The ecology of lesser black-backed gulls (*Larus fuscus*) in the Anthropocene: implications for conservation and management

Submitted by Liam Langley to the University of Exeter as a thesis for
the degree of Doctor of Philosophy in Biological Sciences
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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature: ……… ………………Liam Langley…………………………………..

Thesis Abstract

Context:

Anthropogenic change is affecting many species, with both positive and negative impacts. Human habitat modification and resource subsidies have helped opportunistic species, leading to demographic expansions. However, anthropogenic changes may also harm these opportunists or present future risks, for instance, dependence on subsidies or increased human wildlife interactions. Understanding human influences on these opportunistic species' ecology is essential for their effective conservation and management in a changing world.

Approaches:

Using gulls (*Laridae*) as a model, this thesis first summarises global trends in their abundance and distribution, the drivers of these changes and the challenges for their conservation and management. The three subsequent chapters examine how human activities have influenced the ecology of lesser black-backed gulls (*Larus fuscus*) in northwest England, combining telemetry data, and field sampling and monitoring. First, I investigate changes to gulls' foraging ecology and adult body condition after landfill closures. Second, I investigate population-level differences in movement and breeding ecology between neighbouring urban and coastal colonies. Finally, I examine the degree of individual foraging site fidelity both within and among colonies.

Results:

First, the review highlighted anthropogenic change as a key driver of demographic expansions in gull populations; however, there were geographic biases in the literature and evidence of recent declines suggest ecological processes linking humans and gulls are complex, necessitating care when making decisions about gull conservation and management. Second, telemetry data revealed strong behavioural responses to anthropogenic perturbations, with increased foraging effort and habitat-switching observed following landfill closures. Third, I found evidence for foraging habitat segregation between urban and rural lesser black-backed gulls. However, this did not results in major differences in diet or breeding performance between colonies. Finally, I found a high degree of individual variation in foraging site fidelity, with populations composed of a mixture of site faithful and varied individuals.

Implications:

The review highlights the urgent need to quantify the efficacy of management approaches in mitigating gull impacts and conservation measures in arresting gull declines. The observation of spatial segregation between breeding habitats demonstrates clear differences in foraging ecology between colonies, and highlights measures targeting urban foragers as a useful tool for mitigating human-gull interactions and the need for conservation action, such as the restoration of coastal ecosystems, to boost declining coastal colonies. Additionally, the finding of habitat-switching following landfill closures suggests anthropogenic perturbations will alter the distribution of foraging gulls and increase the incidence of human-gull interactions and possibly conflict. However, we found that site fidelity, use of urban habitats and responses to landfill closures varied among years, colonies, and individual gulls. This demonstrates the need for long-term monitoring of ecological and demographic responses to human activities across a range of colonies. This will provide the requisite ecological evidence to develop landscape-scale management plans for opportunistic species such as gulls, which balance mitigation of negative impacts with conservation.

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Author's Declaration

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All work included in this thesis was conducted by Liam Langley, with the following contributions from co-authors outlined below for each chapter:

Chapter 2 – S Bearhop, N Burton, T Frayling, A Banks, SC Votier

> LL and SVC designed the study with critical input from SB. LL performed the literature review and led the writing of the manuscript with guidance from SCV. SB, NB, TF and AB contributed critically to drafts of the chapter.

Chapter 3 – S Bearhop, N Burton, T Frayling, A Banks, C Thaxter, E Scragg, G Clewley, SC Votier

> In submission at *Movement Ecology* (Submitted 4th December 2020)
>
> LL and SVC designed the study with input from NB, TF, AB and SB. GC and ES collected the data which was archived and managed by CT. LL performed the analysis with some guidance from CT, GC and SCV. All

authors contributed critically to the drafts and gave final approval for publication

Chapter 4 – S Bearhop, N Burton, T Frayling, A Banks, C Thaxter, E Scragg, G Clewley, SC Votier

LL and SVC designed the study. GC and ES collected the data, with the tracking data archived and managed by CT. LL performed the analysis with guidance from SCV. All authors contributed critically to the drafts of the chapter.

Chapter 5 – S Bearhop, N Burton, T Frayling, A Banks, C Thaxter, E Scragg, G Clewley, SC Votier

LL and SVC designed the study with input from NB, TF, AB and SB. GC and ES collected the data which was archived and managed by CT. LL performed the analysis with guidance from CT, GC and SCV. All authors contributed critically to the drafts of the chapter.

With these exceptions, I declare that the work in this thesis is my own and has not been submitted for any other degree of award.

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Chapter 1 – General Introduction

1.1 The Anthropocene: winners and losers

We live in a human world. Human activities now influence global biogeochemical processes to such an extent that the current era has been defined as a new geological epoch, the Anthropocene (Lewis and Maslin, 2015). As such, human activities have had profound and far-reaching impacts on the world's ecosystems (Mckinney and Lockwood, 1999). Habitat destruction, particularly urbanisation and conversion to agriculture, is a major driver of species declines (McKinney, 2006, 2008; Foley *et al.*, 2011). Humans have also introduced non-native invasive species into terrestrial and marine ecosystems, causing reductions in species richness and a loss of ecosystem services (Vitousek *et al.*, 1996; Blackburn *et al.*, 2004; Gallardo *et al.*, 2016). Additionally, the indirect effects of human-induced climate change represent a major threat to many species and ecosystems globally (Bellard *et al.*, 2012). In many cases these drivers have acted in synergy to drive catastrophic declines in biodiversity, resulting in a sixth global mass extinction event (Barnosky *et al.*, 2011; Ceballos, Ehrlich and Dirzo, 2017; Davis, Faurby and Svenning, 2018).

Despite the negative impacts outlined above, human activities have also provided a range of ecological opportunities. A subset of species have benefitted greatly from these opportunities, with the emergence of a few winners (hereafter "Anthropocene opportunists") and a multitude of losers resulting in biotic homogenisation across ecosystems in the Anthropocene (Mckinney and Lockwood, 1999; Olden *et al.*, 2004; McKinney, 2006). For example, species introduced to novel ecosystems by humans often benefit from this redistribution, rapidly increasing in abundance when released from the predators, competitors and pathogens found in their native ranges (Sakai *et al.*, 2001). In some instances, introduced populations may vastly outperform those in their native range, as is the case with the Chinese water deer, where the introduced European animals make up 40% of the global population of this threatened species (Putman *et al.*, 2020). Similarly, a host of species may benefit from the effects of global climate change, expanding their distributions into new areas as conditions become more favourable (Thomas *et al.*, 2011; Bonebrake *et al.*, 2018). Although clearly important components of global ecosystem change, invasive species and climate change are beyond the scope of this thesis and are not discussed further.

Here I focus on the ecological opportunities arising from and the modification of natural landscapes by urbanisation (Møller, 2009; Bateman and Fleming, 2012) and agriculture (Foley *et al.*, 2011; Fox and Abraham, 2017); the provision of predictable anthropogenic food subsidies (hereafter PAFS) in terrestrial and marine ecosystems (Oro *et al.*, 2013); and changes in wildlife management including the widespread removal of large carnivores (Ripple *et al.*, 2014) and legal protection (Côte *et al.*, 2004; Coulson, 2015). These changes have benefitted a subset of adaptable species, often dietary generalists which in some cases also have rapid reproductive rates (Shochat *et al.*, 2006; Møller, 2009; Oro *et al.*, 2013), resulting in changes behaviour, life-history parameters and ultimately population-size (Prugh *et al.*, 2009; Oro *et al.*, 2013; Newsome *et al.*, 2015).

In this chapter I first outline the ways in which habitat modification, PAFS and changes in wildlife management have altered the ecology and demography of Anthropocene opportunists. I then discuss the ecological consequences of population expansions and their implications for human activities before summarising how management has responded to mitigate these impacts.

Although the narrative of Anthropocene opportunists is often framed as one of unbridled success, ongoing human activities may harm these species and I outline the hidden costs of anthropogenic opportunities along with issues relating to shifting PAFS availability and public perceptions. Finally, I introduce gulls as a model system for studying Anthropocene Opportunists and lesser black-backed gulls (*Larus fuscus*) as the case study for this thesis before outlining the scope of the remaining chapters.

1.2 Ecological opportunities in the Anthropocene

1.2.1 Habitat modification

Human activities have resulted in the modification of huge areas of natural habitats around the globe. These changes gathered pace during the last century as the global human population increased rapidly, and shifted to a more urbanised lifestyle, leading to increased urban development (Seto, Fragkias and Gu, 2011; Seto, Güneralp and Hutyra, 2012). In order to feed this burgeoning population, large swathes of natural habitats have been converted to arable land, which now covers c. 11% of the world's land surface (Foley *et al.*, 2005, 2011). Although both urbanisation and agricultural expansion have contributed to biotic homogenisation (McKinney, 2006; Pauchard *et al.*, 2006; Karp *et al.*, 2012; Concepción *et al.*, 2015), there are also opportunities for successful species in these highly modified habitats (Barnett *et al.*, 2004; Møller, 2009).

Modification of natural habitats may increase the availability of natural prey items, such as soil invertebrates in farmland (Kruuk, 1978; Isaksson *et al.*, 2016) and green urban spaces (Mason, 2000; Gaston *et al.*, 2005; Spelt *et al.*, 2019). Additionally, improvement of grassland for livestock provides higher quality resources for successful grazing species such as geese, contributing to population increases (Fox and Abraham, 2017; Mason *et al.*, 2018). In urban areas, colonising species may also benefit from the provision of predator free habitat (Rock, 2005) or the positive effects of a benign urban microclimate which may benefit winter-roosting birds and bats (Partecke, Van't Hof and Gwinner, 2004; Sachanowicz *et al.*, 2019). Finally, the creation of water storage reservoirs for a growing human population has provided breeding and roosting habitat for a range of gull species, facilitating their colonisation of inland areas (Conover, 1983; Lenda *et al.*, 2010; Burton *et al.*, 2013).

1.2.2 PAFS

A key feature of human-modified landscapes is the provision of large volumes of PAFS which represent a major anthropogenic opportunity. These subsidies include street refuse (Contesse *et al.*, 2004; Bino *et al.*, 2010; Huig, Buijs and Kleyheeg, 2016) and supplementary food (Robb *et al.*, 2008; Plummer *et al.*, 2015) in urban areas, livestock feed (van den Bosch *et al.*, 2019) and crops and their residuals (Stewart, McShea and Piccolo, 2002; Abraham, Jefferies and Alisauskas, 2005; Fox *et al.*, 2005; Foley *et al.*, 2011; Patenaude-Monette, Bélisle and Giroux, 2014) in agricultural habitats. Human activities have also produced large quantities of PAFS from two additional sources. In marine ecosystems fisheries discards are the most important PAFS, with global production peaking at 18.8 million tonnes in 1989 (Zeller *et al.*, 2018). Discards can support large communities of scavenging seabirds (Garthe, Camphuysen and Furness, 1996; Sherley *et al.*, 2019), and are consumed by a range of species (Votier *et al.*, 2010; Bicknell *et al.*, 2013; Tyson *et al.*, 2015). In terrestrial ecosystems, humans waste between 30-40% of annual food production, with huge amounts dumped in landfills (Parfitt, Barthel and MacNaughton, 2010; Hoornweg and Bhada-Tata, 2012), providing an important food source for at least 98 recorded vertebrates, with the majority being predatory and scavenging birds and mammals (Plaza and Lambertucci, 2017).

PAFS have directly impacted the behaviour, ecology and evolution of species which consume them (Robb *et al.*, 2008; Bicknell *et al.*, 2013; Oro *et al.*, 2013; Plummer *et al.*, 2015). Altered behaviour in response to PAFS is often in the form of movement changes, from reductions in home range size (Prange, Gehrt and Wiggers, 2004) through selection for habitats with anthropogenic resources (Bozek, Prange and Gehrt, 2007; Kristan and Boarman, 2007; Spelt *et al.*, 2020) to shifts from migratory to resident behaviour at the individual and population-levels (Cozzi *et al.*, 2016; Gilbert *et al.*, 2016). Likewise, given that food supply often limits fitness components (Martin, 1987; Oro *et al.*, 2013), the availability of PAFS has been shown to influence body condition (Hüppop and Wurm, 2000; Auman, Meathrel and Richardson, 2008) and alter life history traits such as annual survival (Annett and Pierotti, 1999), and reproductive performance (Pons, 1992; Pons and Migot, 1995; Oro, 1996).

The demographic impacts of PAFS are often difficult to disentangle from other potential drivers (Oro *et al.*, 2013), however growth rates of rook (*Corvus frugilegus*) and yellow-legged gull (*Larus michahellis*) colonies correlate positively with local availability of landfill refuse (Duhem *et al.*, 2008; Olea and Baglione, 2008). Additionally, population densities of mesopredators such as coyotes (*Canis latrans*), raccoons (*Procyon lotor*) and red foxes (*Vulpes vulpes*), are often higher in urban areas where refuse is abundant (Fedriani *et al.*, 2001; Prange, Gehrt and Wiggers, 2003; Bino *et al.*, 2010). Foraging on PAFS has also been implicated in the expansive population dynamics of a range of Anthropocene opportunists including corvids (Marzluff and Neatherlin, 2006), scavenging seabirds (Sherley *et al.*, 2019), geese (*Anseridae*) (Abraham, Jefferies and Alisauskas, 2005; Alisauskas *et al.*, 2011), and even generalist herbivores such as white-tailed deer (*Odocoileus virginianus*) (Stewart, McShea and Piccolo, 2002; Côte *et al.*, 2004).

1.2.3 Direct wildlife management

Humans have controlled large predators across terrestrial ecosystems, leading to reductions in abundance, range contractions and ultimately extirpation in many areas (Prugh *et al.*, 2009; Ripple *et al.*, 2014). The removal of large predators has had cascading effects on trophic and community dynamics in many ecosystems (Estes *et al.*, 2011; Conner and Morris, 2015; Newsome *et al.*, 2017). "Mesopredator release", defined as the expansion in density or distribution, or change in behaviour of a middle-rank predator resulting from a decline in the density or distribution of an apex predator (Prugh *et al.*, 2009), is a common outcome. This phenomenon has contributed to the expansive population dynamics observed in many generalist mesopredators, particularly mammals such as coyotes, red foxes, and raccoons (Prugh *et al.*, 2009; Henden *et al.*, 2020), which have also benefitted from PAFS availability and urbanisation (Fedriani *et al.*, 2001; Contesse *et al.*, 2004; Prange, Gehrt and Wiggers, 2004; Bino *et al.*, 2010). In addition to mesopredator release, reduced predation pressure has also contributed to the increase in the abundance of large herbivores such as deer (Côte *et al.*, 2004).

Finally, reductions in persecution, overexploitation and improved legal protection have also contributed to the demographic expansion of some species. Scavenging seabirds, such as gulls and their eggs, were widely harvested as a food resource and for feathers during the 19th century (Drury, 1973; Spaans, 1998), and the introduction of protective legislation (i.e. UK Sea Bird Protection Act (1869); North American Migratory Bird Treaty Act (1918)) contributed to subsequent population increases in these species (Coulson, 2015; Anderson *et al.*, 2016). Similarly, the widespread introduction of hunting bans and stricter game laws contributed to the rapid increase in white-tailed deer populations in North America during the 20th century (Brown *et al.*, 2000; Côte *et al.*, 2004).

1.3 The consequences of Anthropocene opportunists

1.3.1 Ecological impacts

As populations of successful species have expanded, there have been consequences for ecosystem and community dynamics as reciprocal interactions such as predation and competition have been modified (Oro *et al.*, 2013). The impacts of predation by Anthropocene opportunists, particularly gulls, corvids and mammalian mesopredators are well documented (Yorio and Quintana, 1997; Marzluff and Neatherlin, 2006; Conner and Morris, 2015; Madden, Arroyo and Amar, 2015; Roos *et al.*, 2018; Henden *et al.*, 2020), and represent a conservation concern for some species (Crooks and Soule, 1999; Scopel and Diamond, 2017; Roos *et al.*, 2018; McMahon *et al.*, 2020). As successful species expand their distributions, they may have similar ecological impacts in their new ranges (Skórka *et al.*, 2014). Hyperpredation may also occur, where Anthropocene opportunists expanding in response to PAFS availability lead to declines in rare prey species (Courchamp, Langlais and Sugihara, 2000). For example, red foxes expanding northwards in Europe in response to urbanisation and PAFS have negatively impacted threatened species (Henden *et al.*, 2020), competing with Arctic foxes (*Vulpes lagopus*) (Angerbjörn *et al.*, 2013; Ims *et al.*, 2017) and predating nesting lesser white-fronted geese (*Anser erythropus*) (Marolla *et al.*, 2019). Such predation impacts may be exacerbated if supplies of alternative resources such as PAFS, on which generalists rely, are removed (Stenhouse and Montevecchi, 1999; Votier *et al.*, 2004; Bicknell *et al.*, 2013).

