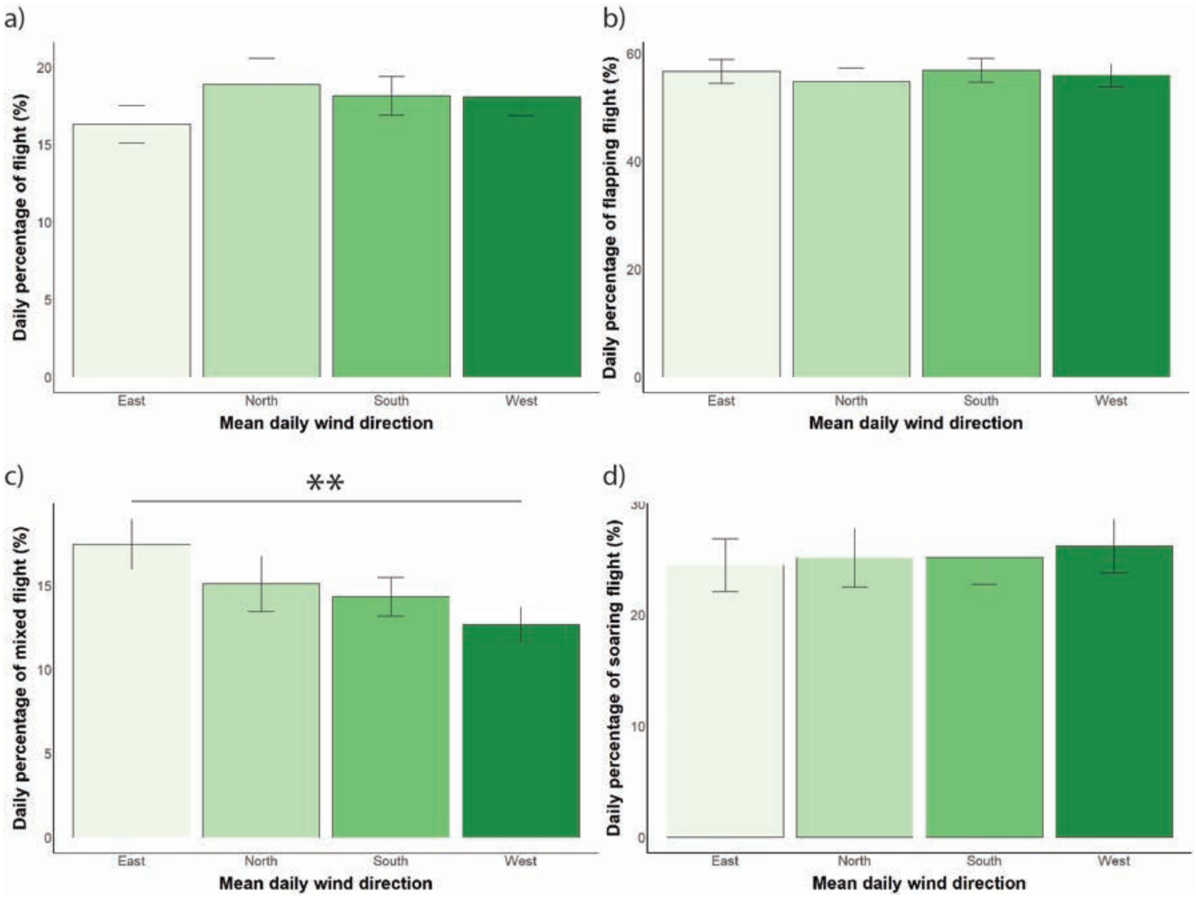

Figure 5.11: The daily flight behaviours of gulls in relation to mean daily wind direction. a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Estimated marginal means ± standard errors are presented. Stars represent significant differences between groups . *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

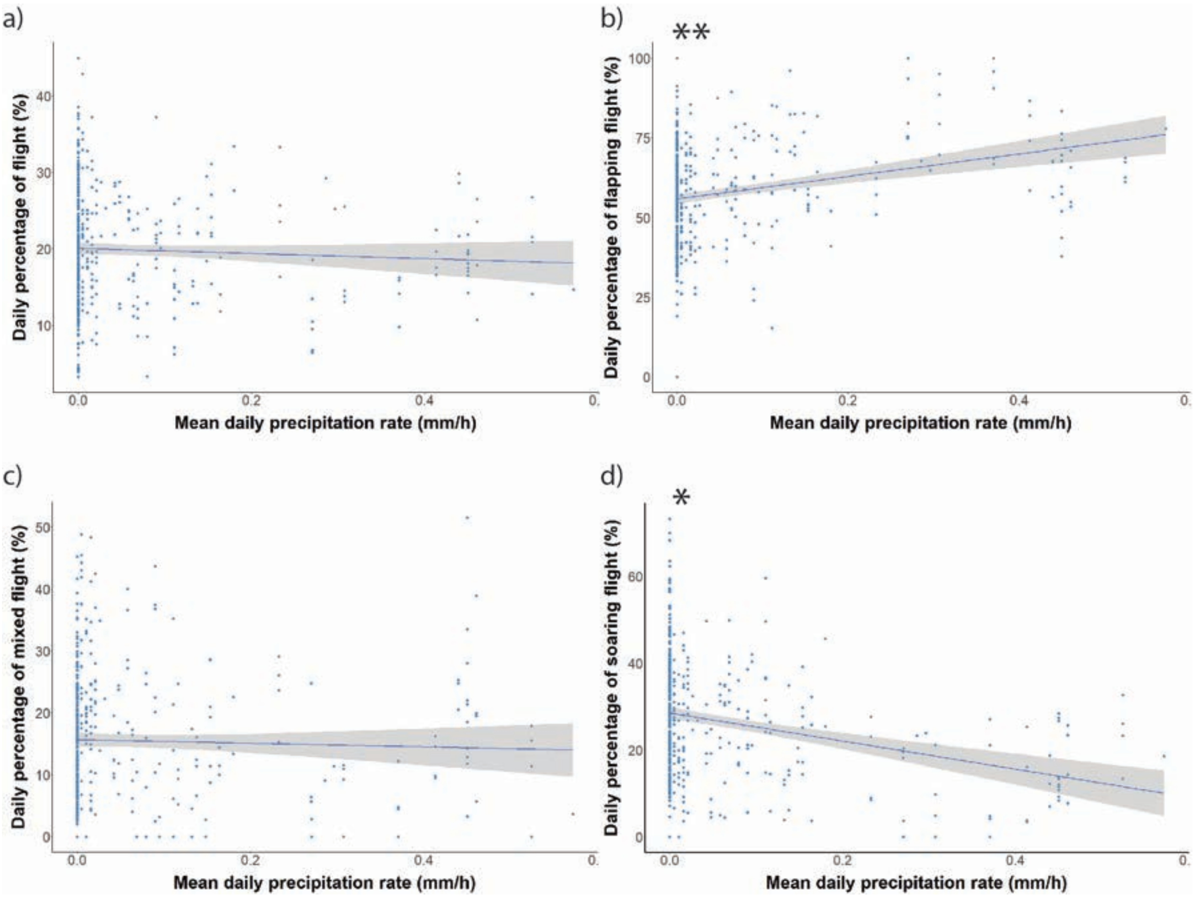

Figure 5.12: The daily flight behaviours of gulls in relation to mean daily precipitation rate (mm/h). a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

5.4.3 Trip analysis

We sampled 1,682 trips from 10 individuals during the early chick-rearing stage of the breeding seasons of 2016, 2017, 2018 and 2019. An overview of the different trip characteristics can be found in Table 5.4. Trip mean wind speed varied from 0.05 m/s to 9.84 m/s and trip mean solar radiation ranged from 0 W/m^2 to 771.41 W/m^2. The mean trip precipitation rate were no rain (1,409 trips), slight rain: 0.01-1.5 mm/h (311 trips) and medium rain: 1.6-3.0 mm/h (14 trips). The mean trip wind directions were winds from the west (663 trips), followed by winds from the south (464 trips), winds from the east (398 trips) and winds from the north (209 trips).

Time investment

Time investment during a trip was examined by the total trip duration in minutes. Increasing wind speeds resulted in a small decrease in trip duration whereas increasing solar radiation resulted in small increase in trip duration (Table 5.5, Figure 5.13). Medium precipitation rates resulted in higher trip durations (130 ± 4.23 min) than no precipitation (116 ± 2.90 min, Table 5.5, Figure 5.13). Both wind direction (χ^2_3 = 2.87, p = 0.412) and the interaction between wind direction and wind speed (χ^2_3 = 2.68, p = 0.443) did not affect the trip duration.

Energy costs

Increasing levels of solar radiation resulted in a small but statistically significant increase in *total trip energy cost* and medium precipitation rates also resulted in higher total trip energy cost (177 ± 6.57 kJ) than trips with no precipitation (152 ± 4.16 kJ, Table 5.5, Figure 5.14). The total trip energy cost was not affected by wind speed (χ^2_1 = 0.11, p = 0.737), wind direction (χ^2_3 = 4.66, p = 0.199) nor the interaction between the two (χ^2_3 = 5.02, p = 0.286). Additionally, the trip *energy cost per unit time* increased with both increasing wind speed and solar radiation (Table 5.5, Figure 5.15). The precipitation rate did not affect this cost (χ^2_2 = 2.90, p = 0.235) nor did wind direction (χ^2_3 = 7.06, p = 0.070) and the interaction of wind direction and speed (χ^2_3 = 4.66, p =

Table 5.4: Overview of mean trip characteristics of the gulls in this study during the early chick-rearing stage (2016-2019). Mean, standard deviation (SD), minimum and maximum are given for trip duration (min), travel distance (km), maximum range (km), mean ground speed in flight (m/s) and directness of the trips. Trip direction shows the number of trip in each direction.

	Mean ± SD	Min	Max	Trip direction	
Trip duration (min)	129 ± 58	67	515	North	942
Trip travel distance (km)	22 ± 14	2.3	107	East	245
Trip max range (km)	8.1 ± 5.3	0.8	47.5	South	275
Mean ground speed in flight (m/s)	10.3 ± 1.4	5.1	15.7	West	220
Directness	2.8 ± 0.8	2.1	8.7	**Total**	**1,682**

0.199). Lastly, the trip *energy cost per unit distance* decreased with increasing solar radiation, was lower during trips with slight rain (7.9 ± 0.3 kJ/km) compared to no rain (8.8 ± 0.3 kJ/km), and was higher during northerly winds (8.8 ± 0.5 kJ/km) compared to southerly (7.9 ± 0.4 kJ/km) and westerly winds (8.0 ± 0.4 kJ/km, Table 5.5, Figure 5.16). Wind speed (χ^2_1 = 2.23, p = 0.136) and the interaction with wind direction (χ^2_4 = 0.50, p = 0.478) did not improve the model.

Flight behaviour

The effect of wind speed (Figure 5.17), solar radiation (Figure 5.18), wind direction (Figure 5.19) and precipitation rate (Figure 5.20) was analysed in relation to the different flight behaviours during a trip. The proportion of time spent in *flight* increased with both increasing wind speed and increasing solar radiation (Table 5.5). Additionally, when winds were coming from the north the proportion of flight was lower (41.2 ± 1.9%) than when winds were coming from the south (45.7 ± 1.4%) or east (45.9 ± 1.5%, Table 5.5). Precipitation did not affect the proportion of flight (χ^2_2 = 0.07, p = 0.964) nor did the interaction between wind speed and direction (χ^2_3 = 3.55, p = 0.314). Secondly, both increasing wind speed and increasing solar radiation decreased the proportion of time spent in *flapping* flight during a trip (Table 5.5). Additionally, when it did not rain during a trip the proportion of time spent in flapping flight was lower (54.8 ± 1.2%) than when it rained slightly (60.3 ± 1.7%), and with westerly winds, the proportion was higher (62.5 ± 2.3%) compared to southerly winds (56.8 ± 2.0%) and easterly winds (58.7 ± 2.2%, Table 5.5). The interaction between wind speed and direction did not improve the model (χ^2_3 = 4.65, p = 0.160). Thirdly, the proportion of time spent in *mixed* flight also increased with both increasing wind speeds and solar radiation (Table 5.5). When the wind was coming from the west, the proportion spent in mixed flight was lower (12.5 ± 1.0%) than when the wind was coming from all other wind directions (east:17.7 ± 1.5%, north:18.3 ± 1.9%, and south:17.1 ± 1.4%, Table 5.5). Both precipitation (χ^2_2 = 0.10, p = 0.949) and the interaction between wind speed and direction (χ^2_3 = 1.99, p = 0.265) did not improve the model. Lastly, the proportion of time spent in *soaring* flight increased with increasing solar radiation and was higher when it did not rain during a trip (24.7 ± 1.4%) compared to slight precipitation (20.3 ± 0.14%, Table 5.5). Wind speed (χ^2_1 = 2.75, p = 0.097), wind direction (χ^2_3 = 3.96, p = 0.266) and their interaction (χ^2_4 = 2.36, p = 0.107) did not improve the model.

Trip characteristics

The effect of wind speed (Figure A.6), solar radiation (Figure A.7), wind direction (Figure A.8) and precipitation rate (Figure A.9) was analysed in relation to the different trip characteristics. Trip *travel distance* increased with increasing solar radiation and was longer during slight precipitation (24.8 ± 1.3 km) compared to no precipitation (20.8 ± 0.9 km, Table 5.5). Both wind speed (χ^2_1 = 1.57, p = 0.209), wind direction (χ_3 = 5.96, p = 0.114) and their interaction (χ^2_4 = 2.07, p = 0.546) did not improve the model. Secondly, the *maximum range* also increased with solar radiation and was longer slight precipitation (8.2 ± 0.5 km) compared to no precipitation (6.7 ± 0.3 km), and was shorter during northerly winds (6.8 ± 0.5 km) compared to easterly (7.7 ± 0.5 km) and southerly winds (7.7 ± 0.5, Table 5.5). Wind speed (χ_1 = 2.34, p = 0.126) and the interaction with wind direction did not improve the model (χ^2_4 = 5.46, p = 0.244). Thirdly, the *directness* of the trip decreased slightly with both increasing solar radiation and increasing wind speeds (Table 5.5). Precipitation (χ^2_2 = 0.03, p = 0.986), wind direction (χ^2_3 = 2.05, p = 0.562) and the interaction with wind speed (χ^2_4 = 2.01, p = 0.569) did not improve the model. Lastly, the *average ground speed during flight* did not change with increasing solar radiation (χ^2_1 = 1.43 p = 0.232) and precipitation (χ^2_2 = 3.02, p = 0.221). Increasing wind speeds seemed to increase the ground speed, but this was not significant (χ^2_1 = 3.74, p = 0.064). Northerly winds resulted in lower ground speeds in flight (10.1 ± 0.1 m/s) than easterly winds (10.4 ± 0.1 m/s, Table 5.5), but interaction with wind speed did not improve the model (χ^2_4 = 4.64, p = 0.744).

Table 5.5: Overview of the response variables and significant explanatory terms, model output and estimates (β-coefficients) of the different models on a *trip* scale. Mean speed = ground speed in flight, WD = mean daily wind direction, WS = mean daily wind speed (m/s), SR = mean daily solar radiation (W/m^2), PR = mean daily precipitation rate (mm/h), df = degrees of freedom, chisq = Chi-square test result, p = p-value. For the β-coefficients, the estimates of the categorical levels for wind direction are compared to East (intercept); 1 = North, 2 = South, 3 = West. For precipitation rate, the β-coefficients are intercept = no rain, 1 = 0-1.5 mm/h, and 2=1.5-3 mm/h.

Response	**Explanatory**	**df**	**chisq**	**p**	**β-coefficients**		
					1	2	3
Trip duration	Intercept				4.75 ± 0.03		
	SR	1	22.4	<0.001 ***	0.05 ± 0.009		
	WS	1	7.17	0.007 **	0.05 ± 0.009		
	PR	2	17.7	<0.001 ***	0.11 ± 0.02	0.07 ± 0.08	
Total energy cost	Intercept				4.936 ± 0.02		
	SR	1	51.4	<0.001 ***	0.004 ± 0.0005		
	PR	2	26.2	<0.001 ***	0.15 ± 0.03	0.10 ± 0.10	
Energy cost per hour	Intercept				4.39 ± 0.03		
	SR	1	23.1	<0.001 ***	0.029 ± 0.006		
	WS	1	20.5	<0.001 ***	0.026 ± 0.006		

Table 5.5: Overview of the response variables and significant explanatory terms, model output and estimates (β-coefficients) of the different models on a *trip* scale. Mean speed = ground speed in flight, WD = mean daily wind direction, WS = mean daily wind speed (m/s), SR = mean daily solar radiation (W/m^2), PR = mean daily precipitation rate (mm/h), df = degrees of freedom, chisq = Chi-square test result, p = p-value. For the β-coefficients, the estimates of the categorical levels for wind direction are compared to East (intercept); 1 = North, 2 = South, 3 = West. For precipitation rate, the β-coefficients are intercept = no rain, 1 = 0-1.5 mm/h, and 2=1.5-3 mm/h.

Response	**Explanatory**	**df**	**chisq**	**p**	**β-coefficients**		
					1	2	3
Energy cost per distance	Intercept				-0.6 ± 0.03		
	SR	1	28.8	<0.001 ***	-0.21 ± 0.009		
	PR	2	15.2	<0.001 ***	0.10 ± 0.02	0.12 ± 0.08	
	WD	3	9.5	0.023 *	-0.02 ± 0.03	-0.03 ± 0.02	0.06 ± 0.02
% in flight	Intercept				-0.76 ± 0.03		
	SR	1	348	<0.001 ***	0.19 ± 0.01		
	WS	1	87.3	<0.001 ***	0.11 ± 0.01		
	WD	3	10.8	0.013 *	-0.11 ± 0.04	-0.005 ± 0.02	-0.05 ± 0.02
% flapping in flight	Intercept				-0.6 ± 0.03		
	SR	1	548	<0.001 ***	-0.21 ± 0.009		
	WS	1	272	<0.001 ***	-0.17 ± 0.01		
	PR	2	10.3	0.005 **	0.10 ± 0.02	0.12 ± 0.08	
	WD	3	19.6	<0.001 ***	-0.02 ± 0.03	-0.03 ± 0.02	0.06 ± 0.02
% mixed in flight	Intercept				-2.56 ± 0.09		
	SR	1	10.9	<0.001 ***	0.05 ± 0.02		
	WS	1	485	<0.001 ***	0.29 ± 0.01		
	WD	3	57.5	<0.001 ***	0.03 ± 0.08	-0.03 ± 0.05	-0.35 ± 0.06
% soaring in flight	Intercept				-1.40 ± 0.06		
	SR	1	463	<0.001 ***	0.32 ± 0.01		
	PR	2	16	<0.001 ***	-0.19 ± 0.05	-0.13 ± 0.21	
Trip travel distance	Intercept				9.92±0.04		
	SR	1	76.2	<0.001 ***	0.14 ± 0.01		
	PR	2	33.4	<0.001 ***	0.20 ± 0.04	0.04±0.15	
Trip max range	Intercept				8.85 ± 0.05		
	SR	1	32.6	<0.001 ***	0.09 ± 0.01		
	PR	2	37.5	<0.001 ***	0.20 ± 0.03	0.10 ± 0.14	
	WD	3	10.9	0.012 *	-0.13 ± 0.0.04	-0.0001 ± 0.04	-0.04 ± 0.03
Directness	Intercept				3.31 ± 0.02		
	SR	1	76.2	<0.001 ***	0.03 ± 0.006		
	WS	1	33.4	0.040 *	0.01 ± 0.006	0.04 ± 0.15	
Mean speed	Intercept				10.4 ± 0.10		
	WD	3	19.6	<0.001 ***	-0.32 ± 0.11	-0.18 ± 0.11	-0.13 ± 0.08

*** p <0.001, ** p <0.01, * p <0.05, . p <0.1

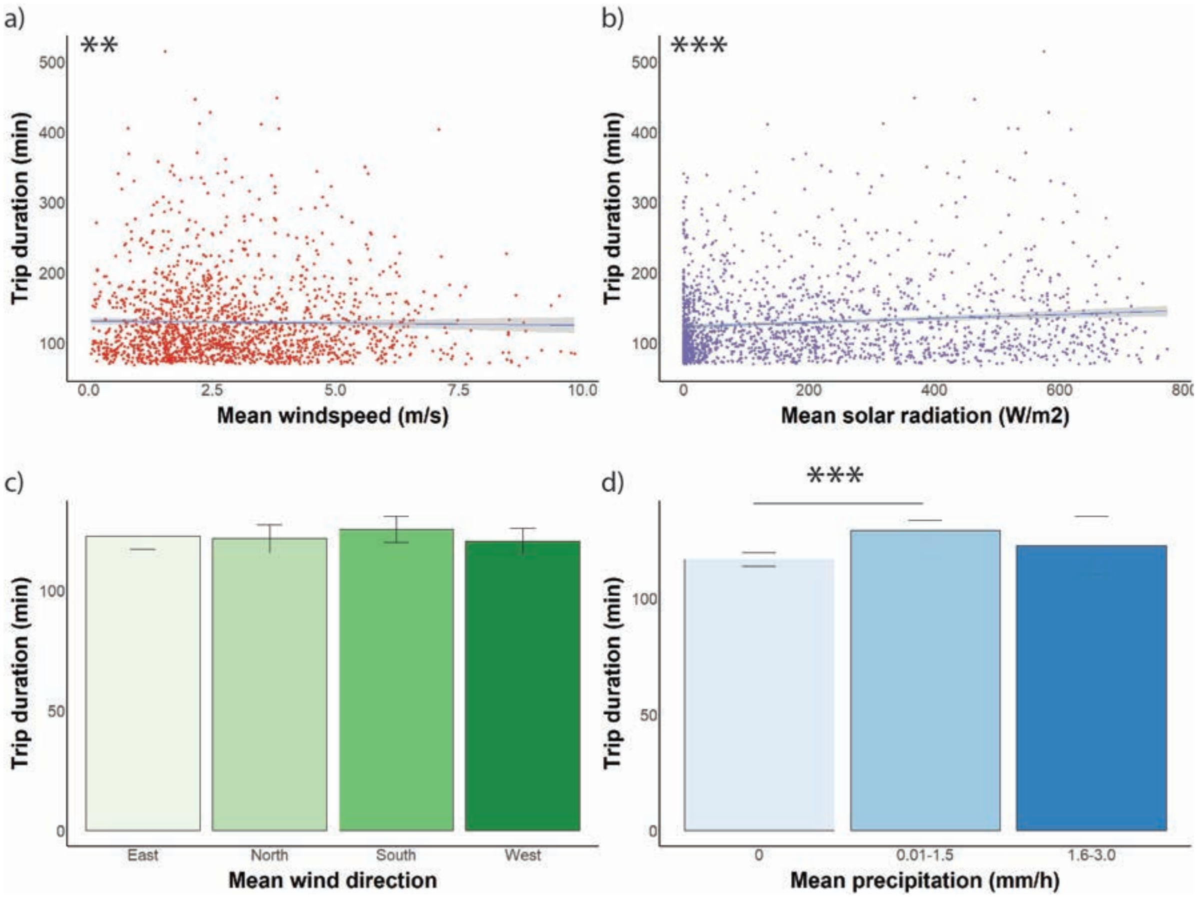

Figure 5.13: Trip duration (minutes) during different weather conditions. a) mean wind speed (m/s), b) mean solar radiation (W/m^2), c) mean wind direction, and d) mean precipitation rate (mm/h). For wind direction and precipitation rate, estimated marginal means ± standard errors are presented. Stars represent significant weather variables (mean wind speed and solar radiation) and significant differences between groups (mean precipitation rate). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