In addition to the direct effects of predation and competition, successful species may influence trophic and ecosystem dynamics indirectly via habitat modification. Growing seabird colonies can alter habitat structure via vegetation removal/trampling (Zelenskaya and Khoreva, 2006) and/or guano deposition (Otero *et al.*, 2015), altering soil chemistry (Otero, 1998; Otero *et al.*, 2018). Such modifications can catalyse irreversible changes in plant community structure (Baumberger *et al.*, 2012), with negative effects on threatened plants and ecosystem dynamics (Vidal, Medail and Tatoni, 1998).

Where successful species are migratory, ecological opportunities in one location may impact ecosystems a continent away, as with the degradation of Arctic ecosystems by overabundant snow geese (*Chen caerulescens*) which have undergone rapid population increases in response to changing agricultural practices in their winter range in the USA (Milakovic and Jefferies, 2003; Abraham, Jefferies and Alisauskas, 2005; Hessen *et al.*, 2017). Additionally, increases in the abundance of browsing species such as deer due to PAFS availability, legal protection and reduced predation pressure, may have cascading impacts on vegetation structure and trophic dynamics in a range of habitats (Côte *et al.*, 2004; Ripple and Beschta, 2012).

1.3.2 Societal impacts

As Anthropocene opportunists have expanded, the potential for human-wildlife interactions have increased (Belant, 1997; Bateman and Fleming, 2012). One major issue is the potential for these species to act as reservoirs for a huge range of zoonotic pathogens (Kruse, Kirkemo and Handeland, 2004), antimicrobial resistant bacteria (Woolhouse *et al.*, 2015), and vector-borne pathogens such as Lyme disease (Kugeler *et al.*, 2016). This is a particular issue in urban areas where humans and animals live in close proximity (Mackenstedt, Jenkins and

Romig, 2015; Navarro *et al.*, 2019). Anthropocene opportunists foraging in agricultural areas may also pose a risk transmission to livestock (Coulson, Butterfield and Thomas, 1983; Böhm, Hutchings and White, 2009; Wilson, Carter and Delahay, 2011).

Human-wildlife conflict may also result from impacts on economic activities. Successful species may move into modified agricultural habitats to forage, consuming crops (Stewart, McShea and Piccolo, 2002) and livestock (Lehner, 1976), creating conflict with farmers (Hill, 2018). Predation pressure from abundant mesopredators can depress populations of ground-nesting game birds, with economic implications for the shooting industry (O'Connell, 1995; Kämmerle and Storch, 2019; Henden *et al.*, 2020). Successful species can also impact transport infrastructure, with deer, geese and gulls posing a considerable risk for aviation collisions during take-off and landing (Rochard and Horton, 1980; Neubauer, 1990; Dolbeer, Wright and Cleary, 2000) and deer frequently involved in road and rail collisions (Putman, 1997; Côte *et al.*, 2004; Huijser *et al.*, 2009). Collisions with animals may have significant costs, both economically and in terms of loss of life (Putman, 1997; Sodhi, 2002; Huijser *et al.*, 2009).

Colonisation of urban areas by successful species has increased human-wildlife interactions including behaviours perceived as a nuisance by the general public (Harris, 1984; Hill, Carbery and Deane, 2007; Trotter, 2019; Nardi *et al.*, 2020). Examples of nuisance behaviours include damage to homes and property (Rock, 2005; Hill, Carbery and Deane, 2007; Delahay and Heydon, 2009), consumption of refuse via bin-raiding (Harris, 1984; Clark, 1994; Contesse *et al.*, 2004), noise pollution (Rock, 2012), and aggressive food-snatching behaviour (Goumas, Boogert and Kelley, 2020). Although rare, more serious nuisance behaviours may include predation of pets (Alexander and Quinn, 2011) and aggressive interactions with people (Timm *et al.*, 2004). These interactions can occasionally lead to fatalities when dangerous large animals are attracted by the ecological opportunities around human settlements (Wilder *et al.*, 2017; Shaffer *et al.*, 2019).

1.4 Management of Anthropocene opportunists

1.4.1 Lethal control

As a consequence of their impacts on human activities and ecologically, Anthropocene opportunists are often the focus of management interventions (Rock, 2005; Conner and Morris, 2015; Payo-Payo *et al.*, 2015; McMahon *et al.*, 2020). The nature of management interventions depends on the species involved and the nature of the conflict, however lethal control via shooting, trapping or poisoned baits, is a common approach for mitigating the impacts of successful species, and may involve blanket culls (Bosch *et al.*, 2000; Brown *et al.*, 2000; Calladine and Park, 2006; Scopel and Diamond, 2017; Marolla *et al.*, 2019; Henden *et al.*, 2020; McMahon *et al.*, 2020) or targeted removal of problem individuals (Sanz-Aguilar *et al.*, 2009). However the long-term efficacy of culling may be limited by dispersal, the relaxation of density-dependent competition or saturation by an overabundant population (Wanless *et al.*, 1996; Bosch *et al.*, 2000; Koons, Rockwell and Aubry, 2014). In some situations, lethal control may be also be undesirable for ethical reasons (Dubois *et al.*, 2017) or impractical due to concerns for public health and safety (Rock, 2005).

1.4.2 Non-lethal control

Where lethal control is unsuitable or undesirable, a range of non-lethal management approaches have been devised to mitigate conservation conflicts. Species may be excluded from specific areas using physical deterrents (Huijser *et al.*, 2009; Malpas *et al.*, 2013), or auditory deterrents (Baxter, 2000; Rock, 2005). However habituation can limit the efficacy of this approach (Rock, 2012).

Alternatively, problem individuals of larger species may be translocated (Linnell *et al.*, 1997; Brown *et al.*, 2000; Mukesh *et al.*, 2015). Limitation of PAFS availability (Prange, Gehrt and Wiggers, 2003; Bino *et al.*, 2010), suppression of reproductive rates via contraception (Barlow, 2000), or the destruction or removal of nests and eggs in avian species (Rock, 2012), are options for controlling population density. However assessing the efficacy and benefits of different mitigation approaches may be hindered by a lack of information on the costs of management (Trotter, 2019), a dearth of appropriately controlled studies (Henden *et al.*, 2020), and the challenges involved in surveying populations to quantify impacts, particularly in urban areas (Rock, 2005; Calladine and Park, 2006; Scott *et al.*, 2014, 2018).

1.5 Threats to Anthropocene opportunists

1.5.1 Hidden costs of exploiting anthropogenic opportunities

The narrative around Anthropocene opportunists is often framed as one of ongoing success. Many species have undergone rapid and sustained increase resulting in overabundant populations which require management to mitigate their impacts on humans and ecosystems (Vidal, Medail and Tatoni, 1998; Payo-Payo *et al.*, 2015). Whilst this may be true for some species, such as the snow goose (Alisauskas *et al.*, 2011; Koons, Rockwell and Aubry, 2014), it also represents an oversimplification which ignores the costs of exploiting anthropogenic opportunities (Oro *et al.*, 2013).

Although anthropogenic subsidies are often predictably available in large quantities, consuming them may involve a quality vs. quantity trade-off, with subsidies representing low value “junk-foods” compared with natural prey (Grémillet *et al.*, 2008; Österblom *et al.*, 2008; Murray *et al.*, 2015). Consuming this poor quality food may lead to impacts on condition or reproductive output compared with natural resources (Annett and Pierotti, 1999; Murray *et al.*, 2015). Additionally, foraging on PAFS such as landfill or urban refuse may increase the risk of exposure to pathogens (Ortiz and Smith, 1994; Höfle and Migura-garcia, 2020), toxic chemicals (Tongue *et al.*, 2019) and solid pollutants such as plastics (Lenzi *et al.*, 2016; Seif *et al.*, 2018). Foraging on fisheries discards may also increase mortality risk due to the possibility of bycatch (Clay *et al.*, 2019).

High density road networks are a feature of human-modified landscapes and road collisions represent a major source of mortality for vertebrates (Forman and Alexander, 1998; Schwartz *et al.*, 2018). Additionally, individuals breeding in anthropogenic habitats may have lower-levels of reproductive performance due to human-interference (Rock, 2005, 2012), or sudden loss of breeding habitats due to human development (Kavelaars *et al.*, 2020; Salas *et al.*, 2020). Although the effect of anthropogenic habitats on population structure requires further research (Ross-Smith, Robinson, *et al.*, 2014), it is possible that anthropogenic habitats such as urban areas function as population sinks (Stillfried *et al.*, 2017), which attract individuals from the wider landscape but represent sub-optimal habitats due to increased mortality risk or reduced reproductive performance.

1.5.2 Future risks of dependence on PAFS

Unlike natural resources, PAFS availability may decline very rapidly either due to management interventions (Bino *et al.*, 2010) or human policy changes aimed at sustainability (Bicknell *et al.*, 2013; Real *et al.*, 2017). This may have negative consequences for species or populations exploiting PAFS, with reduced food availability leading to changes in life-history parameters including reduced survival or reproductive output and ultimately population declines (Pons, 1992; Oro, 1996; Oro, Jover and Ruiz, 1996; Bino *et al.*, 2010). Moreover, changing food availability may increase predation impacts on threatened species, leading to further calls for management of Anthropocene opportunists (Stenhouse and Montevecchi, 1999; Bicknell *et al.*, 2013).

1.5.3 Changing public perceptions

As Anthropocene opportunists shift into closer proximity with humans, it can create a false perception that these species are overabundant and may lead to public calls for management due to human-wildlife interactions (Trotter, 2019). While many successful species are common in the wider landscape, some species may be forced to exploit anthropogenic opportunities due to degradation or destruction of their natural habitats (Pedro *et al.*, 2013; Blight, Drever and Arcese, 2015; Wilder *et al.*, 2017). In some cases, species as diverse as elephants (Shaffer *et al.*, 2019) and herring gulls (*Larus argentatus*) (Nager and O'Hanlon, 2016) which feed and/or breed in anthropogenic environments may be threatened or declining at the landscape-level, with anthropogenic areas acting as sub-optimal substitutes for their natural habitats (Martínez-Abraín and Jiménez, 2016). Moreover, the difficulties involved in surveying urban populations (Rock, 2005; Calladine and Park, 2006; Scott *et al.*, 2014, 2018) can make it difficult to quantify true levels of abundance and determine whether urban colonisations represent numeric increases at the landscape-level or redistributions within a larger metapopulation (Ross-Smith, Grantham, *et al.*, 2014).

Perceptions of apparently successful species may also be skewed by shifting baseline syndrome, defined as a gradual shift in the accepted norm for the natural environment due to a lack of information or experience on past conditions (Soga and Gaston, 2018). Whilst the demographic expansions shown by many successful species since the start of the 20th century appear dramatic, information on past biodiversity states is often poor (Mihoub *et al.*, 2017) and early estimates of abundance may represent historically small populations depressed by previous persecution and over-exploitation (Drury, 1973; Spaans, 1998). In this context, contemporary increases in abundance may, at least in part, represent a recovery to historic baseline levels for some successful species (Côte *et al.*, 2004; Coulson, 2015; Anderson *et al.*, 2016). Conversely, in some instances current declines may represent a return to a more "natural" baseline following population inflation in by anthropogenic opportunities. Despite the challenges involved, it is therefore important to consider appropriate historic baselines when developing and evaluating conservation and management interventions for species which have shown strong demographic responses to anthropogenic change (Bull *et al.*, 2014; Mihoub *et al.*, 2017).

1.6 Gulls as a model system

1.6.1 Gulls as Anthropocene opportunists

Gulls (*Laridae*) are closely linked with humans and, as such, provide a good model to study the effects of ongoing anthropogenic change on the ecology and demography of opportunistic species. Many gulls are generalists with a broad dietary niche and have benefitted from novel PAFS including fisheries discards in marine habitats (Oro, Jover and Ruiz, 1996; Yorio and Caille, 2004; Yoda *et al.*, 2012; Tyson *et al.*, 2015), landfills, urban refuse and agricultural residuals in terrestrial ecosystems (Pons, 1992; Duhem *et al.*, 2008; Patenaude-Monette, Bélisle and Giroux, 2014; Ackerman *et al.*, 2018; Spelt *et al.*, 2019; van den Bosch *et al.*, 2019). The explosion in PAFS availability, combined with reduced persecution (Coulson, 2015; Anderson *et al.*, 2016), has led to increases in gull abundance (Coulson and Coulson, 1998; Spaans, 1998; Nager and O'Hanlon, 2016; Whittington *et al.*, 2016; Yorio *et al.*, 2016). Many gull species have also responded strongly to urban development, visiting urban areas to forage on PAFS and taking advantage of predator-free breeding habitat to expand their ranges into towns and cities around the globe (Dwyer, Belant and Dolbeer, 1996; Rock, 2005; Zelenskaya and Khoreva, 2006; Soldatini *et al.*, 2008; Blight, Bertram and Kroc, 2019; Méndez *et al.*, 2020). As visible colonial breeders, gulls are often more accessible than other Anthropocene opportunists such as mammalian mesopredators. This has allowed researchers to study various aspects of the movement behaviour (Camphuysen, 2013; Navarro *et al.*, 2017), diet (Coulson and Coulson, 2008; Lopezosa *et al.*, 2019) and breeding biology (Vermeer, Power and Smith, 1988; Bolton *et al.*, 1992; Royle, 1998) of a range of species breeding in different habitats.

As gull populations expanded in response to human activities they had impacts both ecologically (Sadoul *et al.*, 1996; Vidal, Medail and Tatoni, 1998; Stenhouse and Montevecchi, 1999; Martínez-Abraín *et al.*, 2003; Sanz-Aguilar *et al.*, 2009; Baumberger *et al.*, 2012; Scopel and Diamond, 2017) and on human activities (Calladine and Park, 2006; Carroll *et al.*, 2015; Dolbeer and Wright, 2015; Goumas *et al.*, 2019; Navarro *et al.*, 2019). In response, gull populations have been managed extensively using a range of lethal (O'Connell, 1995; Wanless *et al.*, 1996; Sanz-Aguilar *et al.*, 2009) and non-lethal approaches (Blokpoel and Tessier, 1984; Blokpoel, Gaston and Andress, 1997; Baxter, 2000; Rock, 2005; Donehower *et al.*, 2007).

Although gull management is widespread, interventions are beset by challenges including high economic and time costs (Calladine and Park, 2006), requirement for repeat applications (Rock, 2012; Evans, Votier and Dall, 2016), and the combination of the longevity, mobility and high site fidelity and natal philopatry of many gull species (Wanless *et al.*, 1996). Moreover, evidence for long-term efficacy is mixed (Coulson, Duncan and Thomas, 1982; Coulson and Coulson, 2009; Payo-Payo *et al.*, 2015; Salas *et al.*, 2020) and recent declines in reproductive performance and abundance in some populations have led to questions of the validity of management interventions (Mitchell *et al.*, 2004; Ross-Smith, Robinson, *et al.*, 2014; Blight, Drever and Arcese, 2015; Eaton *et al.*, 2015; Nager and O'Hanlon, 2016). This has created a conundrum for management organisations tasked with balancing mitigation of gull impacts with their conservation (Ross-Smith, Robinson, *et al.*, 2014).

1.6.2 Study species: lesser black-backed gulls

The lesser black-backed gull provides a useful case study for investigating the influence of PAFS availability and habitat modification on the demography and ecology of opportunistic species. Traditionally, lesser black-backed gulls had a coastal European distribution, breeding in Northern Europe and wintering south to North Africa (Cramp and Simmons, 1983). Although considered more marine in its foraging ecology than the sympatric herring gull (Camphuysen, 2013), the species is a dietary generalist (Ross-Smith, Robinson, *et al.*, 2014), consuming a broad range of prey from marine (Thaxter *et al.*, 2015; Garthe *et al.*, 2016) and terrestrial environments (Gyimesi *et al.*, 2016; Isaksson *et al.*, 2016).