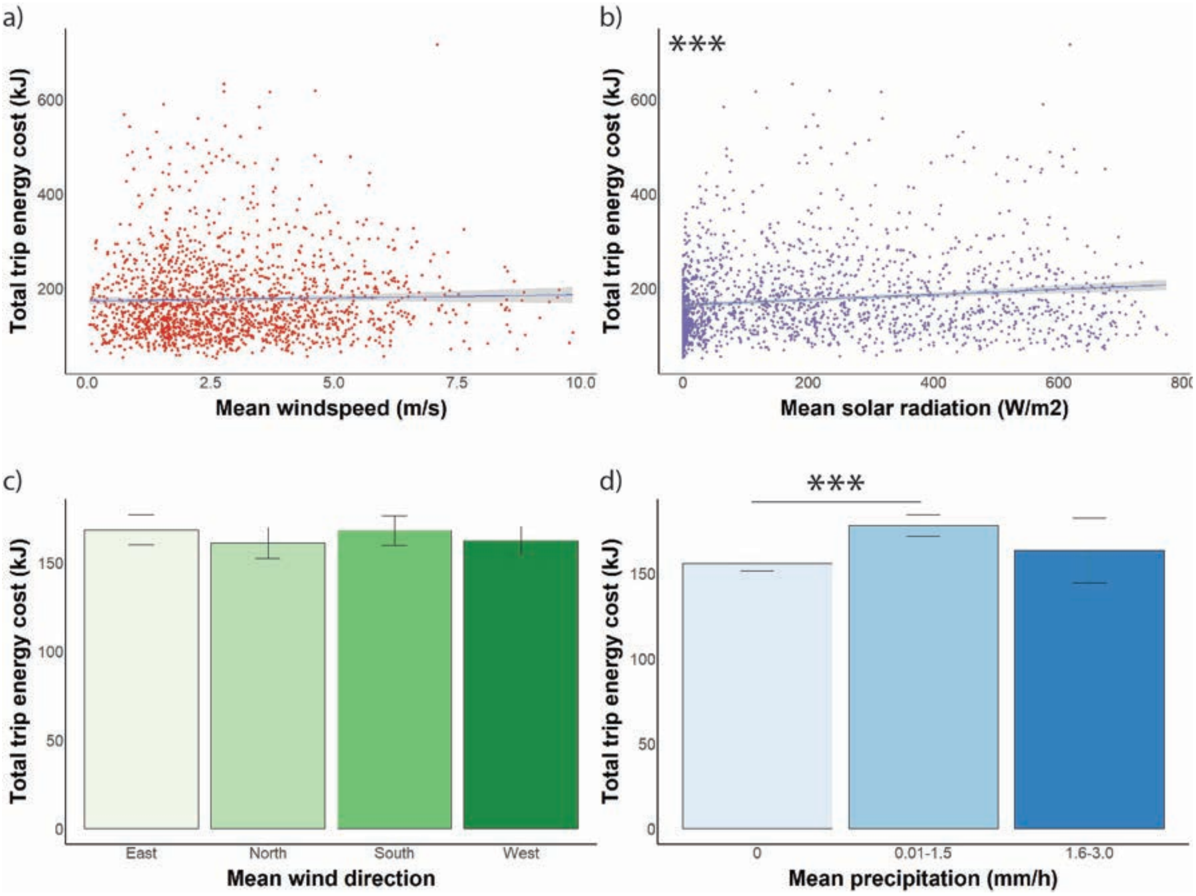

Figure 5.14: Total trip energy cost (kJ) during different weather conditions. a) mean wind speed (m/s), b) mean solar radiation (W/m^2), c) mean wind direction, and d) mean precipitation rate (mm/h). For wind direction and precipitation rate, estimated marginal means ± standard errors are presented. Stars represent significant weather variables (mean solar radiation) and significant differences between groups (mean precipitation rate). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

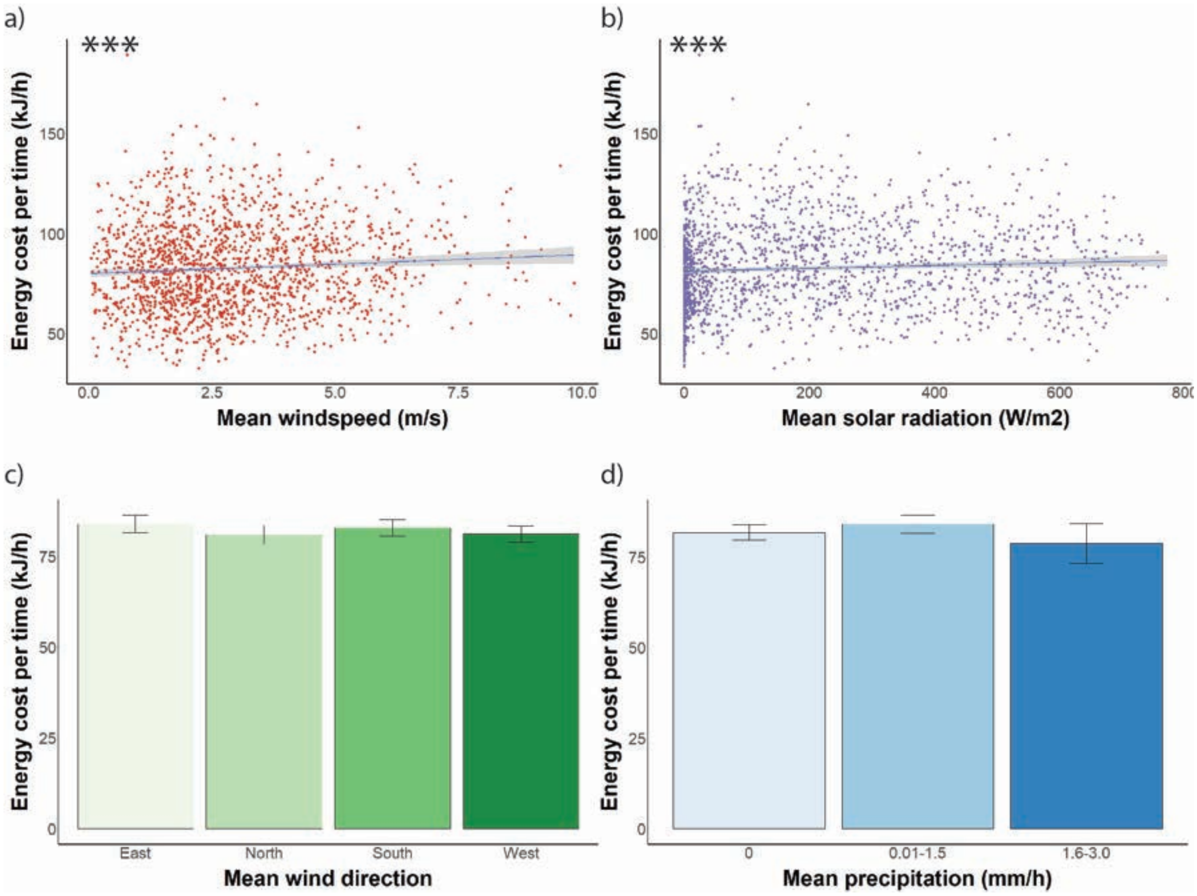

Figure 5.15: Trip energy cost per unit time (kJ/h) during different weather conditions. a) mean wind speed (m/s), b) mean solar radiation (W/m^2), c) mean wind direction, and d) mean precipitation rate (mm/h). For wind direction and precipitation rate, estimated marginal means ± standard errors are presented. Stars represent significant weather variables (mean solar radiation). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

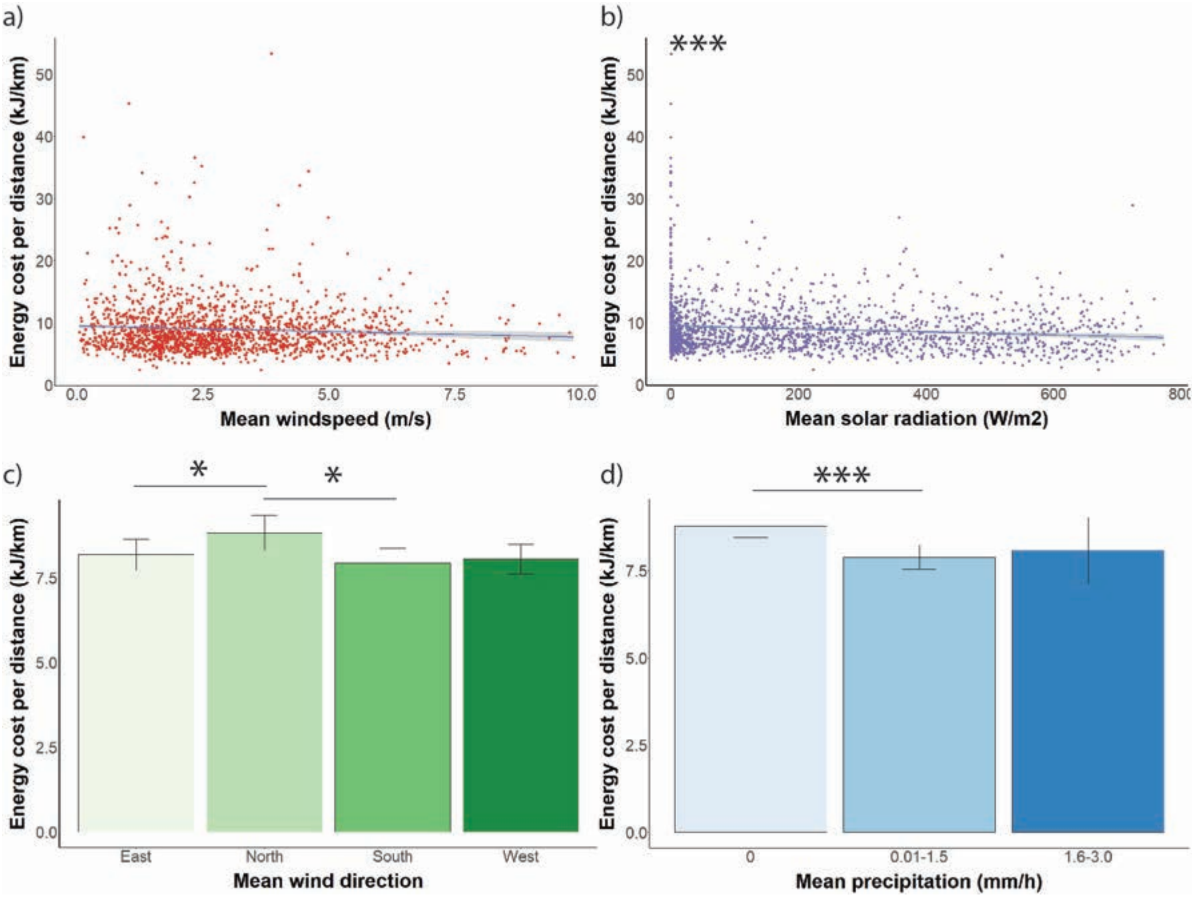

Figure 5.16: Trip energy cost per unit distance (kJ/km) during different weather conditions. a) mean wind speed (m/s), b) mean solar radiation (W/m^2), c) mean wind direction, and d) mean precipitation rate (mm/h). For wind direction and precipitation rate, estimated marginal means ± standard errors are presented. Stars represent significant weather variables (mean solar radiation) and significant differences between groups (mean wind direction and precipitation rate). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

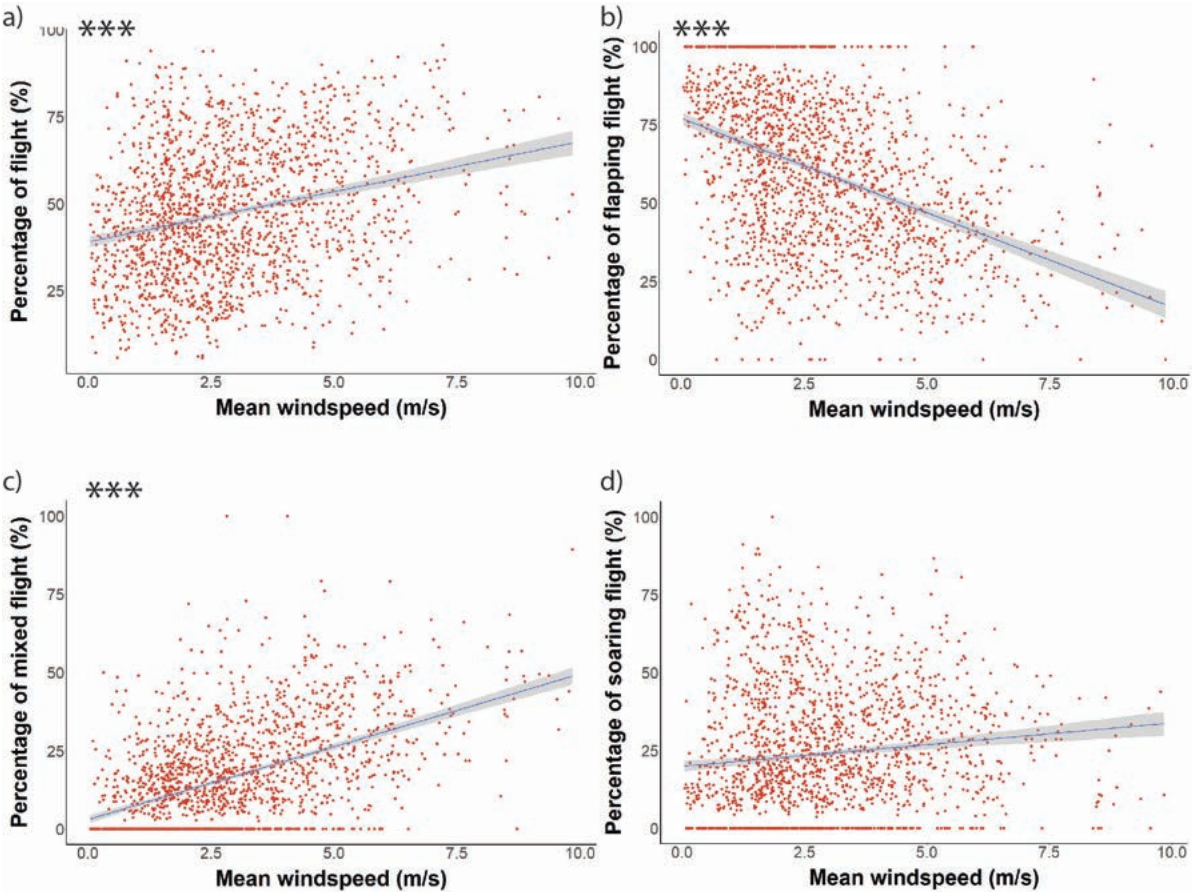

Figure 5.17: The proportion of time spent on different flight behaviours of gulls during trips in relation to mean wind speed (m/s). a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

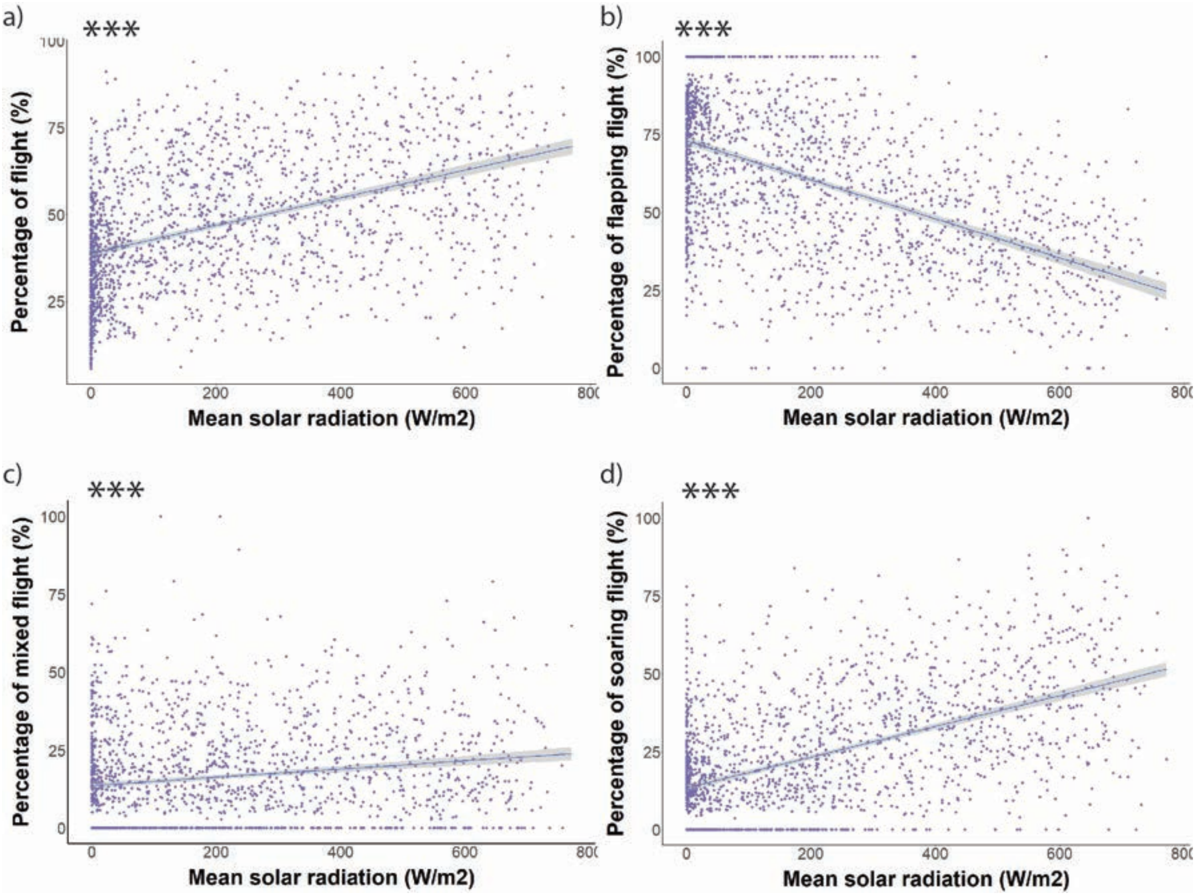

Figure 5.18: The proportion of time spent on different flight behaviours of gulls during trips in relation to mean solar radiation (W/m^2). a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

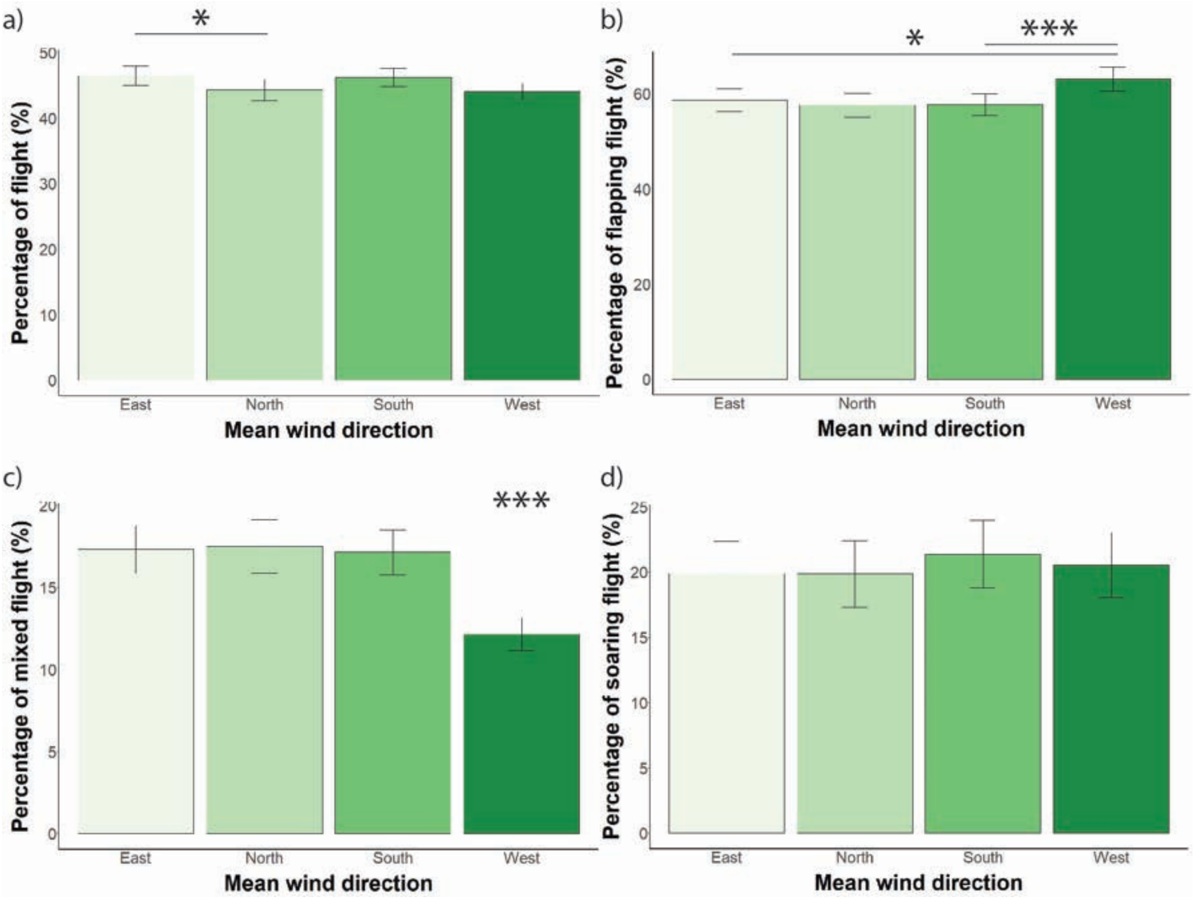

Figure 5.19: The proportion of time spent on different flight behaviours of gulls during trips in relation to mean wind direction. a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Estimated marginal means ± standard errors are presented. Stars represent significant difference between groups. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

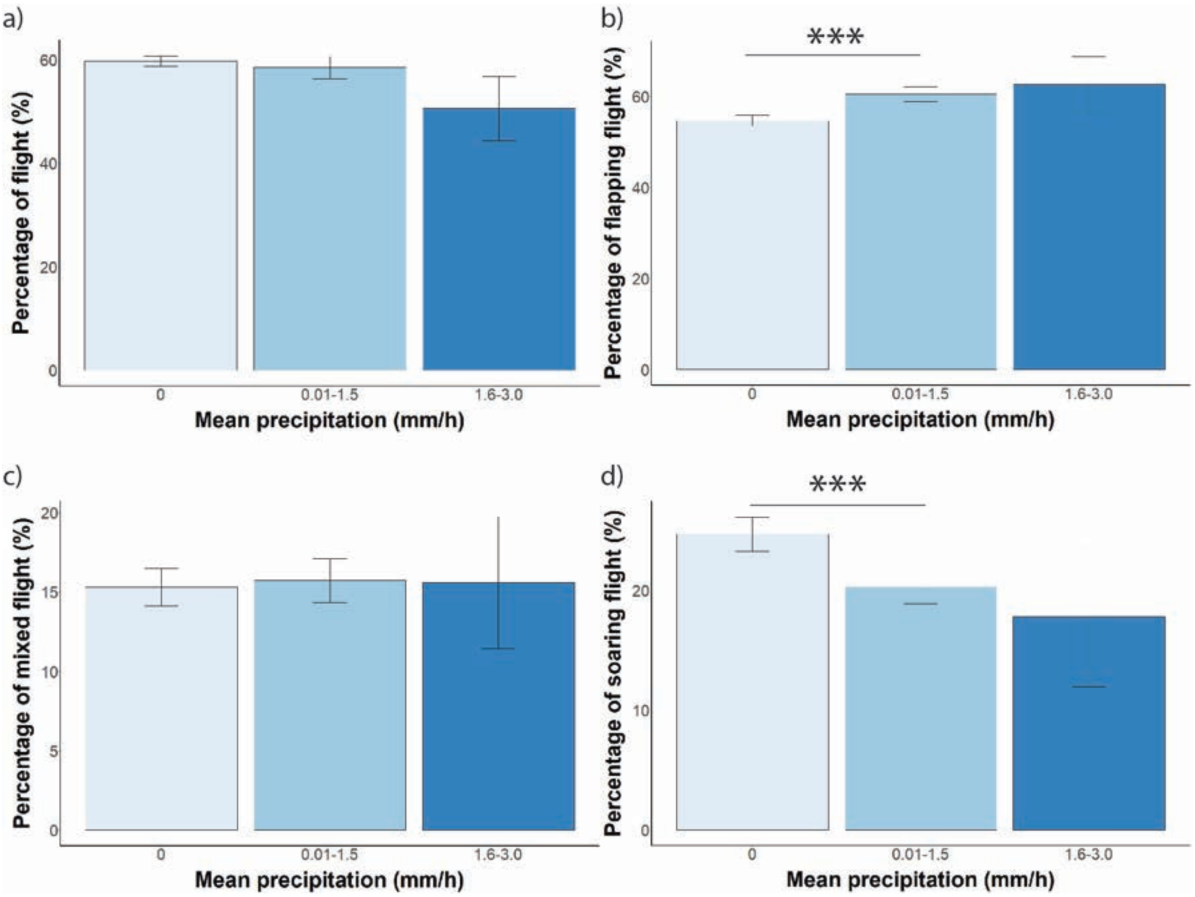

Figure 5.20: The proportion of time spent on different flight behaviours of gulls during trips in relation to mean precipitation rate (mm/h). a) percentage in flight (%), b) percentage flapping in flight (%), c) percentage mixed flight in flight (%) and d) percentage soaring in flight (%). Estimated marginal means ± standard errors are presented. Stars represent significant difference between groups. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

5.5 Discussion

This study showed the extent to which weather conditions (i.e. wind speed, wind direction, solar radiation and precipitation rate) affected both time investment and energy costs attributed to movement of gulls nesting in an urban environment at both the daily and individual trip level (Figure 5.4). Overall, we found that wind speed, wind direction and solar radiation did not show any effect on the daily level but showed small effects on the time investment and/or energy costs at the trip level. Precipitation did increase time investment on both levels, but energy costs were higher only at the trip level (Tables 5.6 and 5.7).

5.5.1 Wind speed and direction

On a daily level, increasing wind speeds and wind direction did not influence the time investment of the gulls, i.e. time spent away from the nest. This is in contrast with studies on other seabird species where either daily foraging time was lower (Furness & Bryant, 1996; Lewis et al., 2015) or higher (Finney et al., 1999; Pistorius et al., 2015) with increasing winds. Wind speed did, however, show a small effect on the trip duration of the gulls, decreasing it slightly when winds got stronger. In comparison, Cape gannets foraging with high wind speeds have been observed to have shorter trip durations (Pistorius et al., 2015), but for Northern gannets trip duration remained unchanged (Lane et al., 2019). The latter result was due to a change in foraging behaviour because these birds did increase their time spent foraging during a trip, but they

Table 5.6: Overview of the results of the effect of weather conditions on the time investment and energy costs at a *daily* level

	Time investment	*Energy costs*
	Time away from nest	Total daily energy cost
Wind speed	NO	NO
Wind direction	NO	NO
Solar radiation	NO	NO
Precipitation	Increase	NO

Table 5.7: Overview of the results of the effect of weather conditions on the time investment and energy costs at a *trip* level.

	Time investment	*Energy costs*		
	Trip duration	Total trip energy cost	Energy cost per unit time	Energy cost per unit distance
Wind speed	Decrease	NO	Increase	NO
Wind direction	NO	NO	NO	North: highest
Solar radiation	Increase	Increase	Increase	Decrease
Precipitation	Increase	Increase	NO	Decrease

compensated this by decreasing their time spent resting on the water. Additionally, birds can increase their ground speeds with increasing wind speeds (Safi et al., 2013; Shamoun-Baranes et al., 2017b), and especially when flying with a tailwind (Lane et al., 2019), which in turn can decrease trip durations when distances are kept constant (Cornioley et al., 2016). In our study, increasing wind speeds seemed to increase mean ground speeds in flight but not significantly, suggesting that there may be another reason for the slight decrease observed in trip duration.

We did not observe any effect of wind speed on daily and trip total energy costs which was not as expected. Gulls are flap-gliders and therefore were expected to decrease their energy costs with higher winds as they can use these conditions to soar using orographic lift, similar to Northern fulmars, *Fulmarus glacialis*, which can use dynamic soaring with higher winds at sea (Furness & Bryant, 1996). However, daily energy costs in Northern gannets, also flap-gliders, increased with higher winds, which is possibly a result of them spending more time foraging in flight (more energetically expensive) and less time resting on the water (Mullers et al., 2009). We did observe a change in flight behaviour with increasing wind speeds as the gulls spent proportionally more time flying, less time in flapping flight and more time in mixed flight. This increased the energy cost per unit time which in combination with a lower trip duration can explain the constant total trip energy cost. The gulls spending more time in flight and less time on the ground could have decreased the trip duration. When in flight with favourable conditions, such as higher wind speeds providing orographic lift, gulls can switch to energetically cheaper soaring flight (Shamoun-Baranes et al., 2016). Interestingly, instead of soaring flight, we observed that the gulls increased the proportion of time spent in mixed flight (a combination of soaring and flapping flight) with increasing wind speeds. This could be attributed to the fact that these gulls are mainly flying through a city environment and the airflows created by different buildings and structures (including gusts) are more complex than orographic lift created from cliffs, dunes and dykes in more open environments.

Although flying is general energetically more expensive than non-flight, it seems that when wind speeds increase, individuals can spend more time in flight without increasing their overall energy cost. We propose two - not mutually exclusive - hypotheses that could explain the increase of proportion in flight with increasing wind speeds. Firstly, gulls flying through an urban environment with strong winds might encounter areas of updrafts, downdrafts and sudden gusts. To optimise their flight path, they should navigate through this complex environment and make use of the structures which could provide them with lift. Therefore, they might not fly directly but choosing an optimum path through the environment (Sage et al., 2019; Williamson et al., 2020). Indeed, increasing wind speeds showed a small effect on the directness of the trip, resulting in less direct trips at higher wind speeds. However, we must note that we did not see an effect of wind speed on the trip travel distance which would have been expected to increase as well. Secondly, spending more time in flight during foraging trips could be advantageous for encountering new ephemeral food sources. Gulls are opportunistic and able to use a fly-and-search foraging strategy (Chapter 3) taking advantage of food sources presented to them when in flight. It could be that when the wind is favourable, they can spend more time in flight without increasing their overall energy cost but increasing the possibility of encountering ephemeral food sources which could potentially increase their energy intake. On the other hand, when weather conditions are not favourable, they would go directly to their foraging grounds as time in flight is more expensive.

The prevailing wind direction in Bristol is westerly resulting in a bias showing a high number of days and trips with westerly winds. Therefore, it was not surprising that we did not find a significant effect of the mean wind direction on the total daily energy cost. Westerly winds did seem to negatively affect the proportion of time spent in mixed flight on both daily and trip level, but did not show an effect on the energy costs. As most trips are not in the westerly direction, we expected the proportion of time in mixed flight not to be different, however, this finding might be a result of the sample bias. The total daily energy cost did increase with wind speed but only during northerly winds. Trips were shorter in range and the trip energy cost per unit distance was higher with northerly winds. Additionally, the gulls spent proportionally less time in flight and when flying their ground speed was lower with northerly winds. The direction of the trips did not depend on the wind direction (Figure A.10) and the majority of the trips were north/north-west bound (942 out of 1,682 trips; Table 5.4). Therefore, during northerly winds, birds seemed to face headwinds during the initial stage of the trip. Flying with headwind can result in slower ground speeds (Pennycuick, 1998; Lane et al., 2019) and is more costly (Amélineau et al., 2014). Flying back to the nest the opposite direction along the reversed track could result in benefits related to wind support (e.g. tailwinds), however, the costs can exceed the benefits as flying with head wind takes longer (Alerstam et al., 2019). Additionally, most of the trips in this study were not direct and contained several stops indicating the gulls might have flown back to the nest from another direction, possibly encountering different wind conditions.

5.5.2 Solar radiation

On a daily level, increasing solar radiation levels did not affect the time investment of the gulls. This was contradictory to our expectations as we expected the gulls to spend more time in thermals which could have increased the time spent in flight and therefore increased the time spent away from the nest. Our gulls did show a small increase in trip duration on the trip level, but apparently, this was not substantial enough to show a difference in time investment on the daily level. This increase is similar to a study with kestrels that increased their foraging trip duration with increasing solar radiation levels due to higher thermal opportunities (Hernández-Pliego et al., 2015). Soaring behaviour such as conducted in thermalling generally results in lower ground speeds in flight compared to flapping flight (Shamoun-Baranes et al., 2016). However, the mean ground speeds in flight did not change with increasing levels of solar radiation, suggesting it is not the ground speed but another factor resulting in slightly higher trip durations.

Additionally, the total daily energy cost did not decrease with increasing solar radiation levels, but our birds did spend proportionally more time in soaring flight and less time in flapping flight on both daily and trip levels. This finding is similar to previous studies showing that a higher probability of thermals resulted in higher proportions of soaring flight in gulls (Shamoun-Baranes et al., 2016) and in California condors, *Gymnogyps californianus* (Poessel et al., 2018). Although the fact that soaring is energetically less expensive than flapping flight (Hedenström, 1993; Pennycuick, 2008; Shamoun-Baranes et al., 2016), the total daily energy cost did not decrease. Although not significantly on the daily level, on the trip level, the gulls spent proportionally more time in flight. Flight is energetically more expensive than non-flight and possibly due to the increase in flight, the total trip energy cost increased slightly too. However, the trip energy cost per unit distance decreased with higher solar radiation levels, suggesting that the gulls could cover more distance for the same energy output. Indeed, we found that the travel distance and maximum range also increased slightly with higher solar radiation levels.

The higher proportion of time spent in flight and more distance covered during trips with increasing solar radiation could be explained by two - also not mutually exclusive - hypotheses. Firstly, using thermals during flight could be less direct than without thermal convection. Thermals are not likely to be present in lines (but see thermal streets - Pennycuick 1998) and could be horizontally displaced by wind (Kerlinger & Moore, 1989). Therefore, birds might have to adjust their flight path for the spatial availability of thermals and potential drift resulting in longer routes than if travelling directly using flapping flight. Indeed, we found that the directness of the trip decreased slightly and the travel distance increased with increasing solar radiation indicating the increased proportion of time spent in flight might be a result of this adjustment to thermal availability. Secondly, some of the foraging grounds that are used by the gulls are further away. On days with higher possibilities of thermals, they could save energy by soaring in these conditions and cover more distance for the same energy cost to fly to foraging grounds further away. Indeed, our study showed that the gulls increased their travel distance and maximum range with increasing solar radiation. Kestrels have shown to fly further away when weather conditions were favourable for soaring and do so at a smaller energy cost (Hernández-Pliego et al., 2015). However, this only seems advantageous when food in these foraging grounds is of higher quality or its availability is more predictable. Indeed, ring-billed gulls selected landfills which were further away from the nesting site but were more predictable and provided a higher energy intake than agricultural lands closer to the nesting area (Patenaude-Monette et al., 2014). In Bristol, some of the foraging grounds further away are waste processing centres such as landfills and transfer stations. These sites are known to contain predictable anthropogenic food sources (Sibly & McCleery, 1983b; Belant et al., 1998), therefore the energy and time spent on foraging further away might be compensated by a higher food intake.

5.5.3 Precipitation

We expected precipitation to affect the proportion spent in flight by our gulls because precipitation might hinder the flight performance of animals. However, we found no effect of precipitation on the proportion of time spent in flight at both the daily and trip level. The plumage of seabirds, such as gulls, is highly water-resistant because the feathers are anointed with the excretion from an oil gland (Elder, 1954) and therefore might not be as affected by precipitation as other flying animals such as bats which have fur or smaller birds. Indeed, the flight behaviour of another seabird species, Northern gannets, was also unaffected by precipitation (Lane et al., 2019).

We did find that precipitation both increased the time away from the nest on a daily level and the trip duration when it was slightly raining. This is similar to Cape gannets which increased their time spent foraging with higher precipitation rates resulting in less time spent at the nest (Pistorius et al., 2015). These and other seabirds mainly forage at the sea, where precipitation could increase the turbidity of the water surface resulting in poor foraging conditions which can, in turn, affect prey delivery rates (Elliott et al., 2014). However, the gulls in Bristol only forage on terrestrial lands during the breeding season (Chapter 3) and therefore this is unlikely to be the reason for the increase in trip duration. Both the travel distance and maximum range of the trip also increased with precipitation indicating that the birds fly further with slight precipitation. One possible explanation could be that Bristol is surrounded by agricultural lands and green areas where rain can increase the availability of earthworms (Sibly & McCleery, 1983b). Spending more energy to fly further to feed on predictable food sources during rain, such as earthworms, might increase the energy intake and therefore compensate the higher total trip energy cost.

Precipitation can also affect the mechanical flight costs of birds, for example, hummingbirds showed a change in body position and increase in wingbeat frequency resulting in higher mechanical expenditure when their feathers were wet (Ortega-Jimenez & Dudley, 2012). In our study, we did not detect any effect of precipitation on the total daily energy cost, however on the trip scale, precipitation resulted in a higher total trip energy cost. This could be explained by the gulls increasing the proportion of time spent in flapping flight and decreasing time spent in soaring flight, but keeping the proportion in flight the same. The trip duration also increased with precipitation, resulting in no change of the energy cost per unit time. The decrease in the proportion of time spent in soaring flight might be related to the fact that during rainy days, thermals are less likely to form, and gulls cannot make use of these favourable conditions to switch to the energetically less expensive soaring flight. Lastly, the energy cost per unit distance decreased with slight rain, suggesting that gulls cover more distance for the same energy cost. This could be explained by the findings of the trip travel distance increased at a higher rate than the total energy cost, but the exact reasons of why this would happen are unclear.

5.5.4 Energy cost comparison

Metabolic rates of moving animals can be calculated by several distinct methods each having their own limitations. In this study, we compared energy expenditure calculations based on dynamic body acceleration with time-energy budgets based on metabolic rate estimations in gulls from previous studies. The two methods were highly correlated on both the daily and trip level (all above 0.80) but there was some variation between DBA and the time-energy budgets which might be contributed to non-movement related factors affecting the DBA values (Halsey et al., 2011; Gómez-Laich et al., 2011), such as the environment (e.g. strong winds) or bird behaviour (e.g. preening, shivering). In gulls, dynamic body acceleration has not yet been validated against oxygen consumption with either double-labelled water or heart-rate measurements, but the results from this study show that at least on a larger scale (daily and trip level) using DBA as a proxy for energy costs in gulls might be promising. However, to use DBA as a proxy, the relationship between DBA and energy expenditure should be validated properly because in other seabirds the relationship is species-specific and dependent on the activity (Halsey et al., 2011; Wilson et al., 2020).

5.5.5 Implications and conclusions

This study aimed to analyse how weather conditions affect both time investment and energy costs of gulls nesting in an urban environment. Specific weather conditions can result in opportunities for some species of birds to save energy by using orographic lift (during strong winds) or thermals for example (Figure 5.1). Cities are heterogeneous environments with both complex wind flows and a higher probability of thermals due to the UHI-effect, therefore the ability to use these conditions to minimise time and energy costs could be another reason why gulls are successful in cities. However, this study found that the gulls in Bristol did not substantially minimise their time or energy costs on a large scale (daily and trip level), but instead maintained the same costs under various wind conditions and solar radiation levels. The energy saved by switching to more energetically cheaper flight strategies under favourable conditions was offset by increasing their overall time in flight during a trip. This initially unexpected behaviour might be beneficial when considering energy intake. Spending more time in flight during a trip could increase the energy intake rate by either increasing the possibility to encounter ephemeral food sources during a trip (higher wind speeds) or by flying further away to predictable foraging grounds (higher solar radiation).

Animals can encounter ephemeral food sources in urban environments when of people discard waste on the street, feed birds or other human-waste related activities. Gulls are opportunistic species which are known to take advantage of a wide range of food sources when presented to them. By adopting a "fly-and-search" strategy in the city (discussed in Chapter 3) they can scan a larger area for feeding opportunities than when using a "sit-and-wait" strategy at a specific high vantage point. Maintaining their energy costs while switching to the "fly-and-search" strategy is beneficial and might increase their total energy gain. Using thermals to fly to foraging grounds further away from the nest might be beneficial if these grounds provide a higher intake rate. Most landfills and waste centres in Bristol are at the border of the city (Figure 3.1) and these foraging grounds are known to be more predictable and have higher intake rates (Sibly & McCleery, 1983b; Belant et al., 1998). Therefore, flying to these locations might benefit the gulls to increase their energy intake. If indeed these gulls increase their energy intake while maintaining their energy cost, this could result in a higher total energy gain, eventually increasing fitness.

The small effect sizes observed and the high variation in this study could be a result of the limitations of the dataset collected. This study looked at a larger scale by averaging weather conditions over days and trips. In combination with only focussing on the breeding season in the summer, this could exclude extreme values resulting in low sample sizes of days and trips with strong winds and high precipitation. This could mean that specific effects of these variables, e.g. strong winds affecting flight ability or decreasing soaring possibilities, could have been missed. Additionally, although the total energy cost calculation between DBA and time-energy budgets based on BMR values were comparable, the latter method defined only one value for each of the different flight strategies (e.g. flapping) regardless of the effort put into that flight strategy. Flying at higher or lower airspeeds will affect the cost of movement, especially when in flapping flight as shown by flight power curves created by Pennycuick (2008). However, a power curve based on commuting flights from these gulls showed a relatively shallow minima indicating that there are only small effects on power and thus energy expenditure with increasing and decreasing airspeeds in flapping flight (Williamson et al., 2020). Lastly, although the gulls did not minimise their daily time or energy costs, they might fly at a cheaper rate than gulls breeding at non-urban colonies due to the favourable weather conditions in the city. The gulls in this study seemed to spend proportionally more time in flight during the whole breeding season (47% spent in flight) than the same species of gulls from a non-urban colony (30% spent in flight) using the same GPS devices and settings (Shamoun-Baranes et al., 2016). This could be a result of the fact that gulls in Bristol can utilise these favourable conditions in the city to extend their flight times while maintaining their energy costs, however, the exact reasons are unclear. Future research comparing the flight behaviour and costs between urban and non-urban gulls might provide a more detailed understanding of how the flight energetics differ between urban and non-urban colonies.

Some seabird species can buffer or compensate for the negative effects of weather conditions on their foraging behaviour and energy costs (Elliott et al., 2014; Lane et al., 2019). Other species can take advantage of favourable weather conditions saving energy in flight by making use of thermals (Duerr et al., 2015; Hernández-Pliego et al., 2015; Shamoun-Baranes et al., 2016; Poessel et al., 2018) and orographic lift created by structures such as cliffs and buildings (Shepard et al., 2016; Poessel et al., 2018; Sage et al., 2019). The gulls in this study utilised the increased wind speeds and solar radiation by altering their flight behaviour and increasing their time spent in flight during foraging trips. This did not substantially affect their time investment nor energy costs because they switched to other, cheaper flight strategies. This implies that although the birds could have minimised their time investment and energy costs, they seemed to have increased the possibility to obtain a higher energy intake by spending more time in flight at the same cost, thus possibly increasing their net energy gain which could benefit life-history traits such as survival and reproduction. Overall, the ability to change their flight behaviour and maintain their time and energy costs under a range of weather conditions could potentially enable gulls to thrive in cities. Having this behavioural flexibility has a range of implications which will be discussed in the general discussion combined with the other flexible behavioural traits found in previous chapters.

CHAPTER 6

GENERAL DISCUSSION

Urbanisation can negatively affect animal communities and their biodiversity. However, some opportunistic animals can benefit from the urban environment for breeding and/or foraging. Many of these urban species are increasing in numbers in cities and one specific example are gulls. The increase in numbers of gulls in cities has resulted in a higher number of human-gull conflicts ranging from damage to property and nuisance to aggression and health threats. Several reasons for the increase in the number of gulls related to favourable conditions in cities have been proposed, such as predictable anthropogenic food sources, favourable weather conditions (e.g. warmer temperatures and opportunities to save energy using atmospheric conditions), ample nesting sites and lower predation pressure. However, the movement behaviour of urban-nesting gulls is relatively unstudied, and little is known about the extent to which they utilise urban environments. Therefore, the overall aim of this thesis was to study the movement ecology of urban-nesting gulls by quantifying their habitat use, foraging behaviour and flight energetics. To meet this aim, the following questions were set out:

1. To what extent do urban-nesting gulls use urban environments and does this change with breeding stage?

2. Are there temporal patterns in the foraging behaviour of urban-nesting gulls and how are these linked to human-related activity and food availability?

3. How do weather conditions affect both time investment and energy costs of urban-nesting gulls in the urban environment?

By combining GPS tracking data of 12 lesser black-backed gulls over four breeding seasons (2016-2019) with behavioural data, habitat maps, field observations, nesting area observations, and weather data, I have aimed to answer these questions to provide more insight into the movement ecology and behaviour of urban-nesting gulls. The results highlighted that urban-nesting gulls are highly flexible behaviourally and able to use a wide variety of terrestrial food sources in different habitats each with distinct foraging strategies but do not make use of the marine environment. Moreover, they have the ability to adapt to temporally available anthropogenic food sources and to maintain their time investment and energy costs over a wide range of weather conditions. These behavioural traits are likely to enable them to be successful in the urban environment. In this final chapter, I will summarise the findings of this thesis and discuss their wider implications. Additionally, I will consider the limitations, highlight future directions and finish with concluding remarks.

6.1 Summary of principal findings

Research question 1: To what extent do urban-nesting gulls use urban environments and does this change with breeding stage?

In chapter 3, I explored the habitat use and time-activity budgets of urban-nesting gulls in the city of Bristol. Although Bristol is situated only 10 km from the sea, the gulls did not make use of the marine environment during the breeding season. Instead, they spent two-thirds of their time away from the nest in suburban and urban environments and one-third in agricultural lands surrounding the city. The gulls used a wide variety of terrestrial habitats during the breeding season using distinct foraging strategies for each of these habitats, possibly reflecting the availability of the food sources in the habitats and the strategies to acquire them. For example at waste processing areas, where gulls were waiting for the food to be unloaded, a "sit-and-wait" strategy was used, whereas urban built-up areas were also characterised by a "fly-and-search" strategy. The breeding stage had an effect on both their habitat use and time-activity budgets. As the chicks grew, the gulls spent less time on the nest and more time in suburban and urban areas. The increased food demand of the chicks seemed to result in an increase in foraging time for anthropogenic food sources, with possible explanations such as these food sources being more predictable, of higher quality, or being closer to the nesting areas. Additionally, the change in the birds' time-activity budgets over the breeding season suggests that at the end of the breeding season the gulls shift their resting behaviour from the nesting area to the foraging grounds. This is possibly due to lower constraints to the nest as the chick are nearly fledged and/or resting at the foraging grounds might increase their foraging efficiency.