Lesser black-backed gulls breed colonially, typically recruiting at the age of four years (Cramp and Simmons, 1983). Females lay a modal clutch size of three eggs between late April and early June which is then incubated for approximately four weeks with chicks taking a further five weeks to fledge (Harris, 1964; Bolton *et al.*, 1992; Oro, 1996; Royle, 1998). When breeding, lesser black-backed gulls act as central-place foragers, routinely travelling 40-80km to forage (Camphuysen *et al.*, 2010), with long-foraging trips of over 100km occasionally recorded (Camphuysen, 2013). Birds show high philopatry, frequently recruiting into the natal colony (Wanless *et al.*, 1996), although they may recruit elsewhere if conditions are unsuitable (Monaghan and Coulson, 1977). Once lesser black-backed gulls reach breeding age, annual adult survival is in the region of 90% (Wanless *et al.*, 1996; Camphuysen and Gronert, 2012; Rock and Vaughan, 2013) with successful birds frequently using the same nest site each year (O'Connell, 1995; Rock, 2005).

Lesser black-backed gulls have adapted to forage on PAFS in the form of fishery discards (Furness, Ensor and Hudson, 1992; Garthe, Camphuysen and Furness, 1996; Tyson *et al.*, 2015; Sherley *et al.*, 2020), landfill waste (Mudge and Ferns, 1982) and refuse in urban environments (Huig, Buijs and Kleyheeg, 2016; Spelt *et al.*, 2019). This increase in PAFS availability, combined with improved legal protection (e.g. UK Migratory Birds Treaty Act (1869) led to a rapid increase in global abundance from the mid-twentieth century onwards (Cramp, Bourne and Saunders, 1974; Spaans, 1998; Mitchell *et al.*, 2004; Nager and O'Hanlon, 2016) accompanied by range expansions (Hallgrimsson *et al.*, 2011; Boertmann and Frederiksen, 2016). The species also responded strongly to habitat modification, frequently foraging in urban (Huig, Buijs and Kleyheeg, 2016; Spelt *et al.*, 2019) and agricultural areas (Gyimesi *et al.*, 2016; Isaksson *et al.*, 2016), and moving into towns and cities to breed (Cramp, 1971; Monaghan and Coulson, 1977; Raven and Coulson, 1997; Rock, 2005).

Currently around 38% of the estimated global lesser black-backed gull population breeds in the UK (http://wpe.wetlands.org/) with 60% of that total in England (Calladine, 2004). As summarised by Ross-Smith *et al.* (2014), in England the species invokes legal protection from the EU Birds Directive 2009 (2009/147/EC) which is enforced in UK Law via the Wildlife and Countryside Act (WCA), and is fully protected as a notified feature of several Sites of Special Scientific Interest (SSSI) and as a qualifying feature of several Special Protection Areas (SPAs).

However, until recently the species could also be controlled under three General Licenses issued under the WCA (1981). For certain purposes, such as in the interests of public health and safety, this permitted lethal control with no requirement for reporting (Ross-Smith, Robinson, *et al.*, 2014). The situation has recently changed and due to awareness of the declines in coastal breeding lesser black-backed gull populations, those seeking to control these species will need to apply for individual licences in 2021. The only exception is airfields which can operate under the class licence (https://www.gov.uk/government/collections/bird-licences)

As lesser black-backed gull populations expanded, they were managed extensively due to impacts on sympatric seabirds (Wanless *et al.*, 1996; Harris and Wanless, 1997; Finney *et al.*, 2001) and human activities (O'Connell, 1995; Rock, 2005, 2012). Despite the dramatic increases during the 20th century, the UK population of lesser black-backed gulls has recently declined, mostly due to losses at several large, coastal colonies (Ross-Smith, Robinson, *et al.*, 2014; Nager and O'Hanlon, 2016). The species is now listed as "Amber" on the UK *Birds of Conservation Concern* list (Eaton *et al.*, 2015) due to the international importance and localised nature of its breeding population. This creates a conservation conundrum for statutory organisations, tasked with balancing the mitigation of negative gull impacts with maintenance of favourable conservation status.

Having sufficient ecological information is key when attempting to address conservation conflicts (Redpath *et al.*, 2013), however, in the case of the lesser black-backed gull such information is lacking (Ross-Smith, Robinson, *et al.*, 2014). Current knowledge gaps relate to the size of urban populations, differences in the ecology of urban and coastal populations, responses to changing anthropogenic resource availability and patterns of dispersal and meta-population dynamics (Ross-Smith, Grantham, *et al.*, 2014; Ross-Smith, Robinson, *et al.*, 2014). These knowledge gaps, combined with a dearth of information on the costs, benefits and efficacy of mitigation (Trotter, 2019), present a considerable barrier to the development of an informed conservation management strategy for this species.

1.7 Thesis outline

In this introductory chapter I have discussed how human activities create ecological opportunities which are exploited by a range of species, leading to consequences both ecologically and for people. The remainder of this thesis investigates how habitat modification and the provision of PAFS has influenced the ecology of gulls, a group containing a number of these Anthropocene opportunists. It begins by synthesising the literature on gulls globally before focussing on lesser black-backed gull breeding populations in northwest England as a case study. Details of the remaining chapters are outlined below:

Chapter 2 reviews the published literature on changes in the abundance and distribution of gulls globally, from the beginning of the twentieth century until the present. It then discusses how anthropogenic ecosystem changes have driven the observed demographic trends, the consequences both ecologically and for human activities and the challenges for management and conservation. Finally, it summarises current knowledge gaps and outlines a research agenda aimed at balancing future conservation and management of gulls.

Chapter 3 examines how gulls alter their foraging behaviour in response to changes in anthropogenic resource availability. Using Global Positioning System (GPS) tracking data from adult lesser black-backed gulls breeding at two colonies in northwest England, I investigate population-level responses to the closure of major landfill sites within the foraging range in terms of movement behaviour (foraging trip metrics) and habitat selection. Additionally, at one colony where morphometric data were available, I test for an effect of the landfill closure on adult body condition.

Chapter 4 compares the foraging ecology and breeding parameters of lesser black-backed gulls breeding at neighbouring coastal and urban colonies. I first use GPS tracking data to quantify the "urbanness" of individual tracked gulls, before investigating colony-level differences in foraging ecology in terms of movement behaviour (foraging trip metrics), space use, habitat selection and diet. Finally, I test for differences in breeding parameters between birds from these colonies in terms of egg metrics and chick condition.

Chapter 5 investigates the incidence and extent of individual foraging site fidelity of adult lesser black-backed gulls breeding at the three colonies considered above, again based on GPS tracking data. I first determine whether gulls exhibit foraging site fidelity by calculating the repeatability of foraging trip metrics at the population-level. I then calculate individual-level repeatability values for the same trip metrics, in order to quantify whether individual gulls differ in their degree of site fidelity and the composition of populations in terms of specialist vs. generalist individuals. Finally, I model differences in the degree of individual site fidelity between the colonies, which vary in terms of conspecific density and their reliance on predictable anthropogenic resources.

Chapter 6 summarises the results of the previous chapters and outlines avenues for further research raised by this work.

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Chapter 2 – Gulls in the Anthropocene: a review of changes in abundance, distribution, conservation and management

2.1 Abstract

Human actions have reduced biodiversity, whilst also creating ecological opportunities. However, the costs and benefits of anthropization require more consideration. Gulls (Laridae) have both suffered and benefitted from people, but we lack a synthesis of these effects. Here we review trends in gull abundance and distribution since the start of the 20th Century, before discussing the likely drivers of these trends and the challenges this has posed for management and conservation. Since 1900, some gull taxa (mostly *Larus* spp.) underwent rapid population growth and range expansion, linked to changing human actions, including: reduced harvesting and persecution, habitat creation and predictable anthropogenic food subsidies (PAFS). More recent population stabilisation and decline may relate to declines in resource availability. Population increases and movement to urban areas brought gulls into closer proximity with humans, amplifying human-wildlife interactions such as nuisance behaviour, disease transmission, aviation collision, agricultural impacts and ecological impacts (e.g. seabird predation and altering vegetation). Mitigating gull impacts involves both lethal and non-lethal approaches. The literature suggests, management is hindered by poor understanding of gull ecology and demography and public perceptions of gulls, as well as habituation or dispersal, highlighting these as important research goals. Recently, as a consequence of natural (e.g. disease, competition and predation) and/or anthropogenic factors (e.g. management, reduced food availability), some gull populations have stabilised or declined. This lack of resilience questions interventions and instead highlights the need for more effective conservation strategies to boost declining gull populations. To better

understand the true population status of gull species and the efficacy of management solutions we recommend more comprehensive demographic monitoring (particularly for urban gulls) and additional research on dispersal. Management could also benefit from a much broader vision, both in terms of spatio-temporal scale and diversity of stakeholders. Finally, we need to do more to consider the positive aspects of sharing our world with gulls.

2.2 Introduction

Anthropogenic change has negatively impacted global biodiversity (Mckinney and Lockwood, 1999), while also creating novel ecological opportunities for some taxa (Crooks & Soule, 1999; Møller, 2009, Oro et al., 2013). Understanding and managing the conservation of both the winners and losers of anthropogenic change is therefore a key goal in ecology.

A number of animals have benefitted from anthropization, particularly opportunist mammals (Prugh et al., 2009; Zeller et al., 2019) and birds (Leu, Hanser and Knick, 2013). For instance, persecution has reduced many top predator populations, leading to meso-predator release (Crooks and Soule, 1999), urbanisation has created novel breeding habitat (Møller, 2009), and predictable anthropogenic food subsidies (PAFS) have created new foraging opportunities (Oro et al., 2013). Such changes have benefited many species (Prugh et al., 2009), but there may also be costs including increased mortality risk from vehicle collisions (Schwartz et al., 2018), lower nutrient content of PAFS compared with natural prey (Österblom *et al.*, 2008; Murray *et al.*, 2015) and increased exposure to pollutants (Tongue *et al.*, 2019; Lenzi *et al.*, 2016) and pathogens (Ortiz and Smith, 1994) when foraging on refuse. Moreover, population increases and range expansion have in turn created new conservation and management challenges in both natural (Vidal, Medail and Tatoni, 1998) and human-impacted habitats (Rock, 2005).

Gulls (*Laridae*) are closely linked with humans. They comprise c. 52 species across nine genera (International Ornithologist's Council taxonomy - https://www.worldbirdnames.org/bow/gulls/), breeding on every continent except Antarctica (Olsen, 2018). For many species, particularly those in the genus *Larus*, human opportunities are thought to have driven population increases and range expansions, which has in turn increased human-gull interactions (Rock, 2012). Nevertheless, such general associations lack a synthesis based on the peer-reviewed literature. Here, we first summarise how global gull abundance and distribution have changed over the past century. We then discuss how anthropogenic factors, specifically legal protection, habitat creation and PAFS, may have driven changes in gull populations. Expanded gull populations have had deleterious impacts on humans and natural ecosystems and we highlight these before synthesizing existing strategies for management and conservation. Finally, we bring this information together to create a roadmap for research aimed at informing future strategies to balance gull conservation and management.

2.3 Methods

We first summarised broad changes in gull abundance and distribution from the start of the 20th century to the present, in order to provide background to the subsequent discussion of the drivers of demographic change and the associated conservation and management challenges they have presented. To find trend information, we searched the peer-reviewed literature using Google Scholar (https://scholar.google.co.uk/) and ISI Web of Science (http://wok.mimas.ac.uk/), using the search terms *gull** and *Larus** alongside relevant demographic terms: *population*, *status*, *increasing*, *declining*, *demography*, *range*, *distribution*, *breeding* and *nesting* up to June 2019. We included species where the change in population status had generated conservation and/or management concerns either for the population in question or in terms of their impacts ecologically or on human activities.

All peer-reviewed papers that fit these criteria were included. Where primary literature was not available, peer-reviewed papers which summarised data from other sources were included. Furthermore, some relevant non peer-reviewed publications were included. This resulted in a taxonomic coverage that mostly included species from the genus Larus, however it also led to the inclusion of Audouin's Gull (recently moved to *Ichthyaetus*).

Studies measured changes in gull abundance using different survey methods and surveys varied markedly in their intensity and frequency. Moreover many papers did not present raw data on changes in abundance, instead reporting percentage change between survey periods. Therefore, in order to provide a high-level summary of demographic change across gull populations, studies were first ordered by location and then summarised in terms of population change (increasing, decreasing or stable (no change or both increasing/decreasing during the decade in question); Table 2.1) and range shifts (expanding or contracting; Table 2.2) by decade from the 1900s to the 2010s.

Subsequent sections discussing drivers of demographic change, gull impacts, management, conservation and the roadmap for research (Table 2.3) were written qualitatively based on a synthesis of the published literature surrounding these topics.

2.4 Changes in gull demography

2.4.1 Changes in gull abundance

The earliest published gull population estimates are from the 1900s (Cramp et al., 1974), when European and North American populations were coming out of a long period of persecution and exploitation (Drury, 1973; Spaans, 1998). From the 1900s to the 1970s gull populations increased across Europe and North America, with similar trends later in Africa, South America and Asia (Table 2.1).

During the 1970s, some European and North American gull populations stabilised or declined, with further declines from the 1980s through to the 2010s (Table 2.1). In the UK, where urban gull populations were historically well-surveyed (Cramp, 1971; Monaghan and Coulson, 1977; Raven and Coulson, 1997), there was a divergence in trajectories between breeding habitats as some coastal populations declined rapidly while urban populations were stable or increasing (Mitchell *et al.*, 2004; Nager and O’Hanlon, 2016). Our results also revealed a strong publication bias on gull abundance in the peer-reviewed literature towards Europe and North America, with an almost complete lack of published population trends from other regions.

Table 2.1. Changing global gull abundance from the 1900s to 2010s, as summarised from the peer-reviewed literature. Green cells with up arrows indicate population increases, yellow cells with horizontal arrows stable populations, purple cells with down arrows population declines. Light grey cells with hyphen marks indicate no data. UK, United Kingdom; ME, Maine; WA, Washington. HG = herring gull (*Larus argentatus*); LBBG = lesser black-backed gull (*L. fuscus*); YLG = yellow-legged gull (*L. michahellis*); GBBG = great black-backed gull (*L. marinus*); AG = Audouin's Gull (*Ichthyaetus audouinii*); CpG = Caspian Gull (*L. cachinnans*); RBG = ring-billed gull (*L. delawarensis*); CfG = California gull (*L. californicanus*); GWG = glaucous-winged gull (*L. glaucescens*); KG = kelp gull (*L. dominicanus*); SBG = slaty-backed gull (*L. schistagus*).

Continent	**Species**	**Region**	**1900s**	**1910s**	**1920s**	**1930s**	**1940s**	**1950s**	**1960s**	**1970s**	**1980s**	**1990s**	**2000s**	**2010s**	**References**
Europe	HG	UK	↑	↑	↑	↑	↑	↑	↑	↓	↓	↓	↓	↓	(Cramp, Bourne and Saunders, 1974; Chabryzk and Coulson, 1976; Coulson, 1991; Lloyd, Tasker and Partridge, 1991; Mitchell *et al.*, 2004; Nager and O'Hanlon, 2016)
	HG	UK (Urban)	–	–	–	–	↑	↑	↑	↑	↑	↑	↑	–	(Parslow, 1967; Cramp, 1971; Monaghan and Coulson, 1977; Raven and Coulson, 1997; Nager and O'Hanlon, 2016)
	HG	Finland	–	–	–	–	–	–	–	–	↓	↓	↓	↓	(Hario and Rintala, 2016)
	HG	Netherlands	↔	↑	↑	↑	↓	↔	↑	↑	↔	↓	↓	–	(Spaans, 1998b; Camphuysen, 2013)
	HG	Belgium	–	–	–	–	–	–	–	↑	↑	↑	–	–	(Seys *et al.*, 1998)
	HG	Canna, Scotland	–	–	–	–	–	–	↑	↑	↑	↓	↓	↓	(Foster *et al.*, 2017)
	HG	Isles of Scilly, England	–	–	–	–	–	–	–	↓	↓	↓	↓	–	(Heaney *et al.*, 2008)

LBBG	UK	↑	↑	↑	↑	↑	↑	↑	↑	↑	↑	↓	↓	(Cramp, Bourne and Saunders, 1974; Lloyd, Tasker and Partridge, 1991; Mitchell *et al.*, 2004; Nager and O'Hanlon, 2016)
LBBG	UK (Urban)	–	–	–	–	↑	↑	↑	↑	↑	↑	↑	–	(Cramp, 1971; Monaghan and Coulson, 1977; Raven and Coulson, 1997; Nager and O'Hanlon, 2016)
LBBG	Netherlands	–	–	↑	↑	↓	↑	↑	↑	↑	↑	–	–	(Spaans, 1998; Camphuysen, 2013)
LBBG	Belgium	–	–	–	–	–	–	–	–	↔	↑	–	–	(Seys *et al.*, 1998)
LBBG	Finland	–	–	–	–	–	–	–	–	↓	↓	↓	↓	(Hario and Rintala, 2016)
LBBG	Canna, Scotland	–	–	–	–	–	–	–	↑	↓	↓	↓	–	(Foster *et al.*, 2017)
LBBG	Isles of Scilly, England	–	–	–	–	–	–	–	–	↓	↓	↓	–	(Heaney *et al.*, 2008)
YLG	Western Mediterranean	–	–	–	–	–	–	↑	↑	↑	↑	–	–	(Thibault *et al.*, 1996)
YLG	France	–	–	↑	↑	↑	↑	↑	↑	↑	↑	–	–	(Thibault *et al.*, 1996)
GBBG	UK	↑	↑	↑	↑	↑	↑	↑	↓	↓	↓	↓	↓	(Cramp, Bourne and Saunders, 1974; Lloyd, Tasker and Partridge, 1991; Mitchell *et al.*, 2004; Nager and O'Hanlon, 2016)
GBBG	Finland	–	–	–	–	–	–	–	–	↓	↓	↓	↓	(Hario and Rintala, 2016)
GBBG	Canna, Scotland	–	–	–	–	–	–	↑	↑	↑	↑	↓	–	(Foster *et al.*, 2017)
GBBG	Isles of Scilly, England	–	–	–	–	–	–	–	↓	↓	↓	↑		(Heaney *et al.*, 2008)

	AG	Western Mediterranean	–	–	–	–	–	–	↑	↑	↑	↑	–	–	(Thibault *et al.*, 1996)
	CpG	Eastern Europe	–	–	–	–	–	–	–	–	–	↑	↑	–	(Lenda *et al.*, 2010)
North America	HG	Eastern North America	↑	↑	↑	↑	↑	↑	↑	↔	↓	↓	↓	↓	(Drury, 1973; Anderson *et al.*, 2016; Bond *et al.*, 2016)
	HG	Great Lakes, North America	–	–	–	–	–	–	↑	↔	↔	↔	–	–	(Morris, Weseloh and Shutt, 2003)
	HG	Atlantic Canada	–	–	–	–	–	–	–	–	–	↓	↓	↓	(Wilhelm *et al.*, 2016)
	HG	Gulf of St Lawrence, Canada	–	–	–	–	–	–	–	–	–	↓	–	–	(Chapdelaine and Rail, 1997)
	HG	ME, USA	–	–	–	–	–	–	–	↓	↓	↓	↓	↓	(Mittelhauser *et al.*, 2016)
	LBBG	Greenland	–	–	–	–	–	–	–	–	–	↑	↑	↑	(Boertmann and Frederiksen, 2016)
	GBBG	Eastern North America	–	–	↑	↑	↑	↑	↑	↑	↑	↔	↓	↓	(Drury, 1973; Anderson *et al.*, 2016)
	GBBG	Greenland	–	–	–	–	–	–	↑	↑	↑	↑	↑	↑	(Boertmann and Frederiksen, 2016)
	GBBG	Atlantic Canada	–	–	–	–	–	–	–	–	–	↓	↓	↓	(Wilhelm *et al.*, 2016)
	GBBG	ME, USA	–	–	–	–	–	–	–	↓	↓	↓	↓	↓	(Mittelhauser *et al.*, 2016)
	RBG	Eastern North America	–	↑	↑	↑	↑	↑	↑	↑	↑	↓	↓	↓	(Giroux *et al.*, 2016)
	RBG	Great Lakes, North America	–	–	↑	↑	↔	↔	↑	↑	↑	↓	↓	↓	(Ludwig, 1974; Giroux *et al.*, 2016)
	RBG	Atlantic Canada, North America	–	–	–	–	–	–	–	–	–	↑	↑	–	(Cotter *et al.*, 2012; Giroux *et al.*, 2016)
	RBG	Western North America	–	–	↑	↑	↑	↑	↑	↑	–	–	–	–	(Conover, 1983)
	CfG	Western North America	–	–	↑	↑	↑	↑	↑	↑	–	–	–	–	(Conover, 1983)

	GWG	WA, USA	–	–	–	–	–	–	↑	↑	↔	↓	↓	↓	(Blight, 2012; Blight, Drever and Arcese, 2015)
	GWG	Vancouver (Urban), Canada	–	–	–	–	–	–	–	–	↑	↑	↑	↑	(Blight, Bertram and Kroc, 2019)
Africa	KG	South Africa	–	–	–	–	–	–	–	–	↑	↑	↔	↓	(Whittington, Martin and Klages, 2006; Whittington *et al.*, 2016)
South America	KG	Patagonia, South America	–	–	–	–	–	–	–	–	↑	↑	↑	–	(Lisnizer, Garcia-Borboroglu and Yorio, 2011; Yorio *et al.*, 2016)
Asia	SBG	Shelikan Island, Russia	–	–	–	–	–	–	–	–	↑	↑	↑	–	(Zelenskaya and Khoreva, 2006)
	SBG	Magadan City, Russia	–	–	–	–	–	–	–	–	–	↑	↑	↑	(Zelenskaya, 2019)

2.4.2 Changing distribution

Many gull species expanded their range during the 20th century (Table 2.2). These shifts in distribution included range expansions into new countries and continents (Lenda *et al.*, 2010; Hallgrimsson *et al.*, 2011; Boertmann and Frederiksen, 2016). Some species also expanded their distributions into new breeding habitats including inland lakes (Frixione *et al.*, 2012) and reservoirs (Conover, 1983; Lenda *et al.*, 2010), in addition to colonising both new and previously inhabited coastal sites (Anderson *et al.*, 2016; Ronconi *et al.*, 2016). Ecologically, the most significant distribution shift was a niche expansion into anthropogenic habitats, particularly urban areas. Roof-nesting gulls were first reported along the Black Sea coast in 1894 (Goethe, 1960), and this shift began in earnest in Britain in the 1940s (Parslow, 1967), with subsequent urban colonisations reported across Europe (Monaghan & Coulson, 1977; Soldatini et al., 2008), North America (Dwyer, Belant and Dolbeer, 1996), South America (Yorio *et al.*, 2016) and Australia (Temby, 2000).

For many species, changing population size and geographic range suggest dispersal from saturated breeding colonies (Monaghan & Coulson, 1977). However, we have a poor understanding of gull dispersal including whether local declines represent redistributions within a larger meta-population (Ross-Smith, et al., 2014). In some instances, urban increases have not matched coastal declines (Blight, Bertram and Kroc, 2019), and this shortfall suggests ongoing complex patterns in abundance and distribution.

Some gull populations may also have changed their migratory behaviour (Burton et al. 2013), although it is unclear whether this has any influence on breeding distribution.

Table 2.2. Range changes for global gull populations from the 1900s to 2010s. Green cells with up arrows indicate range expansion, purple cells with down arrows indicate range contraction and light grey cells with hyphen marks indicate no data available. UK, United Kingdom; ME, Maine; HG = herring gull; LBBG = lesser black-backed gull; YLG = yellow-legged gull; GBBG = great black-backed gull; AG = Audouin's Gull; CpG = Caspian Gull; RBG = ring-billed gull; CfG = California gull; KG = kelp gull.

Continent	Species	Region	1900s	1910s	1920s	1930s	1940s	1950s	1960s	1970s	1980s	1990s	2000s	2010s	References
Europe	HG	UK (Urban)	–	–	–	–	↑	↑	↑	↑	↑	↑	↑	–	(Parslow, 1967; Cramp, 1971; Monaghan and Coulson, 1977; Raven and Coulson, 1997; Nager and O'Hanlon, 2016)
	HG	Netherlands	–	–	↑	↑	↑	↑	↑	↑	–	–	–	–	(Spaans, 1998b; Camphuysen, 2013)
	HG	Belgium	–	–	–	–	–	–	–	↑	↑	↑	–	–	(Seys *et al.*, 1998)
	LBBG	UK	↑	↑	↑	↑	↑	↑	↑	–	–	–	–	–	(Cramp, Bourne and Saunders, 1974; Nager and O'Hanlon, 2016)
	LBBG	UK (Urban)	–	–	–	–	↑	↑	↑	↑	↑	↑	↑	–	(Cramp, 1971; Monaghan and Coulson, 1977; Raven and Coulson, 1997; Nager and O'Hanlon, 2016)
	LBBG	Netherlands	–	–	↑	↑	↑	↑	↑	↑	↑	↑	↑	–	(Spaans, 1998; Camphuysen, 2013)
	LBBG	Belgium	–	–	–	–	–	–	–	–	↑	↑	–	–	(Seys *et al.*, 1998)
	YLG	Western Mediterranean	–	–	–	–	–	–	↑	↑	↑	↑	–	–	(Thibault *et al.*, 1996)

	GBBG	UK	↑	↑	↑	↑	↑	↑	↑	–	–	–	–	–	(Cramp, Bourne and Saunders, 1974; Nager and O'Hanlon, 2016)
	AG	Western Mediterranean	–	–	–	–	–	–	↑	↑	↑	↑	–	–	(Thibault *et al.*, 1996)
	CpG	Eastern Europe	–	–	–	–	–	–	–	–	↑	↑	↑	–	(Lenda *et al.*, 2010)
North America	HG	Eastern North America	↑	↑	↑	↑	↑	↑	↑	–	–	–	–	–	(Drury, 1973; Anderson *et al.*, 2016; Bond *et al.*, 2016)
	HG	ME, USA	–	–	–	–	–	–	–	↓	↓	↓	↓	↓	(Mittelhauser *et al.*, 2016)
	LBBG	Greenland	–	–	–	–	–	–	–	–	–	↑	↑	↑	(Boertmann and Frederiksen, 2016)
	GBBG	Eastern North America	↑	↑	↑	↑	↑	↑	↑	–	–	–	–	–	(Drury, 1973; Anderson *et al.*, 2016)
	GBBG	Greenland	–	–	–	–	–	–	↑	↑	↑	↑	↑	↑	(Boertmann and Frederiksen, 2016)
	GBBG	ME, USA	–	–	–	–	–	–	–	↓	↓	↓	↓	↓	(Mittelhauser *et al.*, 2016)
	RBG	Western North America	–	–	↑	↑	↑	↑	↑	↑	–	–	–	–	(Conover, 1983)
	RBG	Atlantic Canada	–	–	–	–	–	–	–	–	–	↑	↑	↑	(Cotter *et al.*, 2012)
	CfG	Western North America	–	–	↑	↑	↑	↑	↑	↑	–	–	–	–	(Conover, 1983)
Africa	KG	South Africa	–	–	–	–	–	–	–	–	↑	↑	↑	–	(Whittington, Martin and Klages, 2006; Whittington *et al.*, 2016)
South America	KG	Patagonia	–	–	–	–	–	–	–	–	↑	↑	↑	–	(Lisnizer, Garcia-Borboroglu and Yorio, 2011; Yorio *et al.*, 2016)

2.5 Drivers of demographic change

The literature suggests three primary anthropogenic factors are most related to gull demographic change: persecution, habitat creation and PAFS. Here we discuss how each of these drivers have influenced gull population dynamics (Figure 2.1).

2.5.1 Persecution

In the early 1900s, gulls and other seabirds in Europe and North America were at historically low levels, following decades of harvesting and persecution (Drury, 1973; Spaans, 1998a). Around this time, changing public attitudes, and the resultant protective legislation (i.e. UK Sea Bird Protection Act (1869); North American Migratory Bird Treaty Act (1918)) greatly reduced gull persecution enabling numbers to rise (Coulson, 2015; Anderson *et al.*, 2016).

However, throughout the 20th century many gull populations have been subject to periodic control measures, aimed at mitigating deleterious impacts on humans and natural ecosystems. Such culls may have limited increases in gull abundance at local (O'Connell, 1995; Anderson *et al.*, 2016) or even national levels (Camphuysen, 2013). More recently, control measures may have caused localised population declines (Mitchell *et al.*, 2004; Nager and O'Hanlon, 2016) and may be contributing to recent population levelling or declines (Table 1).

2.5.2 Predictable Anthropogenic Food Subsidies (PAFS)

Humans provide large quantities of PAFS in the form of fisheries discards, landfill, urban refuse and agricultural residuals, of which gulls are significant recipients (Oro *et al.*, 2013).

Fisheries discards - Global discard production peaked at 18.8 million tonnes per annum in 1989 (Zeller *et al.*, 2018), benefitting gulls in Europe (Sherley *et al.*, 2020), North America (Chapdelaine and Rail, 1997), South America (González-

Zevallos and Yorio, 2011) and Africa (Steele, 1992). Accordingly, discards likely played a key role in gull population and range changes (Furness, Ensor and Hudson, 1992; Foster *et al.*, 2017). The abundance and predictability of discards (Patrick *et al.*, 2015) has led to benefits in terms of foraging (Oro *et al.*, 2013), body condition (Hüppop and Wurm, 2000), reproductive success (Oro, 1996), survival (Yorio and Caille, 2004) and dispersal (Oro *et al.*, 2004). However, discards may have negative impacts because they may represent 'junk-food' with low nutrient content (Österblom *et al.*, 2008), or increase bycatch risk (Bicknell *et al.*, 2013)

Landfill & urban refuse - Gulls feed on landfills around the globe (Auman, Meathrel and Richardson, 2008; Ackerman *et al.*, 2018) and this subsidy is a recurring feature associated with expanding gull populations (Coulson and Coulson, 1998; Duhem *et al.*, 2008). Nevertheless, landfills likely have complex effects on gull demography. While access to landfills can improve reproductive performance (Pons and Migot, 1995), body condition (Auman, Meathrel and Richardson, 2008) and survival (Annett and Pierotti, 1999), this is not always the case (Belant, Ickes and Seamans, 1998). Depending on the availability of alternative resources (Annett and Pierotti, 1999; O'Hanlon, McGill and Nager, 2017) refuse may also represent 'junk-food' for chicks (Österblom *et al.*, 2008). Additionally, landfill foraging is associated with intense competition (van Donk *et al.*, 2017) and increased exposure to pathogens such as *Clostridium botulinum* (Ortiz and Smith, 1994) and toxic pollutants (Tongue *et al.*, 2019).

Gulls also feed on urban waste such as litter and domestic refuse (Huig, Buijs and Kleyheeg, 2016; Spelt *et al.*, 2020). This behaviour may bring gulls into conflict with people (Goumas *et al.*, 2019; Goumas, Boogert and Kelley, 2020), although urban foraging has been relatively poorly studied.

Agricultural residuals - Gulls commonly forage on agricultural land for invertebrates (Coulson and Coulson, 2008), small mammals (Camphuysen *et al.*, 2010), crop residuals (Patenaude-Monette, Bélisle and Giroux, 2014) and animal feed (van den Bosch *et al.*, 2019). Recent tracking studies highlight the importance of agricultural foraging for some individuals and populations throughout the annual cycle (Schwemmer, Garthe and Mundry, 2008; Isaksson *et al.*, 2016; Baert *et al.*, 2018; Martín-Vélez *et al.*, 2019; van den Bosch *et al.*, 2019), however, such studies are scarce and the demographic consequences are unknown.

Overall effect of PAFS - PAFS buffer natural fluctuations in food availability, increase food biomass and likely led to increased gull numbers and range expansions on a global scale (Ramírez *et al.*, 2020). However, a steep decline or cessation of PAFS availability may have contributed to recent population declines. For instance, policy has greatly reduced fisheries discards (Sherley *et al.*, 2020) and landfill refuse (Giroux *et al.*, 2016; Zorrozua *et al.*, 2020), with negative demographic consequences (Bicknell *et al.*, 2013; Payo-Payo *et al.*, 2015). While gulls may buffer this in the short-term (Tyson *et al.*, 2015), this is likely to explain some recent declines (Mitchell *et al.*, 2004; Blight, Drever and Arcese, 2015; Nager and O’Hanlon, 2016).

2.5.3 Habitat creation

Urban gulls nest on large, flat or gently sloping roofs in industrial districts (Hooper, 1988; Rock, 2005; Blight, Bertram and Kroc, 2019) and the roofs of private residencies in towns and cities. These provide predator-free nesting sites and a benign microclimate (Rock, 2005), and may have initially benefited from lower population densities compared with rural sites (Monaghan and Coulson, 1977). However, increasing urban gull populations do not match the spread of urbanisation suggesting this spread may relate to events elsewhere in their range. Man-made reservoirs also provide bathing, drinking and roosting opportunities (Burton *et al.*, 2013) and artificial islands provide predator-free breeding habitat, allowing colonisation of otherwise unsuitable areas (Conover, 1983; Lenda *et al.*, 2010). Finally, coastal developments, such as the construction of shipping ports have provided attractive breeding habitat for gulls in some areas, leading to range expansions and increases in abundance (Spaans, 1998a; Seys *et al.*, 1998).