Research question 2: Are there temporal patterns in the foraging behaviour of urban-nesting gulls and how are these linked to human-related activity and food availability?

Based on the insights of how urban-nesting gulls use the urban environment, the focus of chapter 4 was on the foraging behaviour at three urban feeding grounds: a park, a school and a waste centre. I analysed if the gulls could adapt to artificial temporal patterns in human-related activity and food availability at these urban feeding grounds. By combining both field observations and GPS tracking data, I found that the gulls were able to match the timing of availability of anthropogenic food sources at two out of three urban feeding grounds. In the park, the gulls were mainly present in the morning when people were absent, suggesting a possible disturbance from people. However, the presence of gulls seemed to be related to the availability of natural food sources, such as earthworms, which are present in the early hours of the day. At the school, the presence of gulls related to people showed a positive pattern on weekdays related to the break times of the school and when food was consumed, and a negative pattern on the weekends related to sports events which disturbed the gulls. Lastly, the waste centre also showed a different pattern between weekdays and the weekends related to the opening times of the waste centre. There was a lower number of total gulls present at the weekends when the centre was closed and no food waste was being unloaded. However, proportionally more gulls were foraging on the food waste pile at the weekend which was a result of less (disturbing) activities happening on the pile. Additionally, the temporal patterns of the GPS tracked individuals at the same feeding grounds supported the field observations, indicating that they have similar foraging schedules to the gulls observed at the three feeding grounds. The temporal patterns of the GPS tracked individuals at multiple feeding grounds of the same type did also show similarities to the three specific feeding grounds suggesting that these are general patterns across feeding grounds of these types. However, there was some variation in these patterns which was probably due to different opening times of schools and waste centres, and distinct utilisation of parks.

Research question 3: How do weather conditions affect both time investment and energy costs of urban-nesting gulls in the urban environment?

The urban-nesting gulls in Bristol spent the majority of their time in suburban and urban areas (Chapter 3). These urban areas can provide opportunities to save time and energy in flight depending on the weather conditions. I analysed how wind speed, wind direction, solar radiation and precipitation affected both the time investment and energy costs on the daily and trip level in these city-living birds. Firstly, the wind direction did not have a substantial effect on the daily or trip time investment and energy costs which might be explained by the bias due to the prevailing westerly winds. Precipitation did not affect the proportion of time spent in flight but did increase daily time spent away from the nest and trip duration. In combination with increased time spent in flapping flight with slight precipitation levels, this resulted in a higher total trip energy cost. The gulls did not minimise daily total time or daily energy costs with increasing wind speeds (a proxy for orographic updraft) nor with increasing solar radiation (a proxy for thermal updraft) and there were only small effects on the trip level. Although the birds saved energy in flight by shifted to energetically cheaper flight behaviours (e.g. mixed and/or soaring flight) with increasing levels of wind speed and solar radiation, they also spent proportionally more time in flight offsetting the energy saved by flying more efficiently. Spending more time in flight at higher wind speeds in the city could be a result of navigating through a complex windy city environment and/or increasing their opportunity to encounter ephemeral food sources during their flight which could increase their energy intake. With increasing solar radiation, spending more time in flight could be a result of the spatial availability and drift of thermals and/or flying further away from the nest at the same costs to foraging grounds which have more predictable food sources and thereby potentially increasing their intake rate. Using these favourable conditions to increase their net energy intake might result in an overall higher net energy gain, and thus result in higher fitness, survival and reproduction. The higher possibility of thermal and orographic lift in cities in combination with flexibility in the flight behaviour to maintain similar time and energy costs could be a useful trait for adapting to and thriving in cities.

Overall, the results of studying urban-nesting gulls in Bristol presented in this thesis indicate that these gulls are highly flexible in their behaviour. Specifically, three different behavioural traits were observed that might enable them to be successful and thrive in urban environments: the ability to take advantage of a wide variety of terrestrial habitats by using a range of foraging strategies, the ability to match their foraging schedules to predictable anthropogenic food sources and the ability to maintain their time investment and energy costs over a range of weather conditions by optimising their use of the aerial environment.

6.2 Implications

Success in the city

The gulls in this study seem to have several flexible behavioural traits which might enable them to be successful in cities. Being able to utilise in a wide variety of habitats by using different foraging strategies could be beneficial when specific feeding grounds or food resources are not available, so they can switch to other resources. This change in behaviour has been observed in various species of gulls (Rock, 2004a; Tyson et al., 2015; Zorrozua et al., 2018). Additionally, being able to acquire multiple food resources can increase their foraging efficiency and thus their energy intake. The ability to match their foraging behaviour to temporal patterns in food availability can also increase efficient foraging because time and energy costs can be reduced

(Fleischer et al., 2003; Goldenberg et al., 2016). Flying directly to these habitats and waiting until the food becomes available is reducing energy spent on searching in flight and also reduces their time spent on searching for food. The urban environment consists of several different predictable anthropogenic food sources, such as waste centres, schools, and feeding stations in gardens (Monaghan & Coulson, 1977; Belant et al., 1998). Being able to make use of these different food sources and possibly at different times of the day, can be very useful for adapting to city life. Additionally, the ability to maintain time and energy costs over a range of weather conditions might increase the range over which the birds are able to forage during the breeding season. Spending more time in flight but not substantially affecting energy costs provides the opportunity to encounter ephemeral food sources or to fly further to more predictable foraging habitats. These opportunities could have increased their energy intake and maximised their net energy gain.

Behavioural flexibility has been proposed as one of the underlying mechanisms needed to exploit or invade novel environments. Behavioural flexibility can be defined as the ability to change behaviour in response to changes in the external or internal environment and this has been widely discussed in the literature. A meta-analysis of over 10,000 species showed that species with behavioural flexibility (e.g. foraging innovation) showed lower extinction rates and more stable or increasing population trends (Ducatez et al., 2020). When looking at gulls, individuals that were relocated to a new area with a different amount of available habitats, utilised different habitats than control birds, suggesting that they did not adapt to these new habitats over time but had the behavioural flexibility to utilise them directly (van Toor et al., 2017). This confirmed that behavioural flexibility is an important trait for gulls to exploit novel environments, such as cities. For example, flexibility in diet or habitat use are important traits for animals invading or exploiting novel environments (Wright et al., 2010). The urbanisation of the landscape can result in significant changes in the habitat structure and can create novel ecological niches (Luniak, 2004). Generalist species, which are considered to be behaviourally flexible, might be more able to adapt to changing changes in the landscape, whereas specialist species might perform better under specific favourable conditions (Andrén et al., 1997). However, some generalists, like starlings, seem to do worse in cities (Mennechez & Clergeau, 2006) and specialists, such as mountain chickadees, *Poecile gambeli*, can be successful in cities (Kozlovsky et al., 2017). It seems that it is difficult to select one specific trait or a set of traits that explains the ability of urban animals to exploit and thrive in urban environments. At least for the gulls in this study, it seems that their flexibility in habitat use, foraging behaviour and flight strategies are supporting them to adapt to cities.

Human-wildlife conflicts

A better understanding of the ecology, behaviour and demography of urban animals is necessary to mitigate human-wildlife conflicts. Combining proper control measures with adequate education about urban animals might reduce these conflicts. This is especially important with vulnerable species that are considered a pest in urban areas, such as gulls. Media coverage mainly focuses on the negative aspects of urban gulls, reporting on stealing food, raiding bins and aggression towards home-owners (Ellis, 2014; D'Albiac & Gibbons, 2019). However, conservation charities are trying to provide the public with better information about these urban gulls (Ross-Smith, 2019) and some city councils are educating their citizens with booklets about how to live with urban gulls (Aberdeen City Council, 2019). Educating the public is highly important in mitigating conflicts as I have also seen during this study. While conducting field observations at several locations and visiting schools for outreach activities, meeting people and talking about urban gulls and the reasons why they are living in cities, gives people a different perspective on the life and behaviour of these gulls. For example, pupils at schools were more interested in the gulls and saw them less as a nuisance after we told them that consuming food during break times and throwing it away in open bins or on the ground is most likely causing the high number of gulls visiting their school every day.

Besides educating the public, control measures seem to reduce conflicts provided that they are regularly evaluated and checked. This study showed that the gulls made use of a wide variety of terrestrial habitats within but also outside the city, therefore focussing on reducing the accessibility of only one or two locations within the city might not be sufficient. Gulls have been observed to switch to other food sources when specific key foraging locations have been closed (Rock, 2004a; Zorrozua et al., 2018). Therefore, the overall reduction of food waste in the streets, gardens, schools and waste centres might be necessary. I believe that to accomplish this, people and companies have to be educated about separating food waste from their landfill waste, not feeding gulls in the street and properly discarding their food waste. Many cities in the UK have put up signs to warn people not to feed gulls and other animals, however, unfortunately, this does not always work (Clark et al., 2015). Bristol City Council has been placing new smart bins around the city centre which are solar-powered, compact rubbish and send a message when they are full (Wilson, 2019). In comparison to the previous bins, these are closed so gulls cannot access the food inside and can contain more rubbish hopefully resulting in less food waste on the street.

In addition to reducing access to food, preventing gulls from nesting on the roofs is one of the major control measures currently conducted. Netting on rooftops have been placed increasingly in Bristol and could be effective provided that they are well constructed and checked regularly (Rock, 2005). During the nest observations in the breeding season, I have witnessed many gulls and their chicks getting stuck in the netting, some being able to escape but others do not and eventually die. The latter was also the case for two of the tracked individuals in this study which then stopped the collection of the data for these individuals. Animal rescue centres in the UK such as RSPCA are receiving many calls of gulls getting stuck in netting during the breeding season and those are only the ones that are either spotted or saved (RSPCA unpublished data).

This suggests that there is a lot of improvement necessary for both reducing access to food sources and preventing gulls from nesting on roofs and therefore we need more information about gulls and their movement behaviour in cities.

Foraging strategies

By combining both GPS tracking data, acceleration data, and field observations, I was able to quantify the habitat use and foraging behaviour of urban-nesting gulls in more detail than when only using one of the two methods. I discovered that gulls used distinct foraging strategies in different habitats, reflecting the availability of the food sources in the habitats and the strategies to acquire them. Attempting to quantifying foraging behaviour in gulls with these different strategies was difficult and rather complex. Some studies quantify foraging behaviour as instantaneous speeds below a certain threshold (Isaksson et al., 2016; Shaffer et al., 2017), while others quantify foraging behaviour using a method called Expectation-Maximization Binary Clustering (EBMC) which quantifies commuting, foraging, and resting based on speed and turning angle (van Donk et al., 2019b). Although I have considered both methods to quantify foraging, I think these methods overlook an important part of their foraging behaviour, especially while foraging in urban areas. For example, while conducting observations in the centre of Bristol, gulls were flying in a straight line (no turning angle) at medium speed following a road while looking around for food. Some individuals were observed abruptly stopping in flight and diving down to feed on food waste they encountered on the street. This "fly-and-search" behaviour is difficult to distinguish from commuting especially at lower frequency GPS intervals. I do want to note that this behaviour might be specific to gulls foraging in cities as ephemeral food sources seem to be more abundant in cities. The decision to include all the GPS data (outside the nesting areas) in the analysis of habitat use and time-activity budgets was partly based on this observation of different foraging strategies and the difficulty to distinguish exact foraging behaviour based on the GPS tracking and acceleration data. Nevertheless, although there is a need to improve these methods to quantify foraging behaviour more exactly, the combination of both GPS tracking, acceleration data and field observations in this study provided a more detailed insight into the foraging behaviour of gulls in the city.

Energy expenditure

This study looked at the daily and trip energetics of gulls nesting in urban environments. To quantify energy expenditure it is important to be able to understand the effects of a range of intrinsic and extrinsic factors on the birds life-history traits linked to energy expenditure, such as fitness, survival and reproduction. Different methods of quantifying energy expenditure in the field have been widely applied and discussed in several species, including the use of body dynamic acceleration extracted from accelerometers placed on the animal's body (Halsey et al., 2008; Green et al., 2009). Although a promising method due to its practicality, the DBA method is also under dispute because studies need to validate DBA measurement with oxygen consumption for each activity and species (Halsey et al., 2011; Wilson et al., 2020). In gulls, the DBA method has only applied to one study to my knowledge to calculate energy expenditure (Sotillo et al., 2019b) but was not validated against the methods of oxygen consumption and heart rate measurements. Although I could not validate DBA properly, I did compare the DBA measurements with estimations of energy expenditure based on metabolic rate values estimated from oxygen consumption published in the literature. On both the daily and trip level, I found that the two methods were highly comparable. However, a more detailed analysis should follow if this is also the case on a smaller scale. Energy expenditure is often analysed on a daily scale, therefore the DBA method seems to be promising for understanding energy expenditure on a larger scale in gulls.

6.3 Limitations and further directions

This thesis is the first study to my knowledge to track multiple urban-nesting gulls over a period longer than 1 year. Although long-term studies are important to be able to account for variability between years, this study focussed on only one urban colony and one gull species. Urban areas such as cities and towns can differ in size and the resources available, for example, smaller cities might have fewer waste centres surrounding them and less food waste in the streets. Hence, the results found in this study might not apply to other smaller or bigger urban areas in and outside the UK. Nevertheless, the findings of this study provide a good baseline about urban gull movement behaviour in cities to compare with future (currently limited) studies in other urban areas and other urban gulls species. To accommodate this, I created an online discussion forum called "the Urban Gull Network", which will hopefully provide a platform for researchers around the world to share their studies and create local or global collaborations. Additionally, comparisons of movement and foraging behaviour between urban and non-urban gull populations are necessary to understand in more detail why gulls in urban areas are increasing in numbers and gulls in non-urban colonies show the opposite pattern (especially in the UK). Data from gulls nesting in Bristol is now available to compare habitat use, foraging behaviour, trip characteristics and energetics with other populations. Hence, future studies should focus on comparing these datasets to understand in more detail if conditions in cities are providing better chances for survival and reproduction than conditions at non-urban colonies.

Although this study tracked individuals for four years, only 12 individuals were tracked during this period. This number is at the lower end of the sample size required to be a representative of the local population, but it seems that it is better to track fewer birds for longer than more birds for less time (Thaxter et al., 2017). I did find that the tracked individuals in this study exhibited similar temporal patterns in visiting urban feeding grounds in comparison to gulls present at these grounds. This suggests that the foraging behaviour of the tracked individuals seem to reflect the general foraging behaviour of gulls in Bristol. Another consequence of the smaller sample size was that only two of the 12 individuals in this study were male. Non-urban gulls have shown differences between sexes in foraging behaviour (Camphuysen et al., 2015) and migration strategies (Baert et al., 2018), therefore it could have been that our general conclusions were more biased towards female preferences than an average urban-nesting gull. Due to the limited sample size of male gulls, I was not able to analyse differences in behaviour between the sexes in this study. Additionally, individual differences might have biased general conclusions. Studies in non-urban gull populations have shown that these populations exhibit individual differences in habitat use (Navarro et al., 2017), foraging behaviour (Tyson et al., 2015; Sotillo et al., 2019b; van Donk et al., 2019a) and migration strategies (Shamoun-Baranes et al., 2017a). Indeed, I also observed differences in habitat use with some individuals using almost exclusively suburban and urban areas and other individuals mainly using agricultural lands. However, I did not explore these individual differences in detail as this was out of the scope of the thesis. The long-term GPS dataset created by this project provides an opportunity for future research to analyse individual differences within and between several years.

In this study, I analysed how habitat, time and weather affected movement and behaviour in urban-nesting gulls. However, other factors that I have not considered might have played a role. For example, I assumed that urban habitats were highly predictable in the availability of food sources, however, this was not quantified during this study. Gulls were able to match their foraging schedule to temporal predictable natural and anthropogenic food sources in three habitat types, however, this might be similar for other habitats. There is a need to quantify food predictability both temporally and spatially in habitats commonly used by gulls such as agricultural lands (ploughing schedule), waste centres (opening times), schools (opening times), streets (e.g. waste collection days), and gardens (e.g. feeding birds). Some studies have looked at the temporal and spatial availability of a subset of these anthropogenic food sources (Sibly & McCleery, 1983b; Coulson & Coulson, 2008; Schwemmer et al., 2008; Yoda et al., 2012), but combining all would give a complete overview and provide better insight into how gulls are using these different predictable food sources. Combining this knowledge with high-resolution GPS tracking data could then be used to further investigate if gulls are tracking both the temporal and spatial availability of food sources. I found that food sources at the three observed habitats were available at different times of the day, therefore the gulls might optimise their use of different habitats by tracking their availabilities in a single day, instead of specialising in one specific habitat and food source. The gulls in Bristol performed on average 3 trips per day but up to 10 per day, suggesting they might use different habitats at different times of the day. More detailed analysis of the GPS tracking data is required to quantify how gulls are able to track availabilities of food sources in time and space.

In general, the use of habitats by an animal is likely to reflect the trade-off between the costs and benefits of acquiring food sources in these habitats. In this study, I only looked at one side of this trade-off when analysing the energy costs under different weather conditions. This analysis of energy costs can be improved to look at a smaller scale and by calibrating and validating the method of estimating energy expenditure based on dynamic body acceleration with oxygen consumption and heart rate loggers. However, to understand the trade-off between costs and benefits, both energy costs and energy intake need to be considered. Energy intake can be quantified by several methods, such as visual observations, diet samples and stable isotope analysis from feathers (Weiser & Powell, 2011). However, in the current study, the nesting areas in Bristol had limited access possibilities and therefore additional data about energy intake based on diet or feather samples could not be collected. Combining energy intake data from diet and stable isotope samples with movement data from GPS tracking is necessary to understand the complex trade-off between costs and benefits of different habitats used by animals.

This study analysed the general habitat use to understand how gulls utilised the urban environment. Other methods exist to analyse habitat use such as several home-range analyses and resource selection functions (RSF) (Manly et al., 2007). The use of resources by an animal is dependent on the resources available in the surrounding environment and is especially limited during the breeding season when gulls are central-place foragers. Therefore, methods which incorporate this resource availability might be useful when comparing habitat use between individuals, colonies or populations in future studies. Additionally, classical analysis methods in movement ecology are based on the discrete-time random walks which turns continuous animal travelling paths into discrete steps and turns with the animal hopping in between. These methods have several disadvantages such as dependency on the sample interval, limited ability to model autocorrelation and likelihood to wrongly estimate movement speed and travel distance (Fleming et al., 2015). Recently, a continuous-time movement models (CTMM) have been applied to movement data which are able to deal with and/or correct for autocorrelated data, irregular sampling regimes and GPS errors in location amongst other advantages (Fleming et al., 2015; Calabrese et al., 2016). Although this is a promising technique, it has been mainly applied to terrestrial animals or flying animals outside the breeding season. This method has not yet been optimised to account for central-place foragers such as gulls and therefore my attempts to use these models for habitat use and trip characteristics were not successful. Futures studies should focus on applying, improving and extending these promising models for central-place foragers.

6.4 Concluding remarks

The present study provides important findings on the general movement behaviour of urban-nesting gulls, expanding our knowledge about how the behavioural flexibility of these birds seems to allow them to be successful in cities. It seems likely that other urban animals behave in a similar way, using a wide variety of resources within and surrounding cities, and profiting from the predictability and abundant availability of anthropogenic food sources. With urbanisation increasing, the number of urban animals will increase, resulting in a higher numbers of human-wildlife conflicts. It is important to mitigate these conflicts, and it is suggested this could be possible with a combination of education of the public and proper control measures, however these measure can only be successful with a better/complete understanding of the ecology, behaviour and demographics of several, if not most, urban animals. However, as natural habitats for many species will keep reducing, we should also focus on finding ways to co-exist with these animals in our cities.

APPENDIX A

APPENDIX

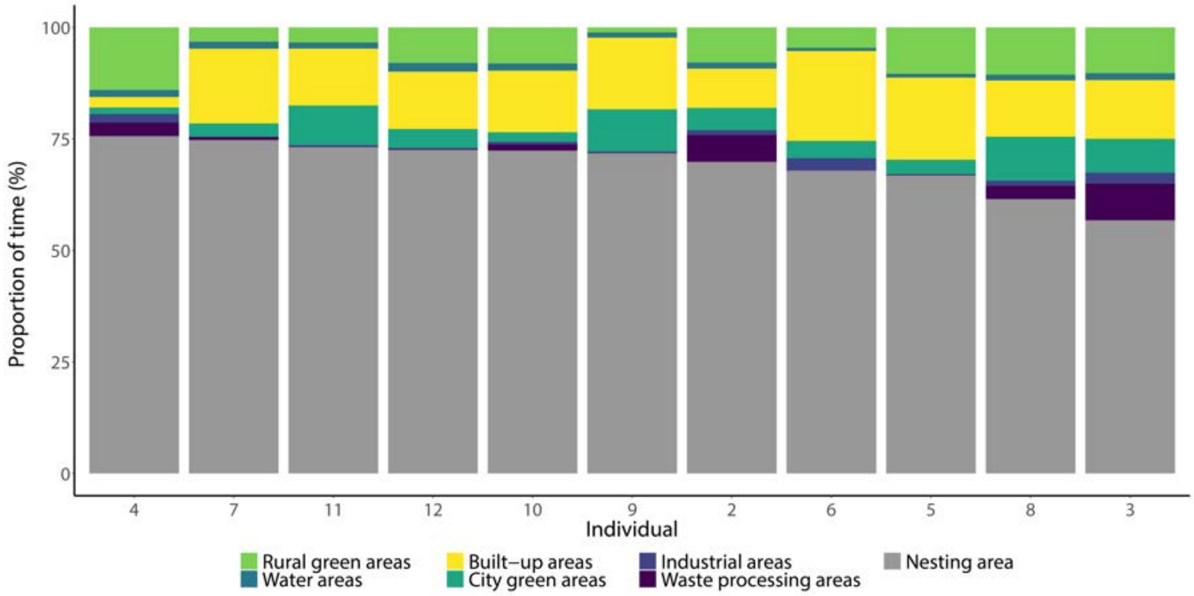

Figure A.1: The mean proportion of time spent in seven different habitats by individual urban-nesting gulls in Bristol during three breeding seasons (2016-2018). Individuals are shown from left to right in descending order of proportion of time spent in the nesting area. The data of individual 1 is not included because it was excluded from this study.