Despite the importance of urban habitats for gulls, survey difficulties mean that even in well-studied countries, current estimates of urban gull numbers are poor (Rock, 2005; Coulson and Coulson, 2015) – more effort using conventional and novel survey techniques (such as drones and aerial surveying) are required to overcome this shortfall (Blight, Bertram and Kroc, 2019). We also know little of the ecology of urban breeding gulls. Recent telemetry studies have provided revealing insights into the habitat use of urban gulls (Spelt *et al.*, 2019; Méndez *et al.*, 2020), however they do not make comparisons with natural populations or examine the fitness consequences of different foraging decisions. More work is required to determine whether urban and rural breeders have different foraging and movement behaviour, and the life-history and applied consequences of this.

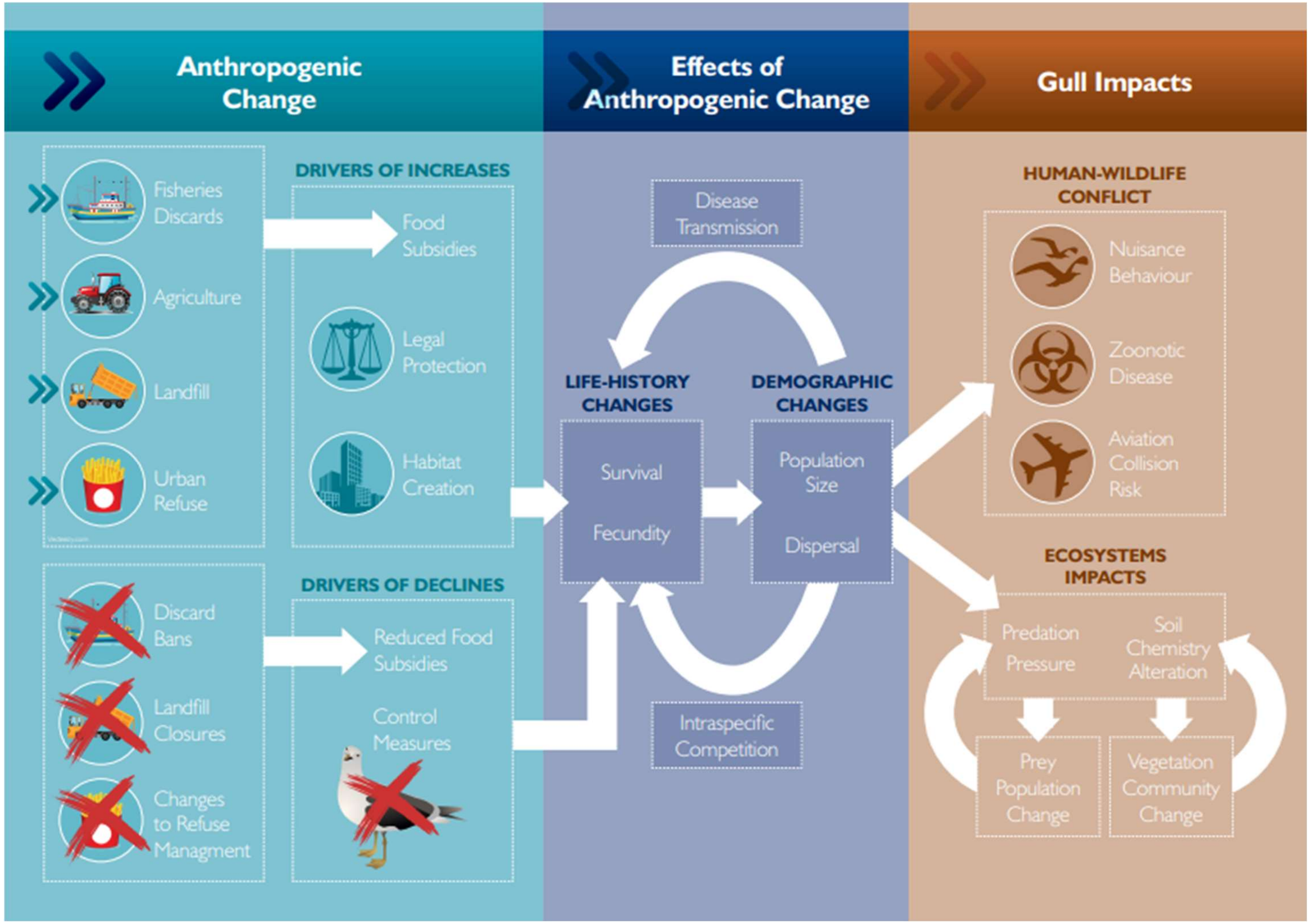

Figure 2.1. Anthropogenic change as a driver of change in gulls. Human activities including changes in resource availability, legal protection, habitat creation and control measures can alter life-history parameters of gulls leading to changes in abundance and distribution. This in turn can lead to downstream impacts on ecosystems and fuel human-wildlife conflict.

2.6 Impacts of expanded gull populations

As gull populations expanded, they had a range of negative impacts in ‘natural’ ecosystems (Vidal, Medail and Tatoni, 1998; Oro *et al.*, 2013). Moreover, range shifts into urban areas brought gulls into close proximity with humans, intensifying human-gull interactions (Figure 2.1).

2.6.1 Human-gull interactions

Nuisance behaviour – Urban gulls are widely considered a problem due to behaviours including noise pollution, eating refuse, stealing food, aggressive behaviour, fouling, blocking drains and damage to buildings (Rock, 2005; Goumas *et al.*, 2019). However, such nuisance behaviour is not consistently documented, nor do we understand the economic costs. Therefore, while nuisance may elicit interventions, this often lacks an evidence base.

Public health impacts – Gulls act as reservoirs for pathogens including enterobacteria (Girdwood *et al.*, 1985) and *Clostridium botulinum* (Ortiz and Smith, 1994), potentially contaminating water supplies (Hatch, 1996) and recreational beaches (Converse *et al.*, 2012) from visits to sewage treatment works and landfills. They may also be reservoirs and dispersal agents for bacterial strains resistant to antibiotics (Dolejska, Cizek and Literak, 2007; Zhao and Hu, 2011). Nevertheless, evidence for direct disease transmission from gulls to humans is limited (Hatch, 1996) and further research is required to quantify the public health risks posed by gulls (Navarro *et al.*, 2019).

Bird strikes - Gulls account for the majority of bird-strikes with aircraft globally (Burger, 1985), with most strikes relating to immature birds (Burger, 1985), which frequently fly at low altitude near airfields (Neubauer, 1990). Human fatality rates are low (Neubauer, 1990), however, economic costs are significant, with aircraft repairs due to bird strikes in the United States costing $400 million annually between 1990 and 1998 (Sodhi, 2002). Attempts to mitigate these risks have focussed on habitat management to reduce the suitability of airfields for foraging and loafing gulls (Buckley and McCarthy, 1994) and occasionally, lethal management (Dolbeer, Belant and Sillings, 1990).

Impacts on agriculture – Gulls forage in agricultural habitats for PAFS (Patenaude-Monette, Bélisle and Giroux, 2014; van den Bosch *et al.*, 2019), providing a pathway for disease transmission to livestock. Gulls have been implicated as the vector in *Salmonella* outbreak in sheep and cattle (Coulson, Butterfield and Thomas, 1983) and could transmit emerging zoonotic diseases and antibiotic resistant bacteria to livestock, with consequences for human health (Carroll *et al.*, 2015; Woolhouse *et al.*, 2015).This highlights the need for further research into agricultural foraging and the public health implications of livestock-gull interactions.

2.6.2 Ecological impacts

Impacts on seabirds – Gulls negatively impact sympatric seabirds, via predation of adults, eggs and chicks (Yorio and Quintana, 1997), kleptoparasitism (Martínez-Abraín *et al.*, 2003) and competition for breeding sites (Sadoul *et al.*, 1996). Hyperpredation may also occur where gulls prevent recovery of scarce prey species (Courchamp, Langlais and Sugihara, 2000; Oro *et al.*, 2013). The demographic impacts of gull predation depend on the size and composition of the seabird assemblage. Gull predation may extirpate small populations of vulnerable species such as terns (*Sterna* sp.), with ongoing management required to restore them (Blokpoel, Gaston and Andress, 1997). However in large, dense seabird colonies, gull impacts may be limited to peripheral nests with negligible impacts on the reproductive performance or demography of sympatric species (Quintana and Yorio, 1998; Yorio *et al.*, 1998).

Food availability for gulls in marine ecosystems is declining due to human activities and climatic change (Bicknell *et al.*, 2013; Sherley *et al.*, 2020). Food stress may result in prey-switching (Payo-Payo *et al.*, 2015), leading to increased predation of sympatric seabirds, with potential demographic impacts (Russel and Montevecchi, 1996; Regehr and Montevecchi, 1997; Stenhouse and Montevecchi, 1999; Votier *et al.*, 2004). Understanding how ecosystem change may alter seabird community dynamics is key to conserving robust gull populations whilst mitigating negative impacts on sympatric species.

Impacts on terrestrial ecosystems – Expanding gull populations alter habitat structure and soil chemistry at colonies via vegetation removal and guano deposition (Otero *et al.*, 2015). This can have negative biodiversity impacts and create conservation challenges by reducing overall vegetation cover and plant diversity (Zelenskaya and Khoreva, 2006) and promoting the growth of generalist ruderal plants over threatened specialists (Baumberger *et al.*, 2012) with severe impacts on ecosystem function and community dynamics observed (Vidal, Medail and Tatoni, 1998). However in some contexts, guano deposition by gulls may have positive consequences, enriching nutrient poor terrestrial ecosystems in polar regions (Zwolicki *et al.*, 2013)

2.7. Gull management

The negative impacts associated with gulls have led to a range of management interventions – we summarise these below and also consider pathways to effective conservation.

2.7.1. Lethal control

Culling has generated mixed results. Indiscriminate culling may improve the outlook for impacted species (Blokpoel, Gaston and Andress, 1997; Scopel and Diamond, 2017) or reduce human-gull conflict (Rock 2012), but it is ethically and politically problematic, especially for declining gull populations. Selective removal of problem individuals/pairs is preferable and can have positive biodiversity impacts (Sanz-Aguilar *et al.*, 2009) or reduce garbage specialists (McCleery and Sibly, 1986). However, the long-term efficacy of lethal control is unclear, as strong density-dependent processes may limit any effects on population density whilst both the rate and distance of dispersal may also increase, simply shifting the problem elsewhere (Coulson, Duncan and Thomas, 1982; Wanless *et al.*, 1996; Bosch, Pocino and Carrera, 2019).

The logistics and ethics of lethal control require careful consideration. Targeted shooting of specialists is time intensive and may not reduce overall predation rates (Donehower *et al.*, 2007). Furthermore, birds may become shy to marksman and shooting is unlikely to be appropriate in an urban setting. Narcotics (such as alpha-chlorolose) do not share the same constraints as shooting, but delayed action and possible spread of dosed bait also raise issues, particularly in towns and cities (Rock, 2005).

2.7.2. Non-lethal deterrents

Physical deterrents – canes, spikes, netting and monofilament wires are effective at deterring nesting gulls (Blokpoel and Tessier, 1984; Rock, 2005) and (along with nest and chick shelters) protecting seabirds from gull predation (Burness and Morris, 1992; Blokpoel, Gaston and Andress, 1997). Physical deterrents have been effective in reducing seabird predation (Blokpoel, Gaston and Andress, 1997) and may be effective at the local scale in urban areas, however, they raise concerns about entanglement of gulls (and non-target species), and may shift problem gulls to neighbouring roofs/areas (Rock, 2005).

Reducing breeding success – removing eggs, oiling eggs and nest removal are all used to deter urban (and rural) gulls (Rock 2012). To be most effective, this should be conducted extensively over multiple breeding cycles to reduce the overall fecundity, conspecific attraction and ultimately recruitment (Evans, Votier and Dall, 2016). Contraception may work, but is costly and requires careful ethical consideration (Barlow, 2000).

Managing food availability – managing food more effectively (such as covering garbage in towns) is important for gull management (Castege *et al.*, 2016), but it may take several years before population-level effects are observed. Red foxes (*Vulpes vulpes*) exhibit rapid population-level responses to food reduction (Bino *et al.*, 2010), however, the mobility and dietary flexibility of gulls (McCleery and Sibly, 1986) may limit the efficacy of this approach.

Birds of prey – birds of prey are used to disturb gulls throughout the year. This approach has successfully prevented foraging at landfills (Arizaga *et al.*, 2013), however, the efficacy on urban-breeding gulls is less clear (Rock, 2005). There is also anecdotal evidence to suggest that some species (falcons) are more effective than others (hawks) (Calladine and Park, 2006).

Human disturbance – gulls may also be deterred by human disturbance, particularly during incubation, leading to reduced reproductive success (Hunt, 1972; Burger, 1981), and occasionally colony abandonment (Conover and Miller, 1978). Human presence may also disrupt gull predation of sympatric seabirds, leading to improved nesting success (Donehower *et al.*, 2007).

2.7.3. Theoretical and practical considerations of gull management

High site fidelity in combination with longevity among gulls means that even with deterrents, individuals may stay faithful to their nest sites. Moreover, differences in philopatry among species and individuals (Wanless *et al.*, 1996) require different approaches across situations. Using a combination of control measures may be more effective in deterring breeding gulls, leading to forced relocations and subsequent local population declines (Coulson and Coulson, 2009; Salas *et al.*, 2020), though not in all cases (Calladine and Park, 2006).

Another challenge is spatio-temporal scale. Many interventions are reactive, responding to a particular nuisance behaviour, rather than taking a broader landscape-scale and long-term approach (Belant, 1997; Trotter, 2019). This is clearly an issue in light of gulls' longevity, their ability to disperse, prey-switch or otherwise overcome management. In tandem, it would be illuminating to quantify both the efficacy and cost of control measures over large spatio-temporal scales – including consideration across international borders, particularly for migrants (Ramírez *et al.*, 2020). Moreover, this should be associated with clear and accessible guidelines for all stakeholders, which are currently lacking (Trotter, 2019).

As well as ecological and economic considerations, there is a need to establish links with social science. Public perceptions of gulls are often framed negatively (Trotter, 2019), yet human-wildlife encounters have potential human health and wellbeing benefits (Keniger *et al.*, 2013). Urban-breeding gulls may also provide important ecosystem services, including public health benefits of roadkill scavenging (Schwartz et al., 2018) and population control of invasive non-native species (Méndez *et al.*, 2020).

Better waste management may discourage gulls from travelling to forage in urban areas (Huig, Buijs and Kleyheeg, 2016), whilst education and public information aimed at reducing gull feeding and understanding food-snatching (Goumas *et al.*, 2019) is crucial to mitigate negative human-gull interactions. Simultaneously, community engagement such as public-facing tracking programmes, which visually demonstrate the diverse foraging behaviours and migratory journeys of local gull populations, provide a platform to move away from the strongly negative narrative surrounding urban gulls.

2.8. Gull conservation

Trends in gull abundance and distribution are necessarily bounded by temporal scale, and these definitions of scale determine the baselines against which conservation decisions are made. For example, large declines in abundance of lesser black-backed gulls at protected sites in the UK have occurred over the past 20 years (Ross-Smith et al. 2014). This has led some Special Protection Areas (SPAs) to set specific targets to restore abundances to baseline levels reflecting pre-decline numbers (see https://designatedsites.naturalengland.org.uk/). In part, these have influenced conservation initiatives such as Site Improvement Plans (*ibid*.) designed to allow protected colonies to grow.

There is a well-established framework of decision-making surrounding potential impacts to gulls, especially where they are features of SPAs and subject to Habitats Regulations Assessment. This process subjects consenting of various activities to a high level of scrutiny to avoid damage to the feature, through avoidance, mitigation, and, where necessary, compensation. The statutory nature conservation bodies in the UK are also leading work to establish definitions of Favourable Conservation Status for lesser black-backed gulls, amongst other species, at national scale. These definitions will be invaluable to ensure any management decisions made will be consistent with national aims for conservation of the same species. Critically, this requires a better understanding of gull meta-population dynamics and thus the linkages between ‘natural’ populations breeding in coastal and freshwater ecosystems and urban populations that have generally been considered and managed as separate (Ross-Smith, Grantham, *et al.*, 2014).

There is often marked variation in demographic trends among gull populations breeding in different habitats or regions (Horswill and Robinson, 2015). Many ‘natural’ populations are in poor condition due to a range of factors including predation, disturbance, habitat degradation, lack of food availability and possibly other anthropogenic factors (Mitchell *et al.*, 2004; Ross-Smith, Robinson, *et al.*, 2014; Nager and O’Hanlon, 2016). Maintaining resilience in gull populations requires these issues to be addressed which requires research to identify relevant factors, and the design, funding and implementation of successful solutions. License regimes, which permit lethal and non-lethal control, may need revision where gull numbers are declining, to ensure systems can track and predict population impacts of direct management interventions. This could introduce flexibility to management decisions based on the conservation status of the gulls which should be underpinned by a national definition of favourable status, and by conservation targets for protected sites where appropriate. Challenges exist, such as ensuring sufficient data are collected to monitor changes in gull abundance.

Conservation is also hampered by knowledge gaps surrounding the scale of gull movement (Ross-Smith, Robinson and Clark, 2015), which are required to quantify possible indirect effects (e.g. unintended control). Moreover, insufficient estimates of urban breeding populations add uncertainty to the conservation status of several gull species (Nager and O’Hanlon, 2016), though progress is being made on developing methods to address this problem (Woodward *et al.*, 2020). Management of urban nesting gulls should recognise that these populations may currently represent significant proportions of national population totals, and that there may be ‘functional linkage’ with protected sites (e.g. birds may switch between (protected) natural sites and urban sites). We believe that gull conservation should begin with a focus on restoring ‘natural’ populations, consistent with published site-specific and national targets reflecting favourable status, to introduce resilience in gull populations and their underlying natural supporting ecosystems. Careful management of urban populations may then be possible to ensure that such measures do not conflict with conservation targets, or with the conservation of other species.

2.9. A roadmap for research

Throughout, we have highlighted current knowledge gaps in our understanding of gull ecology and demography. Building on the work of Lewison *et al.*, (2012) and Ross-Smith, Robinson, *et al.*, (2014), these knowledge gaps are summarised here in a roadmap for research aimed at informing future conservation and management (Table 2.3).

Table 2.3. A roadmap to gull research. Collectively we hope that these proposed priorities might inform conservation management of problematic gull populations that may be of conservation concern.

Research question	Approaches	Outcome
1. How are gull populations changing worldwide?	• Synthesis of existing data from grey literature and national and international monitoring databases • Counts of urban and 'natural' populations. • Annual monitoring of demographic traits at representative sites.	• Reveal true conservation status of different gull taxa, how they change and potential drivers. Relevant for understanding whether divergent population trends between breeding habitats or regions are related to dispersal (see below).
2. What are the patterns and drivers of gull dispersal?	• Ring re-sighting and bio-telemetry among multiple colonies, to determine settlement patterns (see Q1).	• Establish the linkages between urban and "natural" populations and whether local population declines represent redistributions within a wider metapopulation. • Determine the efficacy of different mitigation approaches and the spatial extent of management impacts.
3. How and why have gull migration strategies changed?	• Longitudinal analysis of band/ring re-sighting and recovery. • Tracking studies combined with monitoring of partial migrant populations/species	• Understanding the ecological and anthropogenic drivers of changes in migration strategy. • Understanding the fitness consequences and demographic impacts of changing migratory behaviour. • Understanding changes in the spatial distribution of gull impacts throughout the annual cycle.
4. What are the economic costs and efficiency of different mitigation/control measures?	• Comprehensive review of publicly funded and private interventions.	• Gain an understanding of the true cost and scale of gull impacts and associated management interventions. • Guidelines for stakeholders outlining best practice for managing various gull impacts under different ecological scenarios e.g. urban vs. coastal breeders.

5. What are the cumulative impacts of management and other change?	• Monitor impacts of management as well as other change such as via food availability.	• Understanding how different management interventions interact with factors such as resource availability to drive changes in gull abundance and distribution. • Design more informed management plans that improve efficacy and economic costs of control.
6. Is management more effective when targeted towards problem individuals?	• Experimental removal of problem individuals across a range of species and problems.	• Determine whether such targeted interventions allow for more efficient and sustainable management.
7. What are the ecological differences between urban and rural nesting gulls?	• Comparative tracking, diet, and demographic monitoring in urban and rural sites.	• Understand the ecological differences that may be driving divergent demographic parameters and trends in abundance between breeding habitats and regions (Horswill and Robinson, 2015). • Link gull impacts to breeding populations allowing targeted management interventions.
8. What are the impacts of changing PAFS?	• Tracking, diet, monitoring of populations subject to policy change i.e. discard bans and landfill closures.	• Improved predictions of future changes in gull population and the need for conservation interventions. • Understanding how changes in habitat use may alter the spatial distribution of gull predation impacts and human-gull conflict and the need for management.
9. What is the incidence and implications of transmission of pathogens and antibiotic resistant bacteria?	• Tracking, faecal sampling, environmental sampling at key foraging and roosting locations, as well as comparisons between breeding habitats and species.	• Understanding the potential for gulls to act as a vector for pathogens and antibiotic resistant bacteria and pinpointing sites of acquisition and dispersal is key to mitigate public health threats (Navarro *et al.*, 2019). • Understanding differences in antibiotic resistant bacteria and pathogen prevalence between different components of gull populations - e.g. urban vs. rural breeders and migrants vs. residents.
10. What are the societal benefits of gulls?	• Social science approaches e.g. targeted surveys of the general public.	• Provide a voice to those who value gulls (especially in towns and cities) and allow management authorities to make more balanced decisions regarding control measures.

	• Bait removal experiments to quantify scavenging behaviour.	• Quantify the extent of roadkill and refuse scavenging by gulls and the potential public health benefits.

2.10. Conclusions

During the 20th Century, global gull populations increased and expanded their range, including to urban areas, largely in response to protection and PAFS. As the latter changed, many gull populations declined or stabilised revealing their dependence on human activities and a lack of resilience. It is clear therefore that more should be done to consider gull conservation, not just regulation.

We highlight an urgent need for more information on global gull populations, especially away from Europe and North America, to inform conservation and management. This includes population estimates and effective demographic monitoring, particularly in urban areas. Moreover, we need to better understand gull metapopulation dynamics and dispersal, to reveal the relationships between urban and “natural” populations.

We reviewed gull management approaches, but note these tended to lack published evidence to support their efficacy. There were also knowledge gaps regarding the financial cost and benefit of interventions, and their potential cumulative impacts. Moreover, there is a concerning lack of connectedness among stakeholders – decision-making about control, efficacy of measures, protection and the evidence-base to inform this process appears labyrinthine. Maintaining healthy gull populations in a changing world requires an integrated approach by researchers, conservation organisations, management organisations, local authorities and government bodies.

Finally, probably one of the greatest challenges facing gull populations is public perception. Gulls, especially *Larus* gulls, are widely considered a problem, with financial, public health and safety implications, although this bad press lacks proper quantification. However, gulls also provide pleasure to many, which in turn may have health benefits (Keniger *et al.*, 2013), and deliver ecosystem services such as control of invasive species and removal of refuse and roadkill (Schwartz *et al.*, 2018; Méndez *et al.*, 2020).

Addressing the knowledge gaps identified in this review may enable us to quantify both the benefits and costs of opportunistic species such as gulls, and better understand the influence of ongoing human activities on their ecology and demography. In presenting a roadmap to fill these gaps and drive future research, we hope to inform more sophisticated strategies to protect and manage gulls. More generally, understanding the role of anthropogenic change on the ecology and demography of generalist scavengers, and the resultant impacts on human activities and ecosystem dynamics, are essential to balancing conservation and management in the Anthropocene.

2.11 References

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Chapter 3 – Unpredictable Anthropogenic Food Subsidies: landfill closure induces higher foraging effort and habitat switching in gulls

3.1 Abstract

Predictable anthropogenic food subsidies (PAFS) assist many species, but when they cease this may have consequences, which remain poorly documented. Gulls (*Laridae*) feed extensively on PAFS, such as fisheries discards, agricultural residues and landfill refuse, benefiting fitness and in turn triggering population increases and range expansions. However, changing legislation and practices means resource availability can change abruptly as is the case with widespread landfill closures following the EU Landfill Directive (1999). Landfills are especially important for gulls but the consequences of closures are poorly understood. Here we used GPS-tracking to recreate foraging tracks of lesser black-backed gulls (*Larus fuscus*) breeding at two colonies, and investigate changes in foraging effort and habitat selection in response to the closure of two large landfills. Additionally, we used biometric data from captured adults to test for landfill closure effects on body condition. Following closure, gulls travelled further and for longer to forage. We also found colony-specific differences in habitat selection; birds from one colony shifted to agricultural habitats, while at the other, increased their use of urban areas. Nevertheless, we found no effect on adult body condition. Our results demonstrate how anthropogenic subsidies outside protected area boundaries influence the foraging ecology of gulls, highlighting the need to consider the home ranges and key foraging sites of mobile species in management decisions. Additionally, habitat-switching following landfill closures can alter the spatial distribution of foraging gulls, shifting the focus of human-gull interactions to urban and agricultural habitats.

3.2 Introduction

The negative impacts of human activities on biodiversity are widely recognised (Mckinney and Lockwood, 1999; Fischer and Lindenmayer, 2007). However, humans can also provide ecological opportunities in the form of predictable anthropogenic food subsidies (hereafter PAFS; Oro *et al.*, 2013). However, PAFs are often waste products and the widespread attempts to mitigate this waste means they are becoming less predictable. Given the scale of change and the numbers of species and individuals that take advantage of PAFs (Oro *et al.*, 2013), understanding the ecological consequences of their reduction or cessation is imperative.

Humans produce huge quantities of waste - in 2000, the world's urban residents produced around 3 million tonnes of solid waste per day (Hoornweg, Bhada-Tata and Kennedy, 2013) which is predicted to double by 2025 (Hoornweg and Bhada-Tata, 2012). Whilst much solid waste is inert, it also includes large amounts of food (Parfitt, Barthel and MacNaughton, 2010), that ends up in landfill (Hoornweg, Bhada-Tata and Kennedy, 2013). Landfills therefore represent a major anthropogenic subsidy, providing large quantities of food that is predictable in time and space for at least 98 vertebrate species, predominantly opportunistic birds and mammals (Plaza and Lambertucci, 2017). Landfills may either be a primary food source (Duhem *et al.*, 2008; Ackerman *et al.*, 2018) or be used facultatively when natural prey are scarce (Olea and Baglione, 2008).

Landfills can have complex and far-reaching ecological impacts on animals (Oro *et al.*, 2013), improving body condition (Auman, Meathrel and Richardson, 2008; Steigerwald *et al.*, 2015), reproductive performance (Pons and Migot, 1995; Tortosa, Caballero and Reyes-Lopez, 2002) and immature survival (Annett and Pierotti, 1999), resulting in higher recruitment and subsequent population increases (Smith and Carlile, 1993; Vidal, Medail and Tatoni, 1998; Annett and Pierotti, 1999). Access to landfills may also influence migration, catalysing transitions from migratory to resident behaviour (Cozzi *et al.*, 2016; Gilbert *et al.*, 2016). Alternatively, refuse may be costly because of low nutritional value ("junk-food"; Annett and Pierotti, 1999; Osterblom *et al.*, 2008; O'Hanlon, McGill and Nager, 2017), increased risk of exposure to pollutants (Tongue *et al.*, 2019), pathogens (Ortiz and Smith, 1994), and poisons (Mitchell *et al.*, 2004). Moreover, the high predictability of landfills is contingent on policies that can change rapidly (Bicknell *et al.*, 2013), and predictable approaches to waste production and management methods (Giroux *et al.*, 2016; Zorrozua *et al.*, 2020).

Gulls (*Laridae*) are opportunists that forage at landfills all over the world (Smith and Carlile, 1993; Annett and Pierotti, 1999; Duhem *et al.*, 2008; Frixione *et al.*, 2012; Yoda *et al.*, 2012; Patenaude-Monette, Bélisle and Giroux, 2014; Ackerman *et al.*, 2018; Spelt *et al.*, 2019). As such, landfills have underpinned gull population increases (Coulson and Coulson, 1998; Duhem *et al.*, 2008) and range expansions (Belant, Ickes and Seamans, 1998; Whittington, Martin and Klages, 2006; Lisnizer, Garcia-Borboroglu and Yorio, 2011; Frixione *et al.*, 2012). However, while global waste production is projected to peak next century (Hoornweg, Bhada-Tata and Kennedy, 2013), in Europe refuse availability is declining as landfill sites are phased out (EU Landfill Directive 1999). These closures are likely to have implications for populations of gulls (Pons 1992) and other landfill foragers (Plaza and Lambertucci, 2017).

Monitoring changes in breeding gull numbers following landfill closures may be ineffective because of their bet-hedging life-history strategies leading to lags in response to landfill closures (Votier *et al.*, 2004). However, functional responses are likely to be much more sensitive to changes of this nature (Payo-Payo *et al.*, 2015; Zorrozua *et al.*, 2020). Traditional dietary analyses have revealed responses to landfill closures (Payo-Payo *et al.*, 2015; Zorrozua *et al.*, 2020), but these may underrepresent soft prey items including anthropogenic foods such as carbohydrates and cooked meats (Votier *et al.*, 2003). Therefore, it may be difficult to draw inference about landfill closures from breeding parameters and diet. In contrast, bio-logging, such as GPS tracking provides a much more sensitive monitoring tool because it recreates precise behaviours over relatively short time intervals (Bino *et al.*, 2010). Tracking technology may also help identify management issues arising from changes in gull space use (Cozzi *et al.*, 2016; Huig, Buijs and Kleyheeg, 2016), such as increased predation of sympatric seabirds (Stenhouse and Montevecchi, 1999; Sanz-Aguilar *et al.*, 2009), or conflicts with human activities (Coulson, Butterfield and Thomas, 1983; Goumas *et al.*, 2019).

Here, we provide the first study of the influence of landfill closure on the movement ecology, habitat selection and body condition of adult lesser black backed gulls (*Larus fuscus*) breeding at two colonies in northwest England. We study birds before and after the closure of two very large local open-air landfills that generate significant amounts of waste (150-200,000 tonnes per annum).

3.3 Methods

3.3.1 Study sites and study period

Fieldwork was conducted at two UK lesser black-backed gull colonies: Ribble Marshes in Lancashire (53°42’N, 2°59’W), and South Walney nature reserve in Cumbria (54°40’N, 3°14’W) (hereafter “Ribble” and “Walney” respectively). Both are within Special Protection Areas (SPAs; EC Birds Directive 2009/147/EC) where breeding lesser black-backed gulls are a designation feature. GPS-tagging work was conducted during the breeding seasons (May-July) from 2014 to 2017.

Ribble is a stable mixed colony of herring (*Larus argentatus*) and lesser black-backed gulls (6554-7022 breeding pairs in 2016) in saltmarsh and rank vegetation. Walney contains herring, great black-backed (*Larus marinus*) and lesser black-backed gulls, the latter having declined from an estimated 19,487 apparently occupied nests (AONs) during 1998-2002 to 1,981 AONs in 2018 (https://app.bto.org/seabirds/public/data.jsp).

3.3.2 Landfill habitat

Anecdotal observations and visualisation of foraging tracks suggest extensive use of two separate landfill sites by gulls breeding at Ribble and Walney. Birds from Ribble frequently visited Arpley Tip (53°22'N, 2°37'W), a large landfill with a capacity of c. 200,000 tonnes p.a., 43 km south-southeast of the colony that closed in December 2016 (http://myplanning.warrington.gov.uk). The main landfill at Walney was Jameson Road Landfill Site (53°54'N, 3°01'W), with a capacity of c. 150,000 p.a., 19.5 km south-southeast of the colony that closed in April 2017 (http://planningregister.lancashire.gov.uk/).

3.3.3 Movement

We analysed data during 4-19th June (to coincide with late incubation/early chick-rearing) in both 2016 (immediately before closure) and 2017 (immediately after closure). This resulted in 1,292 foraging trips from 48 individuals (Table 3.1). Breeding adult gulls were caught at the nest using wire mesh walk-in cage traps and then fitted with a solar-powered Global Positioning System (GPS) tag (either a University of Amsterdam Bird-Tracking System (UvA-BiTS) device or a Movetech Flyway-18 GPS-GSM device) which collected regular positional fixes (Thaxter *et al.*, 2019). Devices were attached using a Teflon wing-loop harness, to facilitate long-term deployment without impacting breeding success or survival (Thaxter *et al.*, 2014, 2016). "Permanent" harnesses were replaced with those containing a “weak-link” from 2017 allowing tag detachment without recapture (Table A1). Device and attachment combinations were below the 3% body mass recommended at the time (Phillips, Xavier and Croxall, 2003; Table A2). Although recent work suggests such percentage of body mass thresholds may be inappropriate for mitigating device effects (Bodey *et al.*, 2018), previous work showed no negative influence of this type of tag attachment (Thaxter *et al.*, 2014, 2016). All tagging was performed under license from the British Trust for Ornithology’s independent Special Methods Technical Panel of the UK ringing scheme. All tagged individuals were fitted with uniquely engraved colour rings for subsequent field identification.