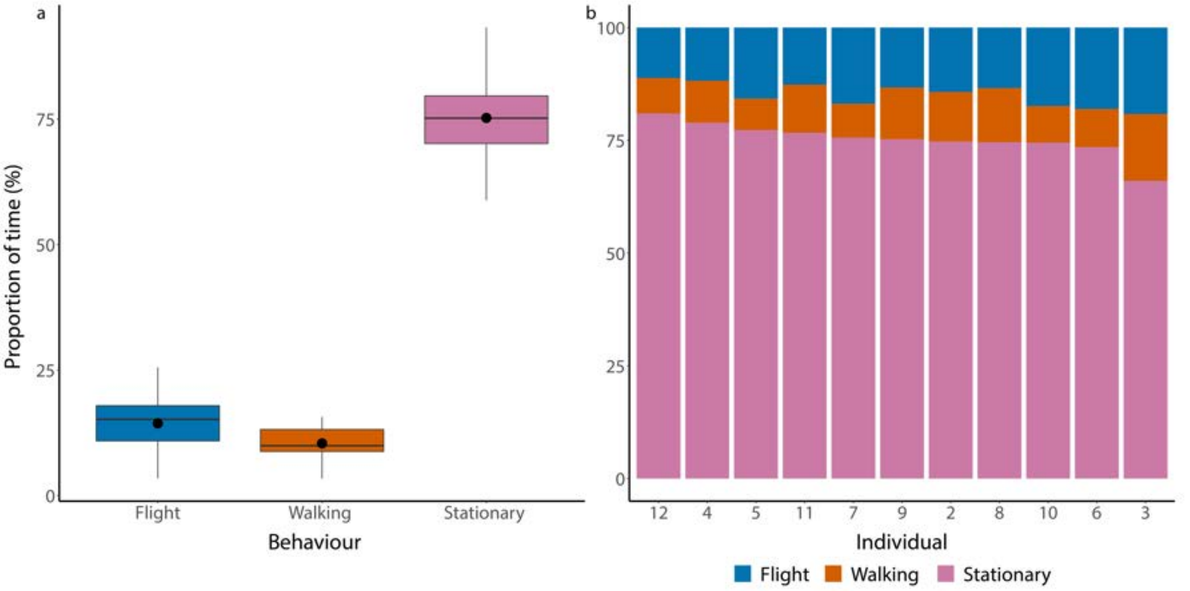

Figure A.2: Mean proportion of time spent on each of the three behaviour types during three breeding seasons (2016-2018). a) Mean over the whole breeding season. b) Mean per individual. The boxplots show the 25%, 50% and 75% quantiles, the upper and lower whiskers are the largest and lowest value up to 1.5 * inter-quartile range (IQR), and the grey points are data outside 1.5 * IQR.

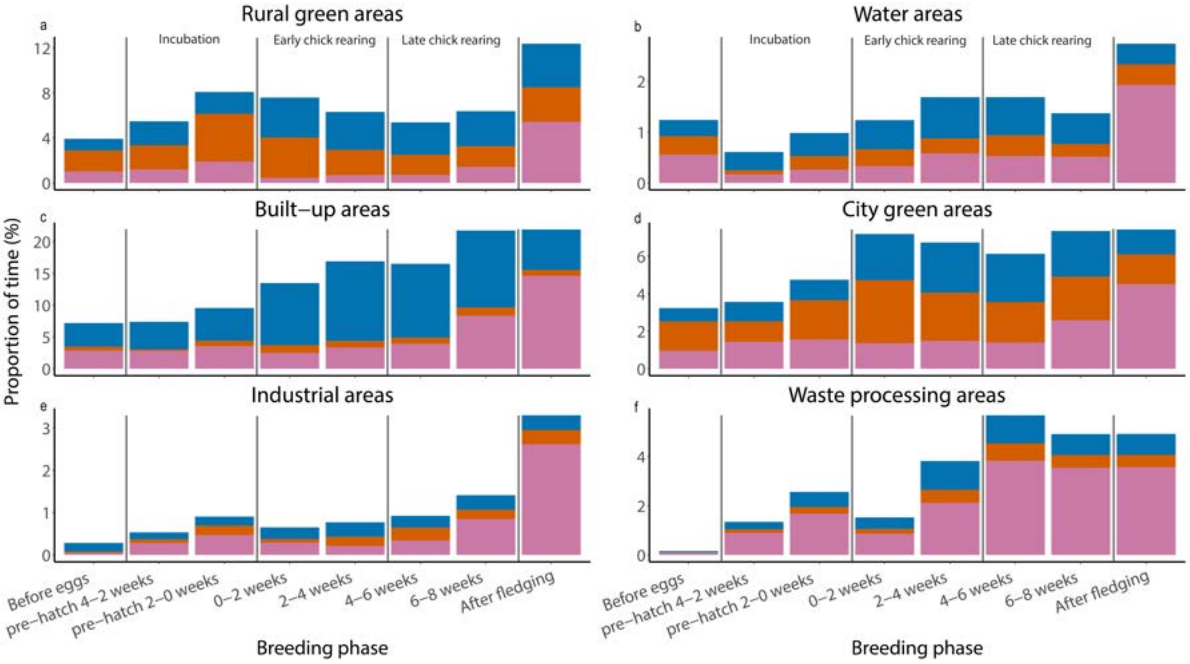

Figure A.3: Mean proportion of time spent on each of the three behaviour types depending on breeding stage for the six habitats when away from the nesting area. a) Rural green areas. b) Water areas. c) Built-up areas. d) City green areas. e) Industrial areas. f) Waste processing areas.

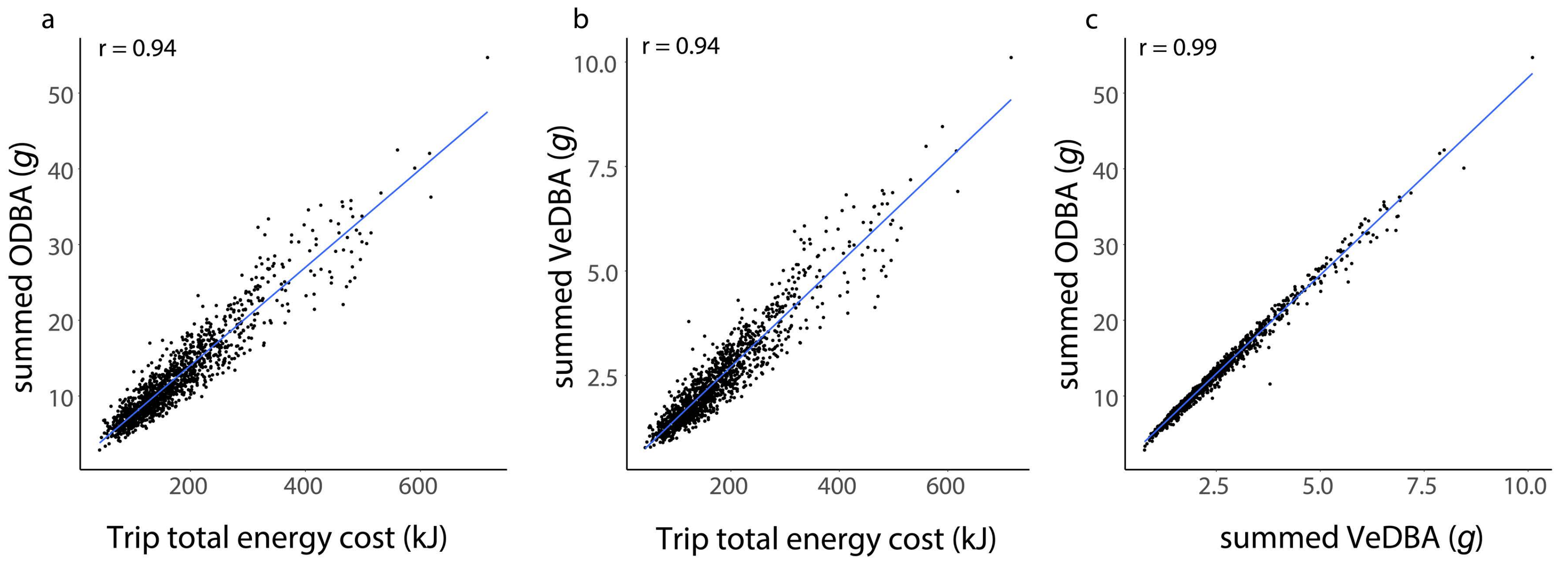

Figure A.4: Comparison between different methods to calculate total trip energy expenditure: trip summed overall dynamic body acceleration (ODBA), trip summed vectorial dynamic body acceleration (VeDBA) and total trip energy cost based on metabolic rate estimations from previous studies. A linear regression line with confidence interval has been plotted to show the correlation.

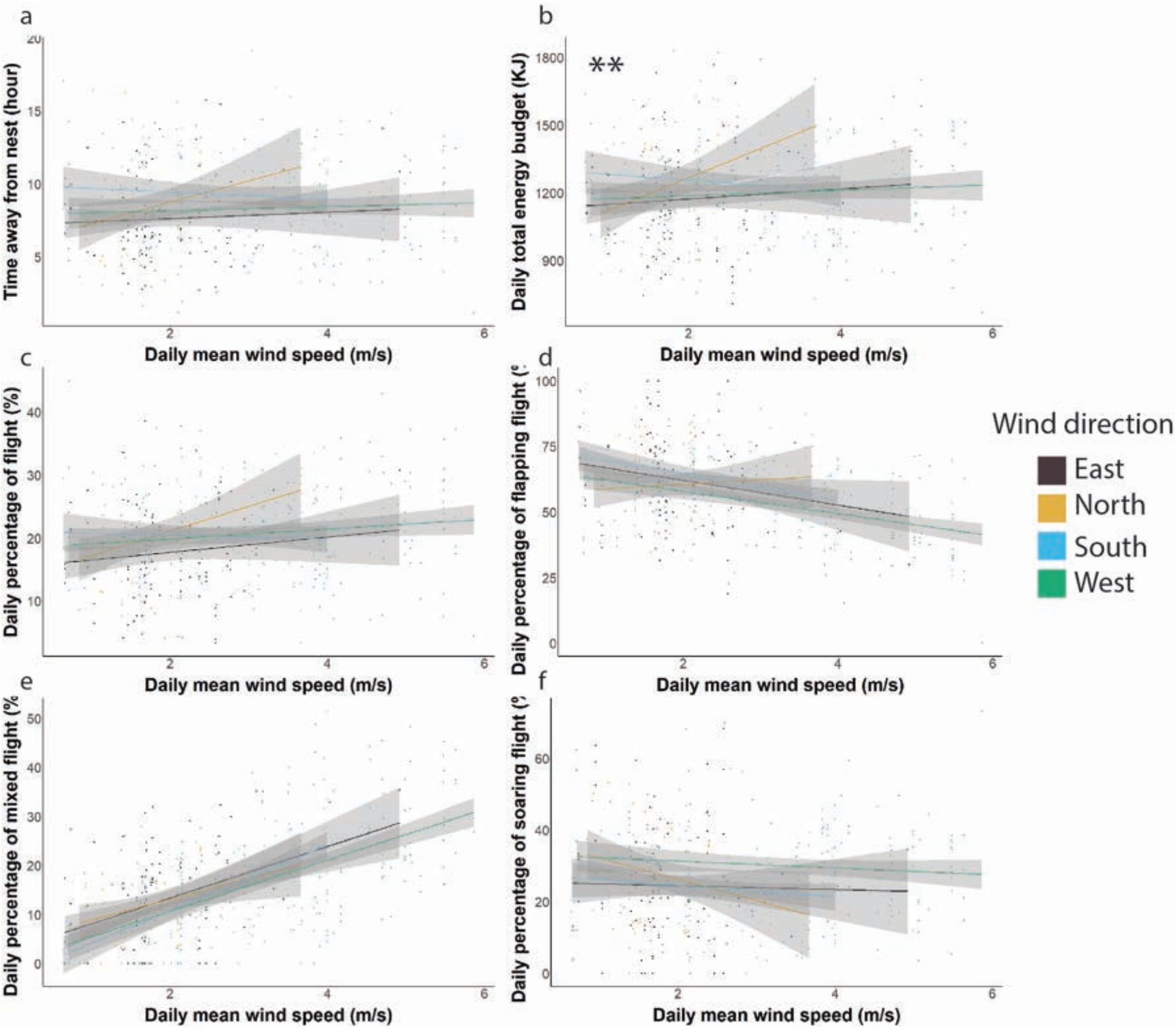

Figure A.5: Interaction between daily mean wind speed (m/s) and wind direction for daily response variables: a) Time spent away from the nest (h), b) daily total energy cost (kJ), c) percentage in flight (%), d) percentage flapping in flight (%), e) percentage mixed flight in flight (%) and f) percentage soaring in flight (%). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

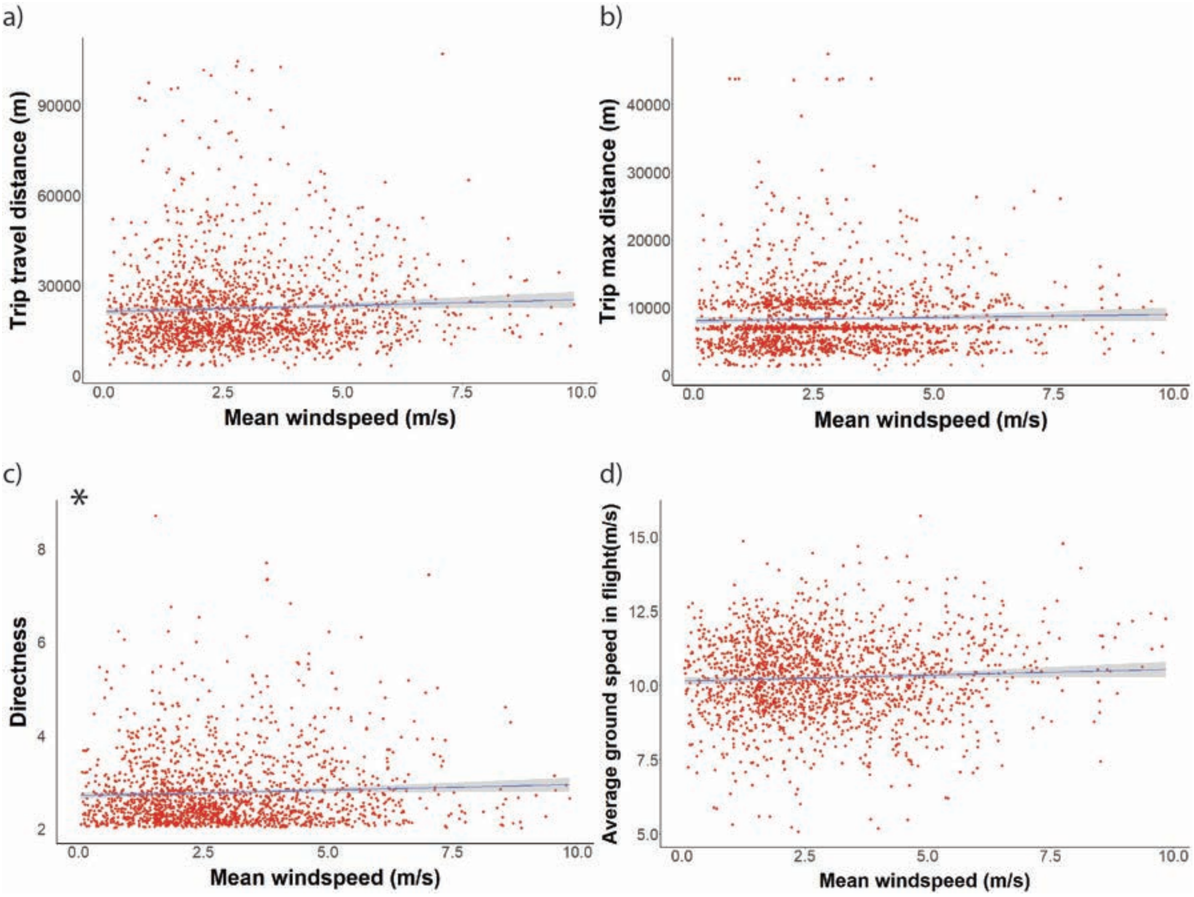

Figure A.6: The trip characteristics in relation to mean wind speed (m/s). a) trip travel distance (m), b) trip maximum distance (m), directness of trip, and mean ground speed in flight (m/s). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

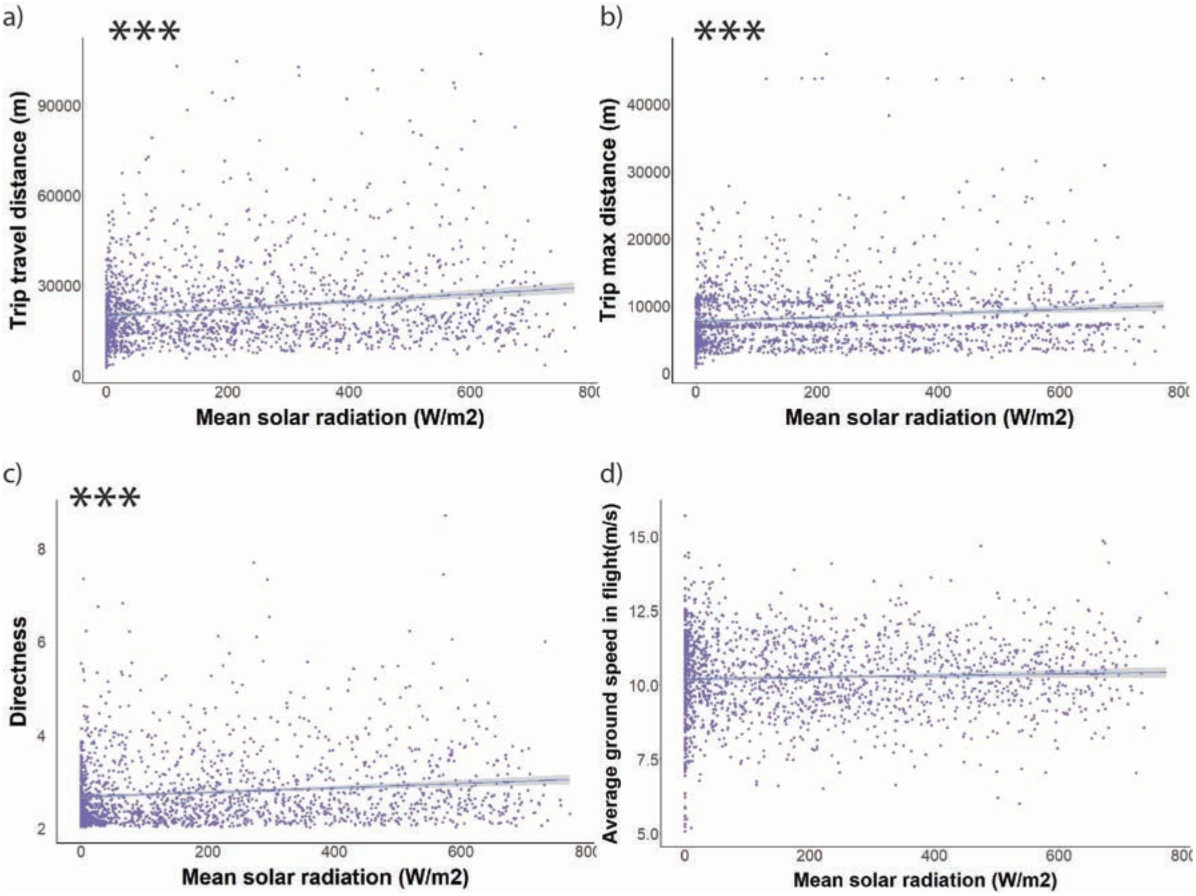

Figure A.7: The trip characteristics in relation to mean solar radiation (W/m^2). a) trip travel distance (m), b) trip maximum distance (m), directness of trip, and mean ground speed in flight (m/s). Stars represent significant variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

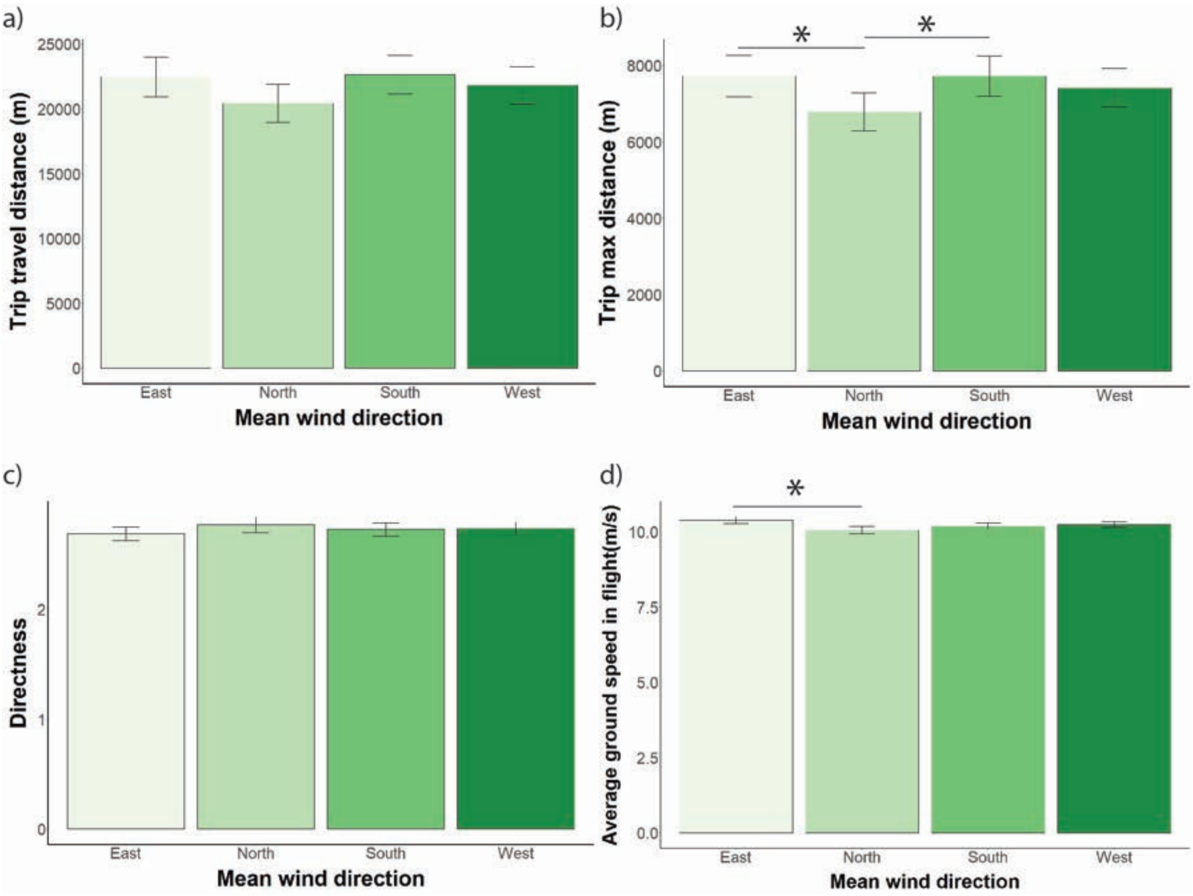

Figure A.8: The trip characteristics in relation to mean wind direction. a) trip travel distance (m), b) trip maximum distance (m), directness of trip, and mean ground speed in flight (m/s). Estimated marginal means ± standard errors are presented. Stars represent significant difference between groups. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

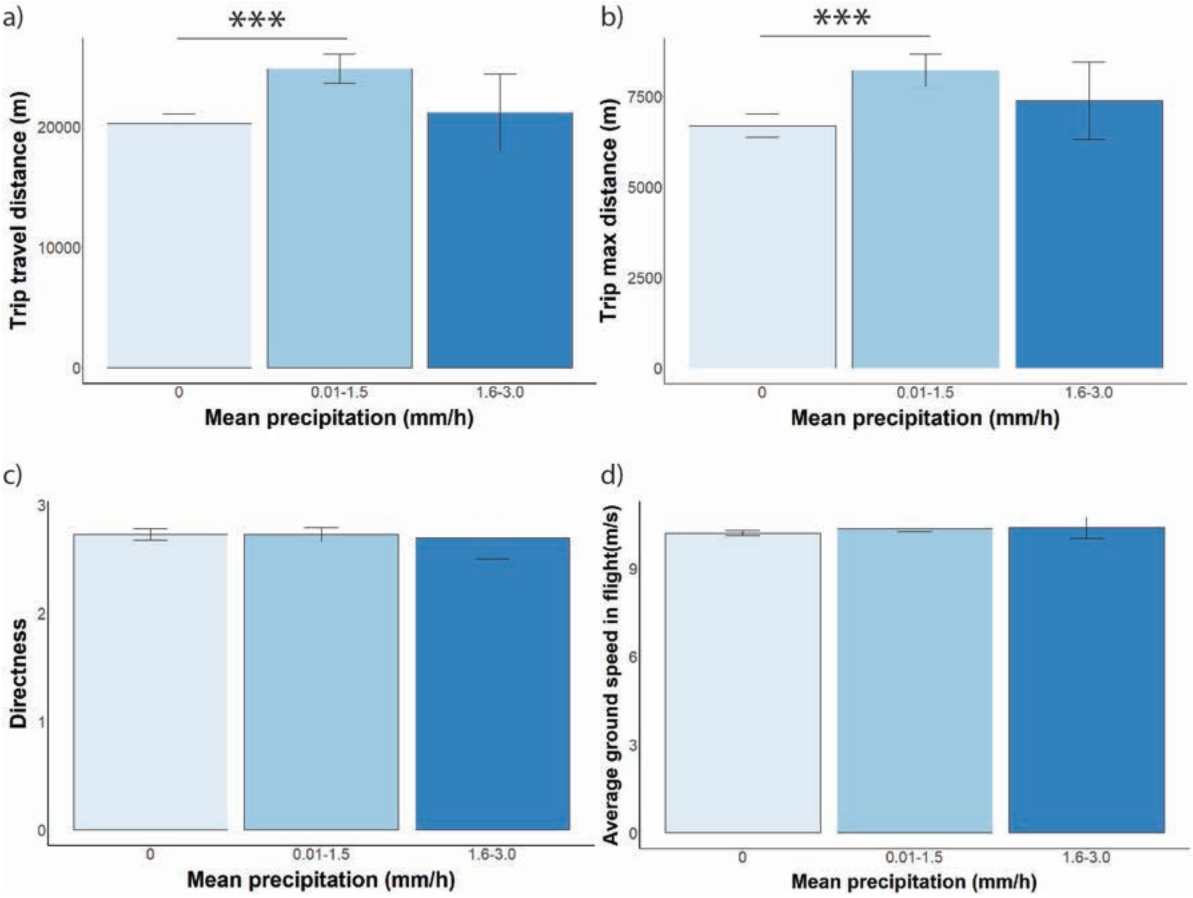

Figure A.9: The trip characteristics in relation to mean precipitation rate (mm/h). a) trip travel distance (m), b) trip maximum distance (m), directness of trip, and mean ground speed in flight (m/s). Estimated marginal means ± standard errors are presented. Stars represent significant difference between groups. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, · $p < 0.1$.