Table 3.1. Sample sizes of tagged adult lesser black-backed gulls and foraging trips at each colony before and after landfill closure, following subsampling and removal of incomplete trips. Total number of individuals which contributed data in both years are shown in brackets.

Colony	**Year**	**Landfill Status**	**Number of Individuals**	**Number of Foraging Trips**
Ribble	2016	Open	5	68
Ribble	2017	Closed	13 (3)	231
Walney	2016	Open	33	759
Walney	2017	Closed	18 (18)	234

3.4 Data analysis

3.4.1 Movement

We limited movement analysis to 2016 and 2017, the years immediately before and after landfill closure. Tracks were resampled to a one-hour resolution, due to differences in sampling frequency between tags. Foraging trips were defined as any positional fix outside the colony boundary (Figs A1 & A2) with no data gaps greater than four hours (i.e. with good satellite coverage). Due to low data resolution, we were unable to distinguish between foraging and resting behaviour, therefore we assumed that all absences from the colony represented foraging trips.

3.4.2 Landfill utilisation

For each foraging trip, we classified all fixes into one of seven habitat categories (agriculture, coastal, freshwater, landfill, marine, other, urban; Table A3) using the 100 m resolution Corine European Landcover raster database (available at: https://land.copernicus.eu/pan-european/corine-land-cover/clc2018) overlaid with active landfill sites (Environment Agency. Permitted Waste Sites - Authorised Landfill Site Boundaries - https://data.gov.uk).

We first investigated whether there was a difference in the relative use of the focal landfills compared to other landfills in the years before and after closure. We classified all landfill fixes as either “focal” (Arpley Tip or Jameson Road; n = 222) or “other” (n = 80) and calculated the proportion of fixes in “focal” and “other” landfills for each site in each year.

We then quantified changes in overall landfill utilisation following landfill closure. We classified the habitat at the distal point (a proxy for foraging habitat; (Hamer *et al.*, 2009)) of each foraging trip as either “landfill” or “other” and modelled the probability of visiting any landfill using a generalised linear mixed effects model (GLMM) with a binomial error structure. The full model contained site, landfill status and the two-way interaction as fixed effects and individual as a random intercept.

3.4.3 Foraging effort

For each foraging trip we calculated duration (hours), total length (straight-line point to point distance km) and distance to distal point (km). We then modelled these response variables separately, using GLMMs with a gamma distribution and log link function. For each response variable we created maximal models containing site, landfill status (open vs. closed) and the two-way interaction between site and landfill status as fixed effects, and individual identity as a random intercept.

3.4.4 Habitat use

We modelled resource selection functions (RSFs) that account for differences in habitat availability by comparing visited habitats with randomly generated pseudoabsences (Aarts *et al.*, 2008). We first removed all birds with <5 location fixes in a given year. For each fix, we generated five pseudo-absences within the 100% minimum convex polygon (MCP) of the colony in that year. This allowed us to adequately capture the composition of available habitat within the foraging range, including rare habitats like landfills, without models becoming too computationally intensive (Northrup *et al.*, 2013) .

Based on observed habitat use, we modelled RSFs for the five most visited foraging habitats (agriculture, coastal, landfill, marine and urban; Fig. B1), fitting separate models for each site and year. For each foraging habitat, probability of gull utilisation was modelled as a function of habitat type (focal habitat vs. other), breeding site and the two-way interaction using binomial generalised linear models (GLM) with a logit link. In all models we assigned a weighting of 5 to real location points, proportional to the ratio of real locations to pseudoabsences in the data set (Muff, Signer and Fieberg, 2020). A significant interaction effect supports the hypothesis that habitat selection varies with breeding site. Model fit was assessed by calculating AUC (Zweig and Campbell, 1993), predictive power, sensitivity and specificity (Warwick-evans, Atkinson and Robinson, 2016; Table B5).

3.4.5 Body condition

All captured birds were measured (wing length, bill depth, bill length and total head and bill length (mm)) and weighed (using a Pesola spring balance to the nearest 10 g). Morphometric data were used when considering tag effects (Table A2) and to calculate adult body condition. For adults breeding at Ribble (2016 tip open n = 19 and 2017 tip closed = 21), we calculated the scaled mass index (Mi), which standardises body mass at a fixed value of a linear body length measurement (here, wing length, the structural measurement most correlated with mass) (Peig and Green, 2010). We compared mean adult body condition in the years before and after landfill closure using a Welch's two-sample t-test for unequal variances.

3.4.6 Model selection

Model selection was based on AIC for all analyses (Tables B1 – B4). Where multiple candidate models had a Δ AIC < 2.0 we selected the model with the fewest parameters (Burnham and Anderson, 2002). Normality plots and visualisation of residuals were used to check assumptions for normality and homogeneity of variance. For mixed effects models, we calculated both marginal (MR^2) and conditional (CR^2) r-squared values (Nakagawa and Schielzeth, 2013), using the trigamma function where available (Nakagawa, Johnson and Schielzeth, 2017). All statistical analyses were conducted in R v3.6.2 (R Core Team 2019).

3.5 Results

3.5.1 Movement

Generally, breeding adult lesser black-backed gulls (n = 48) from both sites travelled inland to forage, either to the southeast or northeast of the colony and largely avoided marine habitats. Foraging trips were broadly similar in terms of distance travelled and spatial distribution before and after the landfill closures (Fig. 3.1).

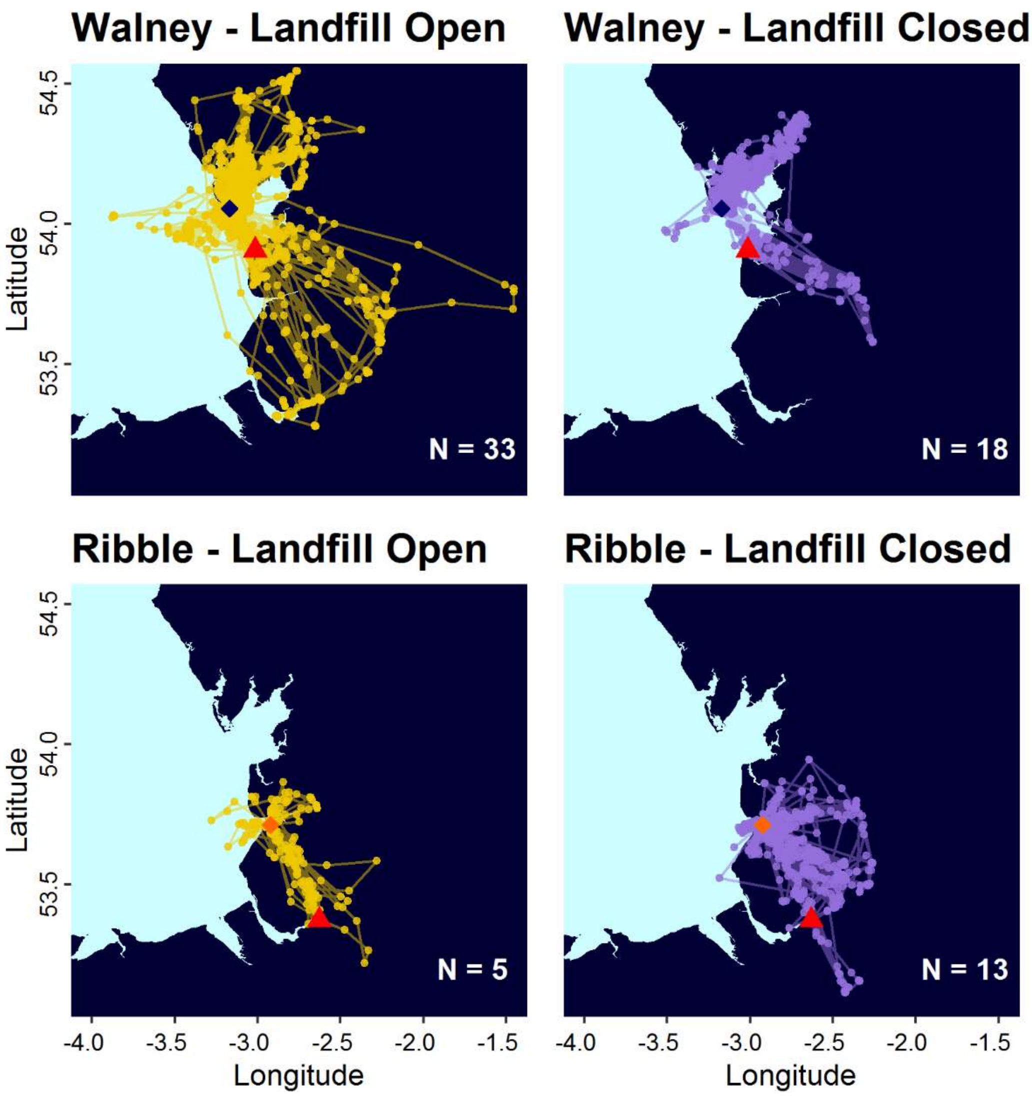

Figure 3.1. Complete foraging trips by all tracked birds from Walney and Ribble before (gold) and after (purple) landfill closures. N denotes the number of birds tracked in each year. Colony locations are marked with navy (Walney) or orange (Ribble) diamonds. Focal landfills, Jameson Road Landfill (Walney) and Arpley Tip (Ribble) are marked with red triangles.

3.5.2 Landfill utilisation

When operational in 2016, the focal landfills fixes were by far the most frequently visited sites at both Ribble (94.8% of landfill fixes) and Walney (77.5% of landfill fixes). However, following landfill closure in 2017 birds from Walney ceased to visit Jameson Road, although Ribble birds occasionally visited Arpley (31.3% of landfill fixes) even after its closure. At both sites, the total landfill fixes were dramatically reduced following the landfill closure (Fig. 3.2). At the colony-level, birds were less likely to forage at any landfill site following the closure of the focal landfill (mean difference ± SE = -1.87 ± 0.43; Fig. 3.3).

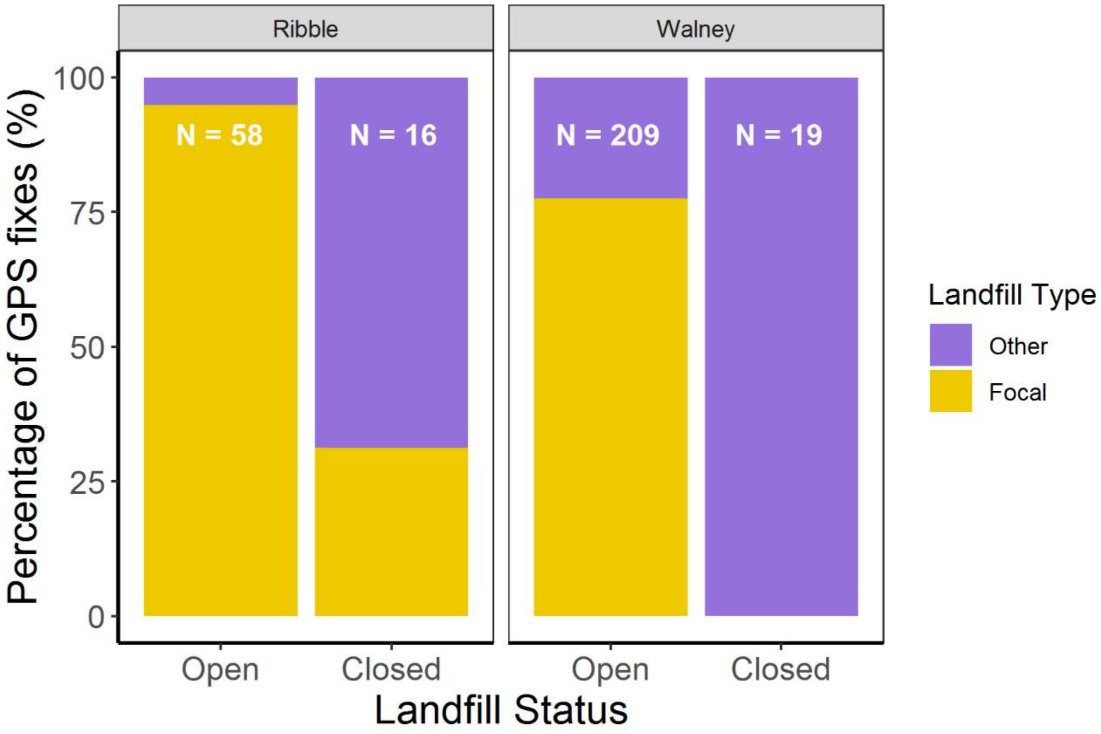

Figure 3.2. Proportion of GPS fixes within landfill sites at focal (gold) and other (purple) landfills in the years before and after landfill closure. Birds from Ribble occasionally visited Arpley Tip following closure whilst birds from Walney ceased visiting Jameson Road Landfill Site altogether. N represents the total number of GPS fixes that fall within all landfill sites in a given year.

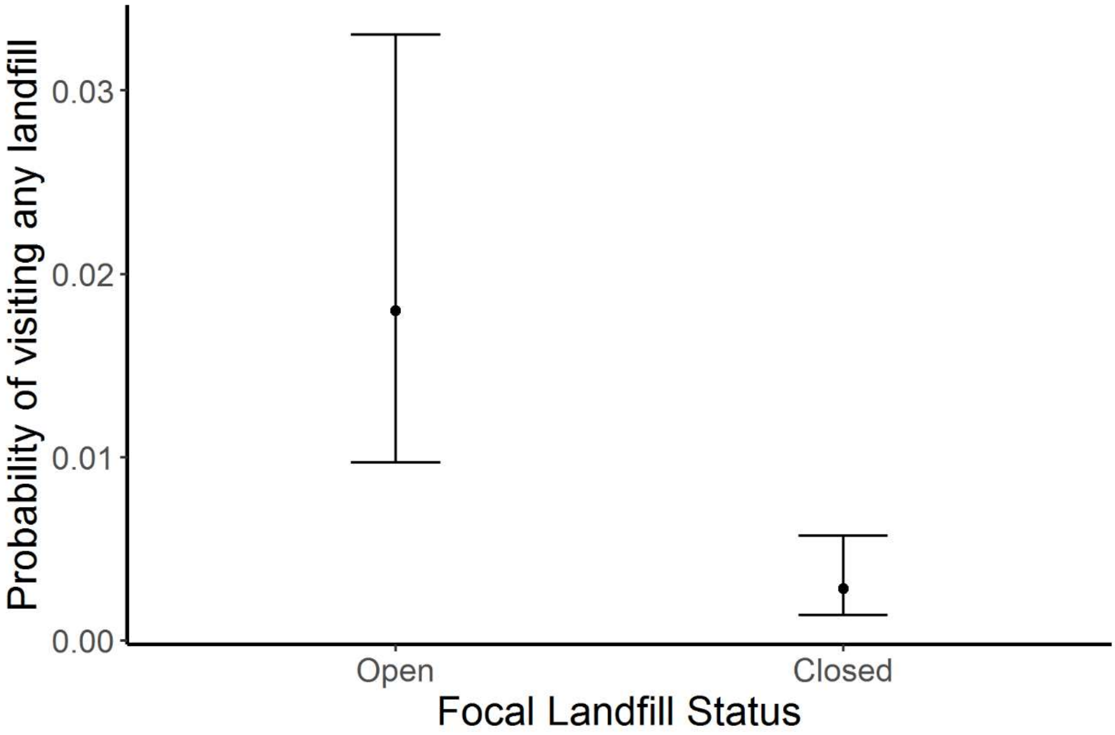

Figure 3.3. Probability of visiting any landfill site for breeding lesser black-backed gulls in the years before and after closure of the focal landfills. Birds breeding at Ribble and Walney were more likely to visit landfills in the year before the closure of the focal landfill (Arpley and Jameson Road respectively).