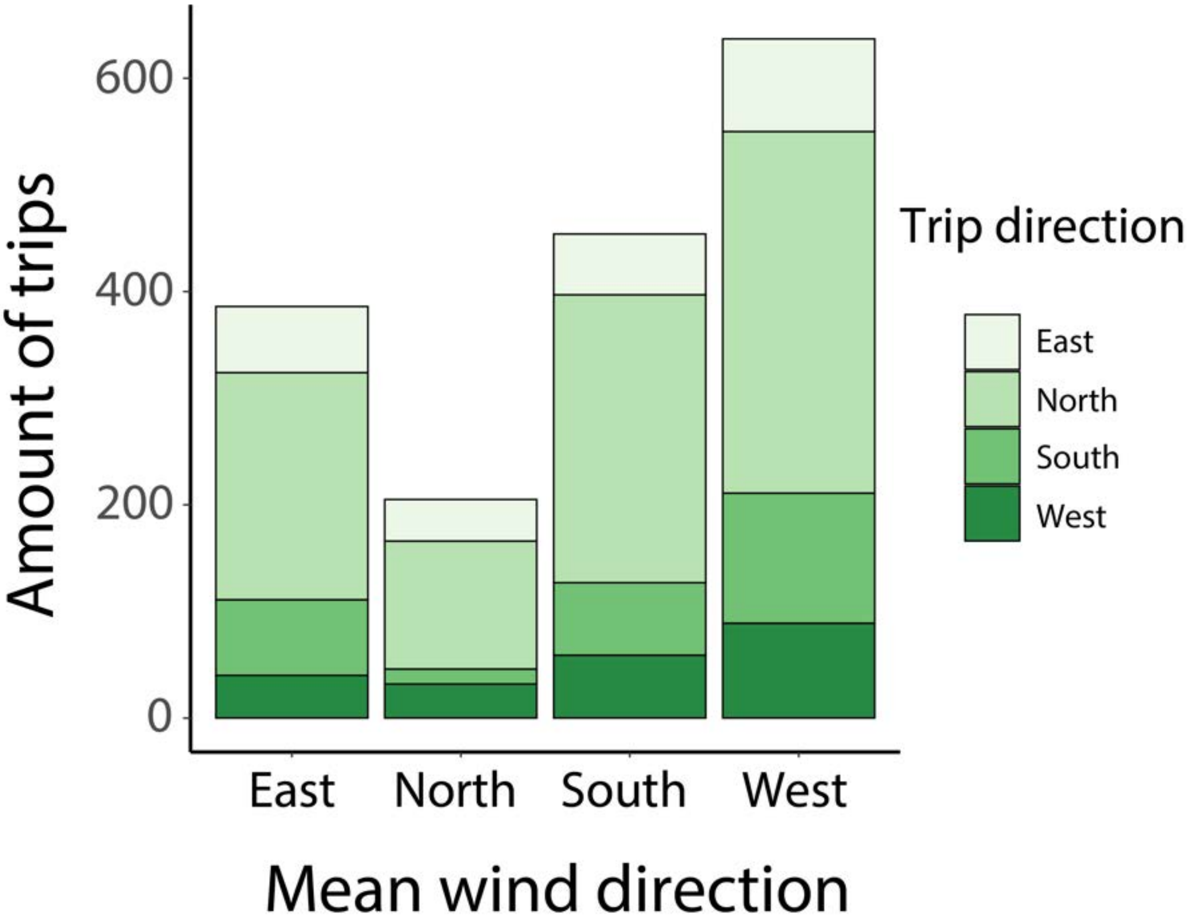

Figure A.10: Number of trips in a specific (initial direction) compared to the mean wind direction during that trip.

Table A.1: Overview of the Akaike Information Criterion adjusted for small sample sizes (AICc) for the models in chapter 4. The models are 1) the number of gulls at the park, 2) the number of gulls at the school, 3) the number of gulls at the waste centre, and 4) the percentage of gulls on the pile at the waste centre. H = total number of humans, F = presence of food, W = day of the week, AL = activity level, U = time since unloading waste, X∗X = interaction between two variables, s(T) = time as a smooth term, df = degrees of freedom, dAICc = difference in AICc between best-fitted model and other models.

Model		**H**	**F**	**W**	**AL**	**U**	**H∗F**	**H∗W**	**s(T)**	**s(T∗W)**	**df**	**AICc**	**dAICc**
1	Park	x							x		14	461	0
		x	x						x		15	461	0
		x		x					x		15	461	0
		x			x				x		16	461	0
		x						x	x		16	461	0
									x		12	487	27
											2	586	126
2	School	x	x					x	x		18	1634	0
		x	x					x	x	x	19	1634	0
		x	x				x	x	x		19	1636	2
		x	x	x					x		17	1680	46
		x	x						x		16	1680	46
		x							x		16	1685	51
									x		15	1720	86
											8	1879	246
3	Waste centre			x					x	x	20	3296	0
				x	x				x		13	3409	113
				x					x		13	3409	113
									x		16	3414	118
											8	3496	200
4	Waste centre			x	x	x					13	7044	0
				x	x						7	7272	228
				x							4	8867	1823
											3	8879	1836

Table A.2: β-coefficients of the categorical explanatory terms included to model the percentage of gulls on the pile at the waste centre: waste-related activity level and time since waste unload. Reference level for waste-related activity is the activity level "0" and for time since waste unload is the level "0-15 min".

Explanatory term	**Category**	**β-coefficient**
Waste-related activity level	1	-0.12 ± 0.03
	2	-0.89 ± 0.03
	3	-1.07 ± 0.03
Time since waste unload (min)	15-30	0.31 ± 0.05
	30-45	0.03 ± 0.04
	45-60	0.08 ± 0.06
	60-75	-0.25 ± 0.07
	75-90	0.05 ± 0.06
	>90	-0.17 ± 0.03

Table A.3: Overview of the Akaike Information Criterion adjusted for small sample sizes (AICc) for the *daily* models in chapter 5. SR = mean daily solar radiation, WS = mean daily wind speed, WD = mean daily wind direction, PR = mean daily precipitation rate, WS*WD = interaction term between wind speed and direction, df = degrees of freedom, dAICc = difference in AICc between best-fitting model and other models.

Model	**Response**	**SR**	**WS**	**WD**	**PR**	**WS*WD**	**df**	**AICc**	**dAICc**
1	Time away from nest (h)			x	x		7	2016	0
					x		4	2017	1
			x		x		5	2018	2
		x			x		5	2019	3
					x	x	8	2020	4
							3	2020	4
2	Total daily energy cost (kJ)			x		x	11	5747	0
			x	x			8	5752	5
				x			7	5752	5
				x	x		8	5753	6
		x		x			8	5753	6
							4	5753	6
3	% in flight		x				4	1706	0
		x	x				5	1706	0
			x		x		5	1707	1
			x			x	7	1708	2
			x	x			7	1709	3
							3	1712	6
4	% flapping in flight	x	x		x		7	4291	0
		x	x		x		6	4294	3
			x	x			10	4296	5
		x	x		x	x	10	4297	6
			x				5	4349	58
							4	4393	102
5	% mixed in flight		x	x			9	3715	0
			x	x		x	12	3716	1
			x				6	3820	5
			x		x		7	3721	6
		x	x				7	3722	7
							5	3786	71
6	% soaring in flight	x			x		7	4080	0
		x	x		x		8	4081	1
		x		x	x		10	4085	5
		x					6	4085	5
		x			x	x	11	4086	6
							5	4154	74

Table A.4: Overview of the Akaike Information Criterion adjusted for small sample sizes (AICc) for the *trip* models in chapter 5. SR = mean daily solar radiation, WS = mean daily wind speed, WD = mean daily wind direction, PR = mean daily precipitation rate, WS*WD = interaction term between wind speed and direction, df = degrees of freedom, dAICc = difference in AICc between best-fitting model and other models.

Model	**Response**	**SR**	**WS**	**WD**	**RC**	**WS*WD**	**df**	**AICc**	**dAICc**
1	Trip duration	X	X		X		7	18551	0
		X	X	X	X		10	18554	3
		X	X		X	X	10	18554	3
		X			X		6	18556	5
		X					4	18570	19
							3	18590	39
2	Trip energy budget	X			X		6	2172	0
		X		X	X		9	2174	2
		X	X		X		7	2174	2
		X			X	X	10	2175	3
		X					4	2194	22
							3	2244	72
3	Energy budget per hour	X	X				5	15926	0
		X	X	X			8	15926	0
		X	X		X		7	15928	2
		X	X			X	8	15932	6
		X					4	15946	20
							3	15967	41
4	Energy budget per distance	X		X	X		9	9046	0
		X		X	X	X	10	9048	2
		X	X		X		7	9050	3
		X			X		6	9050	3
		X					4	9061	15
							3	9087	41
5	% in flight	X	X	X			8	16003	0
		X	X	X		X	11	16006	3
		X	X				5	16008	5
		X	X		X		7	16012	9
		X					4	16094	91
							3	16440	437
6	% flapping in flight	X	X	X	X		10	13297	0
		X	X	X	X	X	13	13297	0
		X	X		X		7	13315	18
		X	X				5	13321	24
		X					4	13591	294
							3	14137	840

Table A.4: Overview of the Akaike Information Criterion adjusted for small sample sizes (AICc) for the *trip* models in chapter 5. SR = mean daily solar radiation, WS = mean daily wind speed, WD = mean daily wind direction, PR = mean daily precipitation rate, WS*WD = interaction term between wind speed and direction, df = degrees of freedom, dAICc = difference in AICc between best-fitting model and other models.

Model	**Response**	**SR**	**WS**	**WD**	**RC**	**WS*WD**	**df**	**AICc**	**dAICc**
7	% mixed in flight	X	X	X			9	9920	0
		X	X	X		X	12	9921	1
		X	X				6	9981	61
		X	X		X		8	9985	65
		X					5	10465	545
							4	10474	554
8	% soaring in flight	X			X		7	11328	0
		X			X	X	11	11329	1
		X		X	X		10	11332	3
		X	X				6	11340	12
		X					5	11341	13
							4	11802	474
9	Travel distance	X			X		6	38336	0
		X		X	X		9	38336	0
		X			X	X	10	38341	5
		X					4	38365	29
		X	X				5	38366	30
							3	38440	104
10	Max distance	X		X	X		9	33421	0
		X		X	X	X	13	33424	3
		X			X		6	33426	5
		X	X				5	33459	38
		X					4	33459	38
							3	33490	69
11	Mean speed in flight			X			7	5944	0
			X	X			6	5944	0
				X	X		8	5946	2
		X		X			7	5946	2
							3	5948	4
				X		X	10	5949	5
12	Directness	X	X				5	11519	0
		X					4	11521	2
		X	X	X			8	11523	4
		X	X		X		7	11523	4
		X	X			X	8	11523	4
							3	11552	33

Table A.5: Overview of flight characteristics per bird-year combination during the early chick-rearing stage and excluding the nesting area. Soar = soaring flight, mixed = mixed flight, flap = flapping flight, exflap = extreme flapping flight. Both the percentages of total flight behaviours as well as the percentages of the flight behaviours when in flight are presented. Individual 1 has been excluded from this dataset due to the limited sample size collected for this individual.

Bird-year	**n**	**% flight**	**% soar**	**% mixed**	**% flap**	**% exflap**	**% soar in flight**	**% mixed in flight**	**% flap in flight**	**% exflap in flight**
2_2016	1427	53.3	13.0	6.3	32.7	1.4	24.3	11.8	61.2	2.6
2_2017	304	59.2	18.1	10.9	28.3	2.0	30.6	18.3	47.8	3.3
2_2018	1062	54.4	14.0	10.8	27.4	2.2	25.8	19.9	50.3	4.0
2_2019	1561	47.5	9.4	8.4	28.3	1.5	19.8	17.7	59.4	3.1
3_2016	1772	52.0	19.5	4.5	26.8	1.2	37.5	8.6	51.5	2.4
3_2017	1757	49.1	18.1	7.2	22.3	1.5	36.9	14.6	45.5	3.0
3_2018	1864	51.7	17.7	9.7	23.0	1.3	34.1	18.8	44.5	2.6
3_2019	2041	46.0	13.7	7.4	23.8	1.0	29.9	16.2	51.7	2.2
4_2019	234	54.7	10.3	12.8	29.5	2.1	18.8	23.4	53.9	3.9
5_2016	233	47.2	9.0	5.6	30.9	1.7	19.1	11.8	65.5	3.6
6_2018	681	55.4	13.1	15.4	26.0	0.9	23.6	27.9	46.9	1.6
7_2017	1626	57.4	17.2	7.4	31.5	1.2	30.0	13.0	54.9	2.1
8_2017	1028	58.4	9.7	10.3	37.6	0.7	16.7	17.7	64.5	1.2
8_2018	1006	66.0	11.3	10.7	42.3	1.6	17.2	16.3	64.2	2.4
9_2017	1541	44.8	18.2	5.3	20.6	0.8	40.6	11.7	45.9	1.7
10_2017	1203	50.6	14.0	9.6	26.4	0.6	27.6	19.0	52.2	1.1
10_2018	1270	50.7	12.6	7.7	29.1	1.3	24.8	15.2	57.3	2.6
10_2019	1248	51.3	10.6	10.3	29.2	1.3	20.6	20.0	56.9	2.5
11_2018	1220	65.6	16.8	10.7	37.2	0.9	25.6	16.3	56.8	1.4
12_2017	919	63.9	18.4	13.6	31.6	0.3	28.8	21.3	49.4	0.5
12_2018	1311	63.5	11.3	15.6	35.1	1.6	17.8	24.5	55.2	2.5
12_2019	1163	55.7	8.7	10.9	35.3	0.9	15.6	19.6	63.3	1.5
	Mean	**54.5**	**13.8**	**9.6**	**29.8**	**1.3**	**25.7**	**17.4**	**54.5**	**2.4**
	Range	**44.8-66.0**	**8.7-19.5**	**4.5-15.6**	**20.6-42.3**	**0.3-2.2**	**15.6-40.6**	**8.6-27.9**	**44.5-65.5**	**0.5-4.0**

BIBLIOGRAPHY

Aberdeen City Council (2019). Survivors guide: Living with urban gulls. Accessible by: www.aberdeencity.gov.uk/.

Agostinelli, C., & Lund, U. (2017). *R package `circular`: Circular Statistics (version 0.4-93)*. CA: Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University, Venice, Italy. UL: Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA. Accessible by: r-forge.r-project.org/projects/circular/.

Ákos, Z., Nagy, M., Leven, S., & Vicsek, T. (2010). Thermal soaring flight of birds and unmanned aerial vehicles. *Bioinspiration & biomimetics*, *5*(4), 045003.

Alerstam, T., Bäckman, J., & Evans, T. J. (2019). Optimal central place foraging flights in relation to wind. *Journal of Ornithology*, *160*(4), 1065–1076.

Alerstam, T., & Hedenström, A. (1998). The development of bird migration theory. *Journal of Avian Biology*, *December*, 343–369.

Amélineau, F., Péron, C., Lescroël, A., Authier, M., Provost, P., & Grémillet, D. (2014). Windscape and tortuosity shape the flight costs of Northern gannets. *The Journal of experimental biology*, *217*(6), 876–85.

Anderson, D. J., Huyvaert, K. P., Wood, D. R., Gillikin, C. L., Frost, B. J., & Mouritsen, H. (2003). At-sea distribution of waved albatrosses and the Galapagos Marine Reserve. *Biological Conservation*, *110*(3), 367–373.

Andrén, H., Delin, A., & Seiler, A. (1997). Population response to landscape changes depends on specialization to different landscape elements. *Oikos*, *80*(1), 193–196.

Annett, C., & Pierotti, R. (1989). Chick hatching as a trigger for dietary switching in the Western Gull. *Colonial Waterbirds*, *January*, 4–11.

Annett, C. A., & Pierotti, R. (1999). Long-term reproductive output in western gulls: Consequences of alternate tactics in diet choice. *Ecology*, *80*(1), 288–297.

Arnfield, A. J. (2003). Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. *International Journal of Climatology: a Journal of the Royal Meteorological Society*, *23*(1), 1–26.

Auman, H. J., Meathrel, C. E., & Richardson, A. (2008). Supersize me: does anthropogenic food change the body condition of Silver Gulls? A comparison between urbanized and remote, non-urbanized areas. *Waterbirds*, *31*(1), 122–126.

Baert, J. M., Stienen, E. W., Heylen, B. C., Kavelaars, M. M., Buijs, R.-J., Shamoun-Baranes, J., Lens, L., & Müller, W. (2018). High-resolution GPS tracking reveals sex differences in migratory behaviour and stopover habitat use in the lesser black-backed gull *Larus fuscus*. *Scientific reports*, *8*(1), 5391.

Baker, P. J., Funk, S. M., Harris, S., & White, P. C. (2000). Flexible spatial organization of urban foxes, *Vulpes vulpes*, before and during an outbreak of sarcoptic mange. *Animal Behaviour*, *59*(1), 127–146.

Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., & Stone, G. N. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1803), 20142849.

Balmer, D. E., Gillings, S., Caffrey, B., Swann, R. L., Downie, I. S., & Fuller, R. J. (2013). *Bird Atlas 2007-11: the breeding and wintering birds of Britain and Ireland*. BTO Thetford.

Barron, D. G., Brawn, J. D., & Weatherhead, P. J. (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution*, *1*(2), 180–187.

Bartumeus, F., Giuggioli, L., Louzao, M., Bretagnolle, V., Oro, D., & Levin, S. A. (2010). Fishery discards impact on seabird movement patterns at regional scales. *Current Biology*, *20*(3), 215–222.

Bateman, P. W., & Fleming, P. A. (2012). Big city life: carnivores in urban environments. *Journal of Zoology*, *287*(1), 1–23.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Baudinette, R., & Schmidt-Nielsen, K. (1974). Energy cost of gliding flight in herring gulls. *Nature*, *248*(5443), 83–84.

Bautista, L. M., Tinbergen, J., Wiersma, P., & Kacelnik, A. (1998). Optimal foraging and beyond: how starlings cope with changes in food availability. *The American Naturalist*, *152*(4), 543–561.

Baxter, A. T., & Robinson, A. P. (2007). A comparison of scavenging bird deterrence techniques at UK landfill sites. *International Journal of Pest Management*, *53*(4), 347–356.

BBC (2018). Endangered birds - miserable deaths - in newcastle netting. Accessible by: www.bbc.co.uk/news/uk-england-tyne-45007207.

Beckmann, J. P., & Lackey, C. W. (2008). Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Human-Wildlife Conflicts*, *2*(2), 168–174.

Belant, J. L. (1993). Nest-site selection and reproductive biology of roof- and island-nesting herring gulls. *Trans North American Wildlife Nature Resource Conference*, *58*, 78–86.

Belant, J. L. (1997). Gulls in urban environments: Landscape-level management to reduce conflict. *Landscape and Urban Planning*, *38*(3-4), 245–258.

Belant, J. L., & Ickes, S. K. (1996). Overhead wires reduce roof-nesting by ring-billed gulls and herring gulls. In *Proceedings of the Vertebrate Pest conference*, vol. 17.

Belant, J. L., Ickes, S. K., & Seamans, T. W. (1998). Importance of landfills to urban-nesting herring and ring-billed gulls. *Landscape and Urban Planning*, *43*(1-3), 11–19.

Belant, J. L., Seamans, T. W., Gabrey, S. W., & Dolbeer, R. A. (1995). Abundance of gulls and other birds at landfills in northern Ohio. *American Midland Naturalist*, *July*, 30–40.

Belant, J. L., Seamans, T. W., Gabrey, S. W., & Ickes, S. K. (1993). Importance of landfills to nesting herring gulls. *Condor*, *95*(4), 817–830.

Bell, J. (1991). *Searching Behaviour: the Behavioural Ecology of Finding Resources.*. London: Chapman and Hall, London.

Bertellotti, M., & Yorio, P. (1999). Spatial and temporal patterns in the diet of the Kelp Gull in Patagonia. *Condor*, *NA*, 790–798.

Blair, R. B. (1996). Land use and avian species diversity along an urban gradient. *Ecological applications*, *6*(2), 506–519.

Blair, R. B. (2001). Creating a homogeneous avifauna. In *Avian ecology and conservation in an urbanizing world*, (pp. 459–486). Springer.

Blight, L. K., Bertram, D. F., & Kroc, E. (2019). Evaluating UAV-based techniques to census an urban-nesting gull population on Canada's Pacific coast. *Journal of Unmanned Vehicle Systems*, *7*(4), 312–324.

Blokpoel, H., Weller, W. F., Tessier, G. D., & Smith, B. (1990). Roof-nesting by Ring-billed Gulls and Herring Gulls in Ontario in 1989. *Ontario birds*.

Borges, C. A., Cardozo, M. V., Beraldo, L. G., Oliveira, E. S., Maluta, R. P., Barboza, K. B., Werther, K., & Ávila, F. A. (2017). Wild birds and urban pigeons as reservoirs for diarrheagenic *Escherichia coli* with zoonotic potential. *Journal of Microbiology*, *55*(5), 344–348.

Bouten, W., Baaij, E. W., Shamoun-Baranes, J., & Camphuysen, K. C. J. (2013). A flexible GPS tracking system for studying bird behaviour at multiple scales. *Journal of Ornithology*, *154*(2), 571–580.

Bristol City Council (2017). Allotment sites. Accessible by: www.data.gov.uk.

Bristol City Council (2019a). Parks and green spaces. Accessible by: www.data.gov.uk.

Bristol City Council (2019b). The population of Bristol. Accessible by: www.bristol.gov.uk.

Brousseau, P., Lefebvre, J., & Giroux, J.-F. (1996). Diet of ring-billed gull chicks in urban and non-urban colonies in quebec. *Colonial Waterbirds*, (pp. 22–30).

Brown, J., Gillooly, J., Allen, A., Savage, V., & West, G. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789.

Bryant, D., & Furness, R. (1995). Basal metabolic rates of north atlantic seabirds. *Ibis*, *137*(2), 219–226.

Buckley, P. A., & McCarthy, M. G. (1994). Insects, vegetation, and the control of laughing gulls (*Larus atricilla*) at Kennedy International Airport, New York City. *Journal of Applied Ecology*, *May*, 291–302.

Butler, P., Green, J., Boyd, I., & Speakman, J. (2004). Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology*, *18*, 168–183.

Cadiou, B. (1999). Attendance off breeders and prospectors reflects the quality off colonies in the kittiwake *Rissa tridactyla*. *Ibis*, *141*(2), 321–326.

Cadiou, B., Pons, J.-M., & Yesou, R. (2004). *Oiseaux marins nicheurs de France metropolitain (1960-2000)*. Biotope.

Calabrese, J. M., Fleming, C. H., & Gurarie, E. (2016). ctmm: An r package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution*, *7*(9), 1124–1132.

Camphuysen, C. J. (1995). Herring gull *Larus argentatus* and lesser black-backed gull *Larus fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. *Ardea-Wageningen*, *83*, 365–380.

Camphuysen, C. J. (2011). Lesser black-backed gulls nesting at Texel. Foraging distribution, diet, survival, recruitment and breeding biology of birds carrying advanced GPS loggers. Tech. rep., Texel: Royal Netherlands Institute for Sea Research.

Camphuysen, K. C. J., Shamoun-Baranes, J., Van Loon, E. E., & Bouten, W. (2015). Sexually distinct foraging strategies in an omnivorous seabird. *Marine Biology*, *162*(7), 1417–1428.

Cannon, A. (1999). The significance of private gardens for bird conservation. *Bird Conservation International*, *9*(4), 287–297.

Caron-Beaudoin, É., Gentes, M.-L., Patenaude-Monette, M., Hélie, J.-F., Giroux, J.-F., & Verreault, J. (2013). Combined usage of stable isotopes and GPS-based telemetry to understand the feeding ecology of an omnivorous bird, the ring-billed gull (*Larus delawarensis*). *Canadian journal of zoology*, *91*(10), 689–697.

Clark, D., Whitney, J. J., MacKenzie, K. G., Koenen, K. K., & DeStefano, S. (2015). Assessing gull abundance and food availability in urban parking lots. *Human–Wildlife Interactions*, *9*(2), 7.

Cooke, S., Hinch, S., Wikelski, M., Andrews, R., Kuchel, L., Wolcott, T., & Butler, P. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution*, *19*, 334–343.

Cornioley, T., Börger, L., Ozgul, A., & Weimerskirch, H. (2016). Impact of changing wind conditions on foraging and incubation success in male and female wandering albatrosses. *Journal of Animal Ecology*, *85*(5), 1318–1327.

Coulson, J. (1963). The status of the kittiwake in the British Isles. *Bird Study*, *10*(3), 147–179.

Coulson, J., & Coulson, B. (2008). Lesser black-backed gulls *Larus fuscus* nesting in an inland urban colony: the importance of earthworms (Lumbricidae) in their diet. *Bird Study*, *55*(3), 297–303.

Coulson, J., & Coulson, B. (2009). Ecology and colonial structure of large gulls in an urban colony: investigations and management at Dumfries, SW Scotland. *Waterbirds*, *32*(1), 1–15.

Coulson, J., & Coulson, B. (2015). The accuracy of urban nesting gull censuses. *Bird Study*, *62*(2), 170–176.

Cox, S. L., Scott, B. E., & Camphuysen, C. J. (2013). Combined spatial and tidal processes identify links between pelagic prey species and seabirds. *Marine Ecology Progress Series*, *479*, 203–221.

Cramp, S. (1971). Gulls nesting on buildings in Britain and Ireland. *British birds*, *64*, 476–487.

D'Albiac, S., & Gibbons, B. (2019). How to survive a seagull attack and avoid being troubled by the feathered pests. Accessible by: www.walesonline.co.uk/news/uk-news/how-survive-seagull-attack-avoid-16642420.

Davison, J., Huck, M., Delahay, R., & Roper, T. J. (2008). Urban badger setts: characteristics, patterns of use and management implications. *Journal of Zoology*, *275*(2), 190–200.

Deepspace Web Services (2019). UK Schools Database. Accessible by: www.schoolswebdirectory.co.uk.

DESA (2018). World urbanization prospects: The 2018 revision, key facts. *United Nations Department of Economics and Social Affairs, Population Division: New York, NY, USA*.

DESA (2019). United nations, department of economic and social affairs, population division. world population prospects 2019: Highlights.

Ditchkoff, S. S., Saalfeld, S. T., & Gibson, C. J. (2006). Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban ecosystems*, *9*(1), 5–12.

Donázar, J. A., Cortés-Avizanda, A., & Carrete, M. (2010). Dietary shifts in two vultures after the demise of supplementary feeding stations: consequences of the EU sanitary legislation. *European journal of wildlife research*, *56*(4), 613–621.

Drent, R., & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. *Ardea*, *68*, 225–252.

Ducatez, S., Sol, D., Sayol, F., & Lefebvre, L. (2020). Behavioural plasticity is associated with reduced extinction risk in birds. *Nature Ecology & Evolution*, (pp. 1–6).

Duerr, A. E., Miller, T. A., Lanzone, M., Brandes, D., Cooper, J., O'Malley, K., Maisonneuve, C., Tremblay, J. A., & Katzner, T. (2015). Flight response of slope-soaring birds to seasonal variation in thermal generation. *Functional Ecology*, *29*(6), 779–790.

Dwyer, C. P., Belant, J. L., & Dolbeer, R. A. (1996). Distribution and abundance of roof-nesting gulls in the great lakes region of the united states. *The Ohio Journal of Science*, *96*(1), 9–12.

Eaton, M., Aebischer, N., Brown, A., Hearn, R., Lock, L., Musgrove, A., Noble, D., Stroud, D., & Gregory, R. (2015). Birds of Conservation Concern 4: the population status of birds in the UK, Channel Islands and Isle of Man. *British Birds*, *108*, 708–746.

Elder, W. H. (1954). The oil gland of birds. *The Wilson Bulletin*, *66*(1), 6–31.

Elliott, K., Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., Osborne, O., Ropert-Coudert, Y., Speakman, J. R., & Hare, J. F. (2014). Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology*, *2*(1), 17.

Elliott, K. H., Le Vaillant, M., Kato, A., Speakman, J. R., & Ropert-Coudert, Y. (2013). Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology letters*, *9*(1), 20120919.

Ellis, C. (2014). Seaside menace: How to avoid gull attacks. Accessible by: www.bbc.co.uk/news/uk-england-26793423.

Elston, D., Moss, R., Boulinier, T., Arrowsmith, C., & Lambin, X. (2001). Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology*, *122*(5), 563–569.

Environment Agency (2019). Permitted waste sites - authorised landfill site boundaries. Accessible by: www.data.gov.uk.

Erni, B., Liechti, F., Underhill, L. G., & Bruderer, B. (2002). Wind and rain govern the intensity of nocturnal bird migration in central Europe: a log-linear regression analysis. *Ardea*, *90*(1), 155–166.

ESRI (2017). ArcGIS Release 10.5.1. Environmental Systems Research Institute.

Estes, W. A., & Mannan, R. W. (2003). Feeding behavior of Cooper's hawks at urban and rural nests in southeastern Arizona. *The Condor*, *105*(1), 107–116.

European Commission (2016). Corine Land Cover 2012. Accessible by: www.land.copernicus.eu/pan-european/corine-land-cover/clc-2012.

Fahlman, A., Wilson, R., Svard, C., Rosen, D., & Trites, A. (2008). Activity and diving metabolism correlate in Steller sea lion *Eumetopias jubatus*. *Aquatic Biology*, *2*, 75–84.

Fernández-Juricic, E., & Tellería, J. L. (2000). Effects of human disturbance on spatial and temporal feeding patterns of blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study*, *47*(1), 13–21.

Ferns, P. N., & Mudge, G. P. (2000). Abundance, diet and Salmonella contamination of gulls feeding at sewage outfalls. *Water Research*, *34*(10), 2653–2660.

Finney, S. K., Wanless, S., & Harris, M. P. (1999). The effect of weather conditions on the feeding behaviour of a diving bird, the common guillemot *Uria aalge*. *Journal of Avian Biology*, (pp. 23–30).

Fischer, J. D., Schneider, S. C., Ahlers, A. A., & Miller, J. R. (2015). Categorizing wildlife responses to urbanization and conservation implications of terminology. *Conservation Biology*, *29*(4), 1246–1248.

Fleischer, A. L., Bowman, R., & Woolfenden, G. E. (2003). Variation in foraging behavior, diet, and time of breeding of Florida scrub-jays in suburban and wildland habitats. *The Condor*, *105*(3), 515–527.

Fleming, C. H., Fagan, W. F., Mueller, T., Olson, K. A., Leimgruber, P., & Calabrese, J. M. (2015). Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology*, *96*(5), 1182–1188.

Forman, R. T., & Alexander, L. E. (1998). Roads and their major ecological effects. *Annual review of ecology and systematics*, *29*(1), 207–231.

Fuirst, M., Veit, R. R., Hahn, M., Dheilly, N., & Thorne, L. H. (2018). Effects of urbanization on the foraging ecology and microbiota of the generalist seabird *Larus argentatus*. *PloS one*, *13*(12).

Furness, R. (1978). Energy requirements of seabird communities: a bioenergetics model. *The Journal of Animal Ecology*, (pp. 39–53).

Furness, R. W., & Bryant, D. M. (1996). Effect of wind on field metabolic rates of breeding Northern fulmars. *Ecology*, *77*(4), 1181–1188.

Gabrielsen, G. W. (1996). Energy expenditure of breeding common murres. *Canadian Wildlife Service Occasional Paper*, *91*, 49–58.

Garratt, J. R. (1994). The atmospheric boundary layer. *Earth-Science Reviews*, *37*(1-2), 89–134.

Garthe, S., Schwemmer, P., Paiva, V. H., Corman, A.-M., Fock, H. O., Voigt, C. C., & Adler, S. (2016). Terrestrial and marine foraging strategies of an opportunistic seabird species breeding in the Wadden Sea. *PloS one*, *11*(8), e0159630.

Gibb, R., Shoji, A., Fayet, A. L., Perrins, C. M., Guilford, T., & Freeman, R. (2017). Remotely sensed wind speed predicts soaring behaviour in a wide-ranging pelagic seabird. *Journal of The Royal Society Interface*, *14*(132), 20170262.

Goethe, F. (1960). Felsbrutertum und weitere beachtenswerte tendenzen bei der Silbermowe. *Proceedings of the International Ornithology Congress*, *12*, 252–258.

Goldenberg, W. P., George, T. L., & Black, J. M. (2016). Steller's Jay (*Cyanocitta stelleri*) space use and behavior in campground and non-campground sites in coastal redwood forests. *The Condor: Ornithological Applications*, *118*(3), 532–541.

Gómez-Laich, A., Wilson, R. P., Gleiss, A. C., Shepard, E. L. C., & Quintana, F. (2011). Use of overall dynamic body acceleration for estimating energy expenditure in cormorants. Does locomotion in different media affect relationships? *Journal of Experimental Marine Biology and Ecology*, *399*(2), 151–155.

Green, J. A., Halsey, L. G., Wilson, R. P., & Frappell, P. B. (2009). Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *The Journal of experimental biology*, *212*(Pt 4), 471–482.

Greig, S. A., Coulson, J., & Monaghan, P. (1983). Age related differences in foraging succes in the herring gull. *Animal Behaviour*, *31*, 1237–1247.

Greig, S. A., Coulson, J. C., & Monaghan, P. (1986). A comparison of foraging at refuse tips by three species of gull (Laridae). *Journal of Zoology*, *210*(3), 459–472.

Gyimesi, A., Boudewijn, T., Buijs, R.-J., Shamoun-Baranes, J., de Jong, J., Fijn, R., van Horssen, P., & Poot, M. (2016). Lesser black-backed gulls *Larus fuscus* thriving on a non-marine diet. *Bird Study*, *63*(2), 241–249.

Halsey, L., Shepard, E., & Wilson, R. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *158*, 305–314.

Halsey, L. G., Shepard, E. L. C., Hulston, C. J., Venables, M. C., White, C. R., Jeukendrup, A. E., & Wilson, R. P. (2008). Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: Tests with an easy model species, *Homo sapiens*. *Zoology*, *111*(3), 231–241.

Halsey, L. G., Shepard, E. L. C., Quintana, F., Gomez Laich, A., Green, J. A., & Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology - A Molecular and Integrative Physiology*, *152*(2), 197–202.

Hardy, K. R., & Ottersten, H. (1969). Radar investigations of convective patterns in the clear atmosphere. *Journal of the Atmospheric Sciences*, *26*(4), 666–672.

Harris, M. (1964). Aspects of the breeding biology of the gulls: Larus argentatus, l. fuscus and l. marinus. *Ibis*, *106*(4), 432–456.

Hartig, F. (2017). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1. 5.

Hatch, J. J. (1996). Threats to public health from gulls (Laridae). *International Journal of Environmental Health Research*, *6*(1), 5–16.

Hedenström, A. (1993). Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *342*(1302), 353–361.

Hernández-Pliego, J., Rodríguez, C., & Bustamante, J. (2015). Why do kestrels soar? *PLoS One*, *10*(12).

Hillstrom, L., Kilpi, M., & Lindstrom, K. (1994). Diet of herring gulls *Larus argentatus* during chick rearing in the Gulf of Finland. *Ornis Fennica*, *71*(3), 95–101.

Hooper, T. (1988). Habitat, reproductive parameters, and nest-site tenacity of urban-nesting glaucous-winged gulls at Victoria, British Columbia. *The Murrelet*, *1*, 10–14.

Huig, N., Buijs, R.-J., & Kleyheeg, E. (2016). Summer in the city: behaviour of large gulls visiting an urban area during the breeding season. *Bird Study*, *3657*(May), 1–9.

Hunt, G. L. (1972). Influence of food distribution and human disturbance on the reproductive success of herring gulls. *Ecology*, *53*(6), 1051–1061.

Irons, D. B. (1998). Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology*, *79*(2), 647–655.

Isaksson, N., Evans, T. J., Shamoun-Baranes, J., & Åkesson, S. (2016). Land or sea? Foraging area choice during breeding by an omnivorous gull. *Movement Ecology*, *4*(1), 11.

Jeanniard-du Dot, T., Guinet, C., Arnould, J. P. Y., Speakman, J. R., & Trites, A. W. (2016). Accelerometers can measure total and activity-specific energy expenditures in free-ranging marine mammals only if linked to time-activity budgets. *Functional Ecology*, *31*(2), 377–386.

Jochen, T., & Christoph, H. (2019). Waterbodies datasets. Accessible by: www.openstreetmapdata.com/data/water.

Jones, D. N., & Thomas, L. K. (1999). Attacks on humans by Australian magpies: management of an extreme suburban human-wildlife conflict. *Wildlife Society Bulletin*, *27*(2), 473–478.

Kavelaars, M. M., Stienen, E., Matheve, H., Buijs, R.-J., Lens, L., & Müller, W. (2018). GPS tracking during parental care does not affect early offspring development in lesser black-backed gulls. *Marine biology*, *165*(5), 87.

Kerlinger, P., & Moore, F. R. (1989). Atmospheric structure and avian migration. In *Current ornithology*, (pp. 109–142). Springer.

Kim, H. H. (1992). Urban heat island. *International Journal of Remote Sensing*, *13*(12), 2319–2336.

Kim, S. Y., & Monaghan, P. (2006). Interspecific differences in foraging preferences, breeding performance and demography in herring (*Larus argentatus*) and lesser black-backed gulls (*Larus fuscus*) at a mixed colony. *Journal of Zoology*, *270*(4), 664–671.

Klaassen, R. H. G., Ens, B. J., Shamoun-Baranes, J., Exo, K. M., & Bairlein, F. (2012). Migration strategy of a flight generalist, the lesser black-backed gull *Larus fuscus*. *Behavioral Ecology*, *23*(1), 58–68.

Koenig, J., Shine, R., & Shea, G. (2002). The dangers of life in the city: patterns of activity, injury and mortality in suburban lizards (*Tiliqua scincoides*). *Journal of Herpetology*, (pp. 62–68).

Kozlovsky, D. Y., Weissgerber, E. A., & Pravosudov, V. V. (2017). What makes specialized food-caching mountain chickadees successful city slickers? *Proceedings of the Royal Society B: Biological Sciences*, *284*(1855), 20162613.

Kroc, E. (2018). Reproductive ecology of urban-nesting glaucous-winged gulls *Larus glaucescens* in vancouver, bc, canada. *Marine Ornithology*, *46*, 155–164.

Kubetzki, U., & Garthe, S. (2003). Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. *Marine Biology*, *143*(1), 199–207.

Kubetzki, U., & Garthe, S. (2007). Nests with a view: Distribution, nest habitats and diets of roof-breeding common gulls (*Larus canus*) in northern Germany. *Waterbirds*, *30*(4), 602–608.

Kumerloeve, H. (1957). Silbermowenbruten auf Hausdachern. *Ornithologische Mitteilungen*, *9*, 112.

Lane, J. V., Spracklen, D. V., & Hamer, K. C. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the Northern gannet. *Marine Ecology Progress Series*, *628*, 183–193.

Lanzone, M. J., Miller, T. A., Turk, P., Brandes, D., Halverson, C., Maisonneuve, C., Tremblay, J., Cooper, J., O'Malley, K., Brooks, R. P., et al. (2012). Flight responses by a migratory soaring raptor to changing meteorological conditions. *Biology Letters*, *8*(5), 710–713.

Lensink, R., De Jong, J., Hartman, J., & Verbeek, R. (2010). Broedende meeuwen in Den Haag in 2010 – Inventarisatie in het broedseizoen van grote meeuwen op daken. Tech. rep., Bureau Waardenburg, Culemborg.

Lepczyk, C. A., Mertig, A. G., & Liu, J. (2004). Landowners and cat predation across rural-to-urban landscapes. *Biological conservation*, *115*(2), 191–201.

Lewis, S., Phillips, R. A., Burthe, S. J., Wanless, S., & Daunt, F. (2015). Contrasting responses of male and female foraging effort to year-round wind conditions. *Journal of Animal Ecology*, *84*(6), 1490–1496.

Liechti, F. (2006). Birds: blowin' by the wind? *Journal of Ornithology*, *147*(2), 202–211.

Lifson, N., & McClintock, R. (1966). Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of theoretical biology*, *12*(1), 46–74.

Lin, T.-H., Akamatsu, T., & Chou, L.-S. (2013). Tidal influences on the habitat use of Indo-Pacific humpback dolphins in an estuary. *Marine biology*, *160*(6), 1353–1363.

Loss, S. R., Will, T., Loss, S. S., & Marra, P. P. (2014). Bird–building collisions in the united states: Estimates of annual mortality and species vulnerability. *The Condor*, *116*(1), 8–23.

Luniak, M. (2004). Synurbization–adaptation of animal wildlife to urban development. In *Proc. 4th Int. Symposium Urban Wildl. Conserv. Tucson*, (pp. 50–55). Citeseer.

Luniak, M. (2008). Fauna of the big city–estimating species richness and abundance in warsaw poland. In *Urban Ecology*, (pp. 349–354). Springer.

Mackenstedt, U., Jenkins, D., & Romig, T. (2015). The role of wildlife in the transmission of parasitic zoonoses in peri-urban and urban areas. *International Journal for Parasitology: Parasites and Wildlife*, *4*(1), 71–79.

Manley, G. (1958). On the frequency of snowfall in metropolitan England. *Quarterly Journal of the Royal Meteorological Society*, *84*(359), 70–72.

Manly, B., McDonald, L., Thomas, D. L., McDonald, T. L., & Erickson, W. P. (2007). *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & Business Media.

Marti, R., & Del Moral, J. C. (2003). *Atlas de las Aves Reproductoras de Espaha*. Direccion General de la Conservacion de la Naturaleza-Sociedad Espanola de Ornitologia, Madrid.

Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. In *Avian ecology and conservation in an urbanizing world*, (pp. 19–47). Springer.

McClennen, N., Wigglesworth, R. R., Anderson, S. H., & Wachob, D. G. (2001). The effect of suburban and agricultural development on the activity patterns of coyotes (*Canis latrans*). *American Midland Naturalist*, (pp. 27–36).

McKinney, M. L. (2002). Urbanization, biodiversity, and conservation. *Bioscience*, *52*(10), 883–890.

Mennechez, G., & Clergeau, P. (2006). Effect of urbanisation on habitat generalists: starlings not so flexible? *Acta Oecologica*, *30*(2), 182–191.

Mitchell, P. I., Newton, S. F., Ratcliffe, N., & Dunn, T. E. (2004). *Seabird populations of Britain and Ireland*. T & AD Poyser, London.

Möller, A. P. (2009). Successful city dwellers : a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia*, *159*(4), 849–858.

Monaghan, P. (1979). Aspects of the breeding biology of herring gulls *Larus argentatus* in urban colonies. *Ibis*, *121*(4), 475–481.

Monaghan, P., & Coulson, J. C. C. (1977). Status of large gulls nesting on buildings. *Bird Study*, *24*(2), 89–104.

Mudge, G. (1978). *Ecological studies of herring gulls (Larus argentatus Pont.) and other Larini, in an urban environment*. Unpublished, University College, Cardiff.

Mudge, G. P., & Ferns, P. N. (1982). The feeding ecology of five species of gulls (Aves: Larini) in the inner Bristol Channel. *Journal of Zoology*, *197*, 497–510.

Mullers, R. H. E., Navarro, R. A., Daan, S., Tinbergen, J. M., & Meijer, H. A. J. (2009). Energetic costs of foraging in breeding Cape gannets *Morus capensis*. *Marine Ecology Progress Series*, *393*, 161–171.

Murray, M., Cembrowski, A., Latham, A., Lukasik, V., Pruss, S., & St Clair, C. (2015). Greater consumption of protein-poor anthropogenic food by urban relative to rural coyotes increases diet breadth and potential for human–wildlife conflict. *Ecography*, *38*(12), 1235–1242.

Nager, R. G., & O'Hanlon, N. J. (2016). Changing numbers of three gull species in the British Isles. *Waterbirds*, *39*(1), 15–28.

Nankinov, D. (1992). The nesting by the herring gull (*Larus argentatus*) in the towns and villages of Bulgaria. *Avocetta*, *16*, 93–94.

Navarro, J., Grémillet, D., Ramirez, F. J., Afán, I., Bouten, W., & Forero, M. G. (2017). Shifting individual habitat specialization of a successful predator living in anthropogenic landscapes. *Marine Ecology Progress Series*, *578*, 243–251.

Neubauer, G., Zagalska-Neubauer, M., Gwiazda, R., Faber, M., Bukaciinski, D., Betleja, J., & Chylarecki, P. (2006). Breeding large gulls in poland: distribution, numbers, trends and hybridisation. *Vogelwelt-Berlin*, *127*(1), 11.

Nogales, M., Zonfrillo, B., & Monaghan, P. (1995). Diets of adult and chick herring gulls *Larus argentatus argenteus* on Ailsa Craig, south-west Scotland. *Seabird*, *17*, 56–63.

Noordhuis, R., & Spaans, A. L. (1992). Interspecific competition for food between herring *Larus argentatus* and lesser black-backed gulls *Larus fuscus* in the Dutch Wadden Sea area. *Ardea*, *80*(1), 114–132.

Nudds, R., Gardiner, J., Tickle, P., & Codd, J. (2010). Energetics and kinematics of walking in the barnacle goose (*Branta leucopsis*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *156*(3), 318–324.

Oke, T. R. (1973). City size and the Urban Heat Island. *Atmospheric Environment (1967)*, *7*(8), 769–779.

Oro, D., Genovart, M., Tavecchia, G., Fowler, M. S., & Martinez-Abrain, A. (2013). Ecological and evolutionary implications of food subsidies from humans. *Ecology letters*, *16*(12), 1501–1514.

Oro, D., Ruiz, X., Jover, L., Pedrocchi, V., & Gonzalez-Solis, J. (1997). Diet and adult time budgets of Audouin's gull *Larus audouinii* in response to changes in commercial fisheries. *Ibis*, *139*(4), 631–637.

Ortega-Jimenez, V. M., & Dudley, R. (2012). Flying in the rain: hovering performance of Anna's hummingbirds under varied precipitation. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1744), 3996–4002.

Ortiz, N., & Smith, G. (1994). Landfill sites, botulism and gulls. *Epidemiology & Infection*, *112*(2), 385–391.

Parslow, J. (1967). Changes in status among breeding birds in Britain and Ireland: part 3. *British Birds*, *60*(5), 177–202.

Patenaude-Monette, M., Bélisle, M., & Giroux, J.-F. (2014). Balancing energy budget in a central-place forager: which habitat to select in a heterogeneous environment? *PLoS ONE*, *9*(7).

Pennycuick, C. (2008). *Modelling the Flying bird*. Elsevier Academic Press.

Pennycuick, C. J. (1998). Field observations of thermals and thermal streets, and the theory of cross-country soaring flight. *Journal of Avian Biology*, *3*, 33–43.

Perlut, N., Bonter, D., Ellis, J., & Friar, M. (2016). Rooftop nesting in a declining population of herring gulls (*Larus argentatus*) in Portland, Maine. *Waterbirds*, *39*(1), 68–73.

Petit, J. G., Gabernet, M. E. M., Gimeno, J. T., & Gallisà, E. C. (1986). Urban nesting of yellow-legged gulls in Barcelona (Spain). In *Mediterranean Marine Avifauna*, (pp. 509–511). Springer.

Pierotti, R., & Annett, C. (1987). Reproductive consequences of dietary specialization and switching in an ecological generalist. In *Foraging behavior*, (pp. 417–442). Springer, Boston, MA.

Pierotti, R., & Annett, C. (2001). The ecology of western gulls in habitats varying in degree of urban influence. In *Avian ecology and conservation in an urbanizing world*, (pp. 307–329). Springer.

Pistorius, P. A., Hindell, M. A., Tremblay, Y., & Rishworth, G. M. (2015). Weathering a dynamic seascape: influences of wind and rain on a seabird's year-round activity budgets. *PloS ONE*, *10*(11).

Poessel, S. A., Brandt, J., Miller, T. A., & Katzner, T. E. (2018). Meteorological and environmental variables affect flight behaviour and decision-making of an obligate soaring bird, the California condor *Gymnogyps californianus*. *Ibis*, *160*(1), 36–53.

Pons, J. (1992). Effects of changes in the availability of human refuse on breeding parameters in a herring gull *Larus argentatus* population in Brittany, France. *Ardea*, *80*(1), 143–150.

Prange, S., Gehrt, S. D., & Wiggers, E. P. (2004). Influences of anthropogenic resources on raccoon (*Procyon lotor*) movements and spatial distribution. *Journal of Mammalogy*, *85*(3), 483–490.

Pütz, K. (2002). Spatial and temporal variability in the foraging areas of breeding king penguins. *The Condor*, *104*(3), 528–538.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C., & Wilson, R. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE*, *7*(2), e31187.

R Core Team (2019). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Accessible by: www.R-project.org.

Raven (1997). *Aspects of the ecology of gulls in the urban environment.*. Ph.D. thesis, Durham University.

Raven, S., & Coulson, J. (1997). The distribution and abundance of *Larus* gulls nesting on buildings in Britain and Ireland. *Bird Study*, *44*(October), 13–34.

Reiser, D. (1894). *Materialien zu einer Ornis balcanica. Bulgarien*. Wien.

Rock, P. (2004a). A study of the effects of deterring gulls from Gloucester landfill site for a two week period in March 2004. Tech. rep., NA.

Rock, P. (2004b). Roof-Nesting Gulls in Bristol. Survey conducted in May & June 2004. Tech. rep., Bristol City Council, Bristol.

Rock, P. (2005). Urban gulls: Problems and solutions. *British Birds*, *98*(7), 338–355.

Rock, P. (2010). Roof-Nesting Gulls in Bristol. Survey conducted in May 2010. Tech. rep., Bristol City Council, Bristol.

Rock, P. (2012). Urban gulls. Why current control methods always fail. *Rivista Italiana di Ornitologia*, *82*, 58–65.

Rock, P., Camphuysen, C. J., Shamoun-Baranes, J., Ross-Smith, V. H., & Vaughan, I. P. (2016). Results from the first GPS tracking of roof-nesting herring gulls *Larus argentatus* in the UK. *Ringing and Migration*, *31*(1), 47–62.

Rock, P., & Vaughan, I. P. (2013). Long-term estimates of adult survival rates of urban herring gulls *Larus argentatus* and lesser black-backed gulls *Larus fuscus*. *Ringing & Migration*, *28*(1), 21–29.

Rodewald, A. D., Kearns, L. J., & Shustack, D. P. (2011). Anthropogenic resource subsidies decouple predator–prey relationships. *Ecological Applications*, *21*(3), 936–943.

Ross-Smith, V. H. (2019). Gulls allowed? understanding gulls. Accessible by: www.bto.org/understanding-birds/articles/gulls-allowed.

Ross-Smith, V. H., Grantham, M. J., Robinson, R. A., & Clark, J. A. (2014a). Analysis of lesser black-backed gull data to inform meta-population studies. Research report 654, BTO, Thetford, Norfolk.

Ross-Smith, V. H., Robinson, R. A., Banks, A. N., Frayling, T. D., Gibson, C. C., & Clark, J. A. (2014b). The lesser black-backed gull *Larus fuscus* in England: how to resolve a conservation conundrum. *Seabird*, *27*, 41–61.

Russ, A., Ruger, A., & Klenke, R. (2015). Seize the night: European blackbirds (*Turdus merula*) extend their foraging activity under artificial illumination. *Journal of Ornithology*, *156*(1), 123–131.

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proaño, C., Takekawa, J. Y., Newman, S. H., et al. (2013). Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecology*, *1*(1), 4.

Sage, E., Bouten, W., Hoekstra, B., Camphuysen, K. C., & Shamoun-Baranes, J. (2019). Orographic lift shapes flight routes of gulls in virtually flat landscapes. *Scientific reports*, *9*(1), 1–10.

Sample, B. E., Cooper, R. J., & Whitmore, R. C. (1993). Dietary shifts among songbirds from a diflubenzuron-treated forest. *The Condor*, *95*(3), 616–624.

Santos, C. D., Hanssen, F., Muñoz, A.-R., Onrubia, A., Wikelski, M., May, R., & Silva, J. P. (2017). Match between soaring modes of black kites and the fine-scale distribution of updrafts. *Scientific reports*, *7*(1), 1–10.

Schaub, M., Liechti, F., & Jenni, L. (2004). Departure of migrating European robins, *Erithacus rubecula*, from a stopover site in relation to wind and rain. *Animal behaviour*, *67*(2), 229–237.

Schoener, T. W. (1971). Theory of feeding strategies. *Annual review of ecology and systematics*, *2*(1), 369–404.

Schreiber, E., & Burger, J. (2001). Climate and weather effects on seabirds. In *Biology of marine birds*, (pp. 197–234). CRC Press.

Schwemmer, P., & Garthe, S. (2005). At-sea distribution and behaviour of a surface-feeding seabird, the lesser black-backed gull *Larus fuscus*, and its association with different prey. *Marine Ecology Progress Series*, *285*, 245–258.

Schwemmer, P., Garthe, S., & Mundry, R. (2008). Area utilization of gulls in a coastal farmland landscape: habitat mosaic supports niche segregation of opportunistic species. *Landscape ecology*, *23*(3), 355–367.

Sellers, R., & Shackleton, D. (2011). Numbers, distribution and population trends of large gulls breeding in Cumbria, northwest England. *Seabird*, *24*, 90–102.

Shaffer, S. A. (2011). A review of seabird energetics using the doubly labeled water method. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *158*(3), 315–322.

Shaffer, S. A., Cockerham, S., Warzybok, P., Bradley, R. W., Jahncke, J., Clatterbuck, C. A., Lucia, M., Jelincic, J. A., Cassell, A. L., & Kelsey, E. C. (2017). Population-level plasticity in foraging behavior of western gulls (*Larus occidentalis*). *Movement Ecology*, *5*(1), 27.

Shamoun-baranes, J., Bouten, W., Camphuysen, C. J., & Baaij, E. (2011). Riding the tide: intriguing observations of gulls resting at sea during breeding. *Ibis*, *153*(2), 411–415.

Shamoun-Baranes, J., Bouten, W., van Loon, E. E., Meijer, C., & Camphuysen, C. J. (2016). Flap or soar? How a flight generalist responds to its aerial environment. *Phil. Trans. R. Soc. B*, *371*(1704), 20150395.

Shamoun-Baranes, J., Burant, J. B., Loon, E. E., Bouten, W., & Camphuysen, C. J. (2017a). Short distance migrants travel as far as long distance migrants in lesser black-backed gulls *Larus fuscus*. *Journal of Avian Biology*, *48*(1), 49–57.

Shamoun-Baranes, J., Liechti, F., & Vansteelant, W. M. (2017b). Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *Journal of Comparative Physiology A*, *203*(6-7), 509–529.

Shepard, E., Cole, E.-L., Neate, A., Lempidakis, E., & Ross, A. (2019). Wind prevents cliff-breeding birds from accessing nests through loss of flight control. *eLife*, *8*, e43842.

Shepard, E. L. C., Williamson, C., & Windsor, S. P. (2016). Fine-scale flight strategies of gulls in urban airflows indicate risk and reward in city living. *Phil. Trans. R. Soc. B*, *371*(1704), 20150394.

Shepard, E. L. C., Wilson, R. P., Halsey, L. G., Quintana, F., Laich, A. G., Gleiss, A. C., Liebsch, N., Myers, A. E., & Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology*, *4*(3), 235–241.

Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A., & Vosper, S. B. (2013). Energy landscapes shape animal movement ecology. *The American Naturalist*, *182*(3), 298–312.

Shochat, E. (2004). Credit or debit? Resource input changes population dynamics of city-slicker birds. *Oikos*, *106*(3), 622–626.

Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to emerging processes in mechanistic urban ecology. *Trends in ecology & evolution*, *21*(4), 186–191.

Sibly, R., & McCleery, R. H. (1983a). Increase in weight of herring gulls while feeding. *Journal of Animal Ecology*, *52*(1), 35–50.

Sibly, R., & McCleery, R. H. (1983b). The distribution between feeding sites of herring gulls breeding at Walney island, U.K. *Journal of Animal Behaviour*, *52*, 21–68.

Smith, S., Wang, J., Fanning, S., & McMahon, B. J. (2014). Antimicrobial resistant bacteria in wild mammals and birds: a coincidence or cause for concern? *Irish Veterinary Journal*, *67*(1), 1–3.

Sokolov, L. (2011). Modern telemetry: new possibilities in ornithology. *Biology Bulletin*, *38*(9), 885–904.

Sol, D., Santos, D. M., Garcia, J., & Cuadrado, M. (1998). Competition for food in urban pigeons: the cost of being juvenile. *The Condor*, *100*(2), 298–304.

Sol, D., Timmermans, S., & Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal behaviour*, *63*(3), 495–502.

Soldatini, C., Albores-Barajas, Y. V., Mainardi, D., & Monaghan, P. (2008a). Roof nesting by gulls for better or worse? *Italian Journal of Zoology*, *75*(May 2013), 295–303.

Soldatini, C., Albores-Barajas, Y. V., Torricelli, P., & Mainardi, D. (2008b). Testing the efficacy of deterring systems in two gull species. *Applied Animal Behaviour Science*, *110*(3-4), 330–340.

Sorace, A., & Gustin, M. (2009). Distribution of generalist and specialist predators along urban gradients. *Landscape and Urban Planning*, *90*(3-4), 111–118.

Sotillo, A., Baert, J. M., Müller, W., Stienen, E. W., Soares, A. M., & Lens, L. (2019a). Recently-adopted foraging strategies constrain early chick development in a coastal breeding gull. *PeerJ*, *7*, e7250.

Sotillo, A., Baert, J. M., Müller, W., Stienen, E. W., Soares, A. M., & Lens, L. (2019b). Time and energy costs of different foraging choices in an avian generalist species. *Movement Ecology*, *7*(1), 1–11.

Soulsbury, C. D., & White, P. C. L. (2016). Human-wildlife interactions in urban areas: a review of conflicts, benefits and opportunities. *Wildlife research*, *42*(7), 541–553.

Spaans, A. L. (1971). On the feeding ecology of the herring gull *Larus argentatus Pont* in the northern part of the Netherlands. *Ardea*, *55*, 73–189.

Spaar, R., & Bruderer, B. (1996). Soaring migration of steppe eagles *Aquila nipalensis* in southern israel: flight behaviour under various wind and thermal conditions. *Journal of Avian Biology*, (pp. 289–301).

Spear, L. B., & Ainley, D. G. (1997). Flight behaviour of seabirds in relation to wind direction and wing morphology. *Ibis*, *139*(2), 221–233.

Spelt, A., Williamson, C., Shamoun-Baranes, J., Shepard, E., Rock, P., & Windsor, S. (2019). Habitat use of urban-nesting lesser black-backed gulls during the breeding season. *Scientific Reports*, *9*(1), 10527.

Steenhof, K., & Kochert, M. N. (1985). Dietary shifts of sympatric buteos during a prey decline. *Oecologia*, *66*(1), 6–16.

Stephens, D. W., & Krebs, J. R. (1986). *Foraging theory*. Princeton University Press.

Stienen, E. W. M., Desmet, P., Aelterman, B., Courtens, W., Feys, S., Vanermen, N., Verstraete, H., Van De Walle, M., Deneudt, K., Hernandez, F., Houthoofdt, R., Vanhoorne, B., Bouten, W., Buijs, R. J., Kavelaars, M. M., Müller, W., Herman, D., Matheve, H., Sotillo, A., & Lens, L. (2016). GPS tracking data of lesser black-backed gulls and herring gulls breeding at the southern north sea coast. *ZooKeys*, *2016*(555), 115–124.

Stofberg, M., Cunningham, S., Sumasgutner, P., & Amar, A. (2019). Juggling a "junk-food" diet: responses of an urban bird to fluctuating anthropogenic-food availability. *Urban Ecosystems*, *22*(6), 1019–1026.

Strucker, R., Arts, F., & Hoekstein, M. S. (2015). Kustbroedvogels in het Deltagebied in 2014. Tech. Rep. BM 14.12, Rijkswaterstaat Waterdienst, Lelystad., Lelystad.

Thaxter, C., Ross-Smith Viola, H., Clark, N., Conway, G., Johnston, A., & Wade, H. (2014a). Measuring the interaction between marine features of Special Protection Areas with offshore wind farm development zones through telemetry: final report. Tech. Rep. 649, BTO Research Report.

Thaxter, C. B., Clark, N. A., Ross-Smith, V. H., Conway, G. J., Bouten, W., & Burton, N. H. (2017). Sample size required to characterize area use of tracked seabirds. *The Journal of Wildlife Management*, *81*(6), 1098–1109.

Thaxter, C. B., Ross-Smith, V. H., Bouten, W., Clark, N. A., Conway, G. J., Rehfisch, M. M., & Burton, N. H. K. (2015). Seabird-wind farm interactions during the breeding season vary within and between years: A case study of lesser black-backed gull *Larus fuscus in the UK*. *Biological Conservation*, *186*(April), 347–358.

Thaxter, C. B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Marsh, M., Leat, E. H. K., & Burton, N. H. K. (2014b). A trial of three harness attachment methods and their suitability for long-term use on lesser black-backed gulls and great skuas. *Ringing & Migration*, *29*(2), 65–76.

Thaxter, C. B., Ross-Smith, V. H., Clark, J. A., Clark, N. A., Conway, G. J., Masden, E. A., Wade, H. M., Leat, E. H. K., Gear, S. C., & Marsh, M. (2016). Contrasting effects of GPS device and harness attachment on adult survival of lesser black-backed gulls *Larus fuscus* and great skuas *Stercorarius skua*. *Ibis*, *158*(2), 279–290.

Thiériot, E., Molina, P., & Giroux, J.-F. (2012). Rubber shots not as effective as selective culling in deterring gulls from landfill sites. *Applied animal behaviour science*, *142*(1-2), 109–115.

Thompson, B., Jang, J., & Dion, J. (1995). Wing performance in moderate rain. *Journal of Aircraft*, *32*(5), 1034–1039.

Tucker, V. A. (1972). Metabolism during flight in the laughing gull, *Larus atricilla*. *American Journal of Physiology-Legacy Content*, *222*(2), 237–245.

Tyson, C., Shamoun-baranes, J., Van Loon, E. E., Camphuysen, K. C. J., & Hintzen, N. T. (2015). Individual specialization on fishery discards by lesser black-backed gulls (*Larus fuscus*). *ICES Journal of Marine Science*, *72*(6), 1882–1891.

van Donk, S., Shamoun-Baranes, J., Bouten, W., van Der Meer, J., & Camphuysen, K. C. (2019a). Individual differences in foraging site fidelity are not related to time-activity budgets in herring gulls. *Ibis*.

van Donk, S., Shamoun-Baranes, J., Van Der Meer, J., & Camphuysen, K. C. (2019b). Foraging for high caloric anthropogenic prey is energetically costly. *Movement ecology*, *7*(1), 17.

van Toor, M. L., Arriero, E., Holland, R. A., Huttunen, M. J., Juvaste, R., Müller, I., Thorup, K., Wikelski, M., & Safi, K. (2017). Flexibility of habitat use in novel environments: insights from a translocation experiment with lesser black-backed gulls. *Royal Society open science*, *4*(1), 160164.

Vermeer, K., Power, D., & Smith, G. E. J. (1988). Habitat selection and nesting biology of roof-nesting glaucous-winged gulls. *Colonial waterbirds*, *1*, 189–201.

Villavicencio, C., & Bahamonde, M. (2019). Mew gull *Larus canus* breeding in a residential area of malmö, sweden. *Ornis Svecica*.

Voigt, C. C., Schneeberger, K., Voigt-Heucke, S. L., & Lewanzik, D. (2011). Rain increases the energy cost of bat flight. *Biology letters*, *7*(5), 793–795.

Washburn, B. E., Bernhardt, G. E., Kutschbach-Brohl, L., Chipman, R. B., & Francoeur, L. C. (2013). Foraging ecology of four gull species at a coastal-urban interface. *The Condor*, *115*(1), 67–76.

Weiser, E. L., & Powell, A. N. (2011). Evaluating gull diets: a comparison of conventional methods and stable isotope analysis. *Journal of Field Ornithology*, *82*(3), 297–310.

Westerterp, K. R. (2017). Doubly labelled water assessment of energy expenditure: principle, practice, and promise. *European journal of applied physiology*, *117*(7), 1277–1285.

Williamson, C. (2020). *Bio-inspired path planning for Unmanned Air Vehicles in urban environments*. Ph.D. thesis, University of Bristol.

Williamson, C. J., Spelt, A., & Windsor, S. P. (2020). Bird-inspired velocity optimization for uavs in the urban environment. In *AIAA Scitech 2020 Forum*, (p. 1948).

Wilson, K. (2019). More than 100 high-tech super bins will start to appear across bristol from today. Accessible by: www.bristolpost.co.uk/news/bristol-news/more-100-high-tech-super-2954834.

Wilson, R. P., Börger, L., Holton, M. D., Scantlebury, D. M., Gómez-Laich, A., Quintana, F., Rosell, F., Graf, P. M., Williams, H., Gunner, R., et al. (2020). Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, *89*(1), 161–172.

Wilson, R. P., Quintana, F., & Hobson, V. J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1730), 975–80.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R., & Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology*, *75*(5), 1081–1090.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, *73*(1), 3–36.

Woodcock, A. H. (1975). Thermals over the sea and gull flight behavior. *Boundary-Layer Meteorology*, *9*(1), 63–68.

Wright, T. F., Eberhard, J. R., Hobson, E. A., Avery, M. L., & Russello, M. A. (2010). Behavioral flexibility and species invasions: the adaptive flexibility hypothesis. *Ethology Ecology & Evolution*, *22*(4), 393–404.

Yoda, K., Tomita, N., Mizutani, Y., Narita, A., & Niizuma, Y. (2012). Spatio-temporal responses of black-tailed gulls to natural and anthropogenic food resources. *Marine Ecology Progress Series*, *466*, 249–259.

Young, G. S. (1988). Convection in the atmospheric boundary layer. *Earth-Science Reviews*, *25*(3), 179–198.

Zelenskaya, L. (2019). Ecology of an urban population of the slaty-backed gull (*Larus schistisagus*) in comparison with natural colonies: 1. Features of nest location and productivity. *Biology Bulletin*, *46*(9), 1108–1123.

Zorrozua, N., Aldalur, A., Herrero, A., Diaz, B., Delgado, S., Sanpera, C., Jover, L., & Arizaga, J. (2018). Breeding yellow-legged gulls increase consumption of terrestrial prey after landfill closure. *Ibis*.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). Mixed-effects modelling for nested data. In *Mixed effects models and extensions in ecology with R*, (pp. 101–142). Springer.