3.5.3 Foraging effort

Trip durations were longer following landfill closure than when open (mean difference ± SE = 0.73± 0.05; Fig. 3.4a) and Walney birds spent more time on trips than those from Ribble (mean difference ± SE = 0.59 ± 0.20; Fig. 3.4b.)**.** Birds travelled greater distances following landfill closure (mean difference ± SE = 0.62 ± 0.08; Fig. 3.4c) and distal points were further from the colony (mean difference ± SE = 0.26 ± 0.15). This latter shift was stronger at Walney, as shown by the interaction between landfill status and colony (mean difference ± SE = 0.33 ± 0.17). Regardless of landfill status, birds from Walney foraged closer to the colony (mean difference ± SE = -0.52 ± 0.23; Fig. 3.4d).

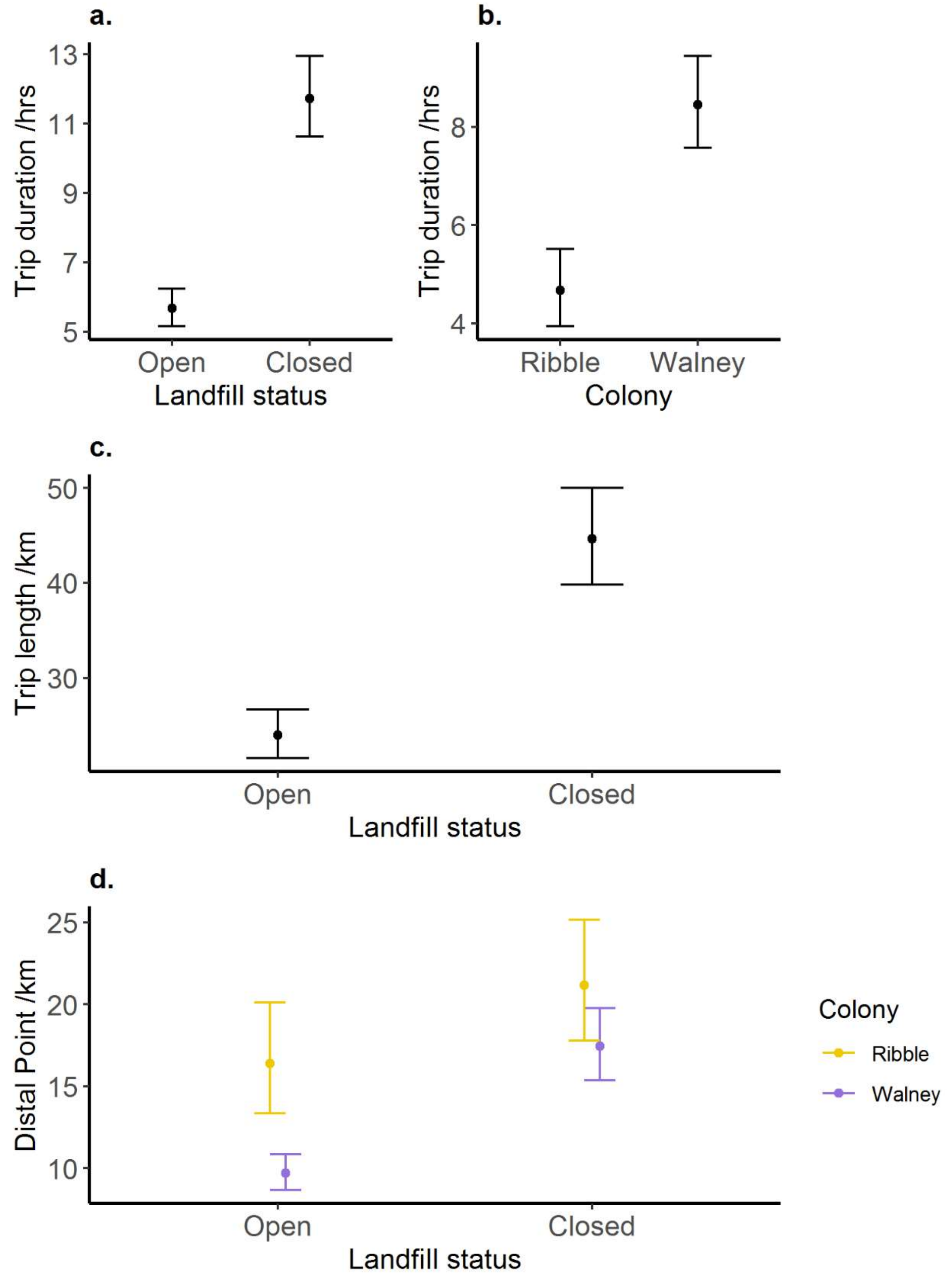

Figure 3.4. Back-transformed model estimates and SEs from the best supported models explaining variation in foraging trip characteristics at the colony-level. a. Trip durations (hrs) were greater following the closure of the focal landfill across both sites. b. Trip durations were greater higher for birds at Walney than those breeding at Ribble regardless of landfill status. c. Trip lengths (km) were greater when the landfill was closed than when it was open across both sites. d. Distal

points (km) were further following the closure of the focal landfill, with a greater increase in distal point following landfill closure at Walney compared to Ribble.

3.5.4 Habitat selection

The probability of landfill foraging declined at both colonies following closure of the focal site, however this probability was much more variable in the year prior to closure, suggesting landfills were not visited by all individuals or on all foraging trips (Fig. 3.3). Although selections for landfills declined overall, they remained an important foraging destination and were still actively selected for relative to their availability. Ribble breeders increased their utilisation of urban habitats following landfill closure whilst birds from Walney used urban habitats less frequently, instead increasing their selection for agricultural habitats. At both colonies, selection for marine habitats was weaker following the landfill closure, however selection for coastal habitats remained high at both colonies across both years of the study (Table 3.2; Fig. 3.5).

Table 3.2. Estimates for the effect of an interaction between the habitat variable and breeding site on the probability of a location being a real gull location or a pseudo-absence. Delta (Δ) AIC refers to the change in AIC caused by removing the interaction. Δ AIC values > 2, suggest that selection for that habitat type differs significantly following landfill closure. Stars next to p-values represent significance levels (* < 0.05; ** < 0.01; *** < 0.001).

Habitat Variable	Site	Estimate for landfill status interaction	p value	Δ AIC
Agriculture	Ribble	0.14 (± 0.09)	0.143	0.2
Coastal	Ribble	0.18 (± 0.21)	0.380	-1.2
Landfill	Ribble	-2.29 (± 0.45)	$<0.001^{***}$	26.1
Marine	Ribble	-3.11 (± 0.37)	$<0.001^{***}$	99.8
Urban	Ribble	0.83 (± 0.11)	$<0.001^{***}$	58.2
Agriculture	Walney	1.02 (± 0.04)	$<0.001^{***}$	752.4
Coastal	Walney	0.24 (± 0.06)	$<0.001^{***}$	12.1
Landfill	Walney	-1.68 (± 0.37)	$<0.001^{***}$	14.8
Marine	Walney	-1.76 (± 0.06)	$<0.001^{***}$	942.6
Urban	Walney	-0.85 (± 0.07)	$<0.001^{***}$	162.9

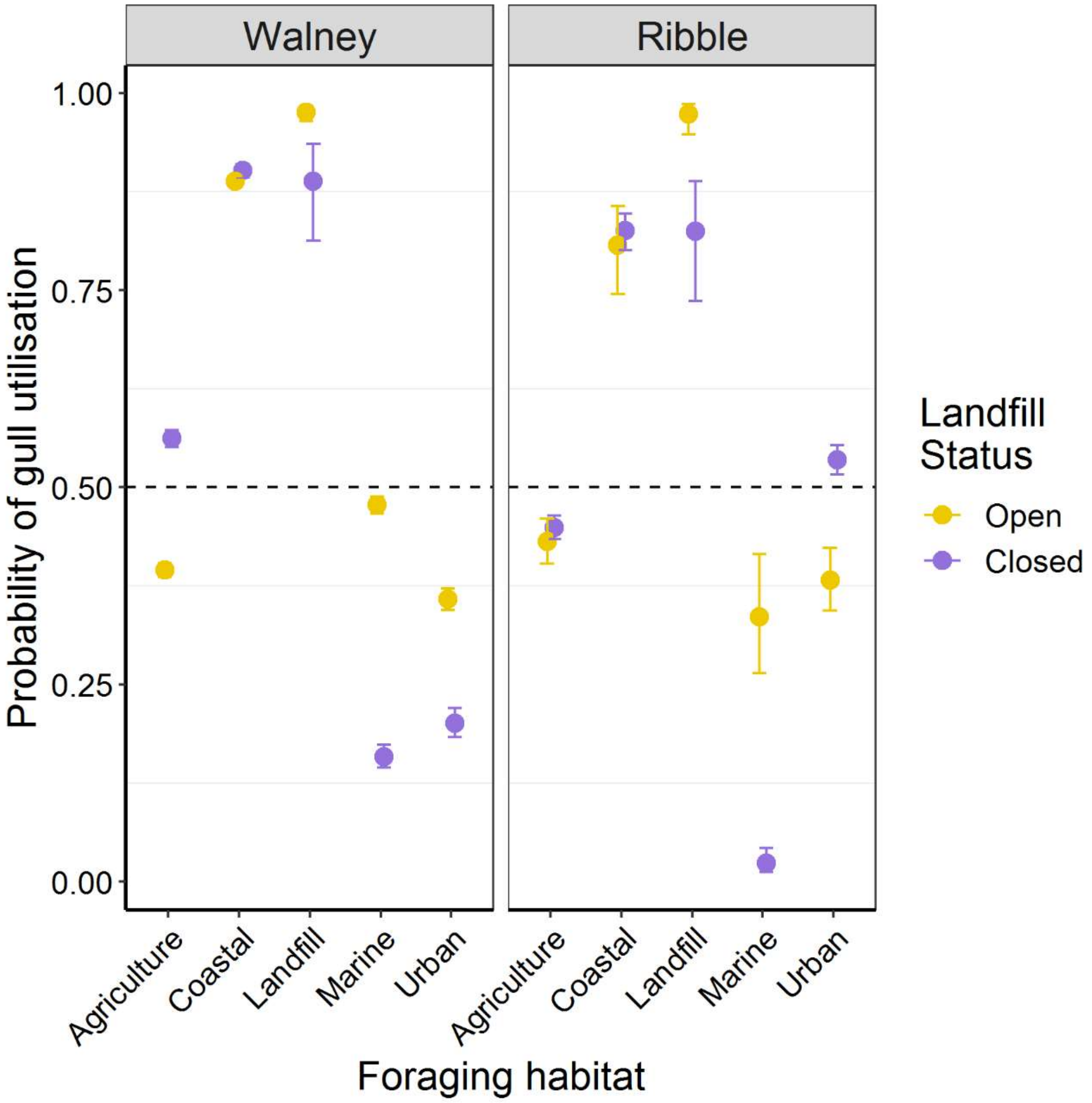

Figure 3.5. Estimates and 95% confidence intervals from resource selection models for all gulls breeding at Ribble and Walney before (gold) and after (purple) closure of the focal landfill site. Models estimate the probability of a given location point being a real gull location rather than a pseudo-absence in response to five main foraging habitat categories (agriculture, coastal, landfill, marine, urban). A probability of 0.50 indicates that birds used habitat in proportion to its availability whilst values of > 0.50 indicate selection for that habitat type at the colony-level.

3.5.5 Adult body condition

There was no significant effect of landfill status on adult body condition at Ribble (Mi) (t = -0.56, df = 32.548, p = 0.577). A power analysis, using the difference between group means (0.56) as the effect size, revealed a relatively low power of 41.1%.

3.6 Discussion

We found that gulls travelled further and spent longer on foraging trips following landfill closures (Fig. 3.4). Moreover, while some birds were able to find alternative landfills to forage on (Fig. 3.3), they increased their use of agricultural habitats or urban areas, depending on colony (Table 3.2; Fig. 3.5).We found no effect of landfill closure on adult body condition.

3.6.1 Movement

Landfills provide predictable food (Oro *et al.*, 2013), although this is clearly not the case if they close. The increased trip duration following landfill closure found here suggests birds spent more time travelling, searching for and/or handling food. This may be due to low quality foods in agricultural habitats (Coulson and Coulson, 2008; van den Bosch *et al.*, 2019), or ephemeral resources (Huig, Buijs and Kleyheeg, 2016) and difficult to learn foraging behaviours in urban areas (Goumas *et al.*, 2019; Spelt *et al.*, 2019).

Alternatively, longer foraging trips may be a direct consequence of breeding failure, which removes the constraint to act as central place foragers (Votier *et al.*, 2017). However, this seems unlikely to explain our results because, while there were high levels of failure at Ribble in 2017 (due to flooding), breeding success was similar between years at Walney. Whatever the reason, longer foraging trips mean longer absences from the nest site, which could increase the risk of chick mortality or conspecific intrusions.

3.6.2 Habitat selection

While gulls were able to find landfills following closure of two very large dumps, they still showed a sharp decline in landfill use. Instead, birds selected either agricultural (Walney) or urban (Ribble) habitats (Fig.3.5). This highlights the rapidity with which gulls can alter their foraging behaviour in response to change and has been found in other species (van Toor *et al.*, 2017; Zorrozua *et al.*, 2020). This also shows how fine-scale tracking is effective at monitoring short-term effects of changing waste management.

The selection of alternative foraging habitats may relate to colony-level differences in habitat availability, with urban habitats more available at Ribble (29% pseudoabsences) than Walney (15% pseudoabsences). Additionally, Walney birds did not forage in Barrow-in-Furness, the closest urban area, possibly due to competitive exclusion by urban breeders (Wakefield *et al.*, 2013; Corman *et al.*, 2016). Longer journey times may therefore make urban foraging unprofitable for Walney birds, prompting a shift to agricultural habitats, despite relatively low energetic rewards (van den Bosch *et al.*, 2019; van Donk *et al.*, 2019).

Another striking result from this analysis is the reduction in marine foraging following landfill closure. Breeding lesser black-backed gulls often forage extensively in marine environments (Camphuysen, 2013; Thaxter *et al.*, 2015), however, rates of marine foraging were relatively low in these populations. This may be due to an abundance of terrestrial foraging opportunities or possibly due to a degraded local marine environment with a low availability of fishery discards (Tyson *et al.*, 2015; Garthe *et al.*, 2016). This change could also result from increased profitability of agricultural foraging due to the high rainfall in 2017, which makes soil invertebrates more accessible (Isaksson *et al.*, 2016). Alternatively, birds may have had to spend longer searching for food in terrestrial habitats (Fig. B1), or colony-wide reproductive failures reduced the requirement for high quality marine prey (Annett and Pierotti, 1999; Thaxter *et al.*, 2015).

3.6.3 Methodological considerations

We included all foraging trip points in our analysis due to low data resolution (1 hr fixes) (Spelt *et al.*, 2019; Méndez *et al.*, 2020), which risks including commuting and not just foraging locations. To address this, we repeated the analysis on a filtered data set containing distal trip locations, where we assumed gulls were foraging (Hamer *et al.*, 2009). General patterns of habitat selection for the distal points were similar to those from all trip foraging trip fixes (Fig B2; Table B6), suggesting that differences in habitat selection presented here represent real shifts in foraging behaviour following landfill closure.

Although gulls are considered generalists at the population-level, some species exhibit sex-specific foraging (Tyson *et al.*, 2015) and individual foraging specialisation to varying degrees (van den Bosch *et al.*, 2019; Westerberg *et al.*, 2019). Our analysis focusses on population-level responses to landfill closures, however, we might also expect variation in landfill foraging resulting from sex differences or individual preferences and future work should investigate the consistency of individual foraging strategies in the face of anthropogenic perturbations.

3.6.4 Body condition

We observed no closure effects on adult body condition at Ribble, which contrasts with previous work demonstrating negative impacts of landfill closures on yellow-legged gull body condition (Steigerwald *et al.*, 2015). The low power (41.1%) suggests the likelihood of a Type II error due to modest sample sizes (n = 40) was relatively high. Alternatively, we may not have detected an effect as birds were able to rapidly switch to alternative habitats. Moreover, not all birds visited the focal landfills when open and we don't know whether individuals measured following closure visited them in the previous year, limiting our ability to detect subtle effects of landfill closures on the body condition of individual gulls. Finally, adult body condition may be influenced by conditions during winter before being carried over to the breeding season (Harrison *et al.*, 2011).

3.6.5 Conservation and management implications

Here we demonstrated the reliance of SPA breeding gulls on landfills outside protected area boundaries, highlighting the need to consider the home ranges and key foraging sites of mobile species in management decisions (Oro, 2003; Thaxter *et al.*, 2012). However, we did not detect fitness costs associated with landfill closures, suggesting that behavioural flexibility of adult gulls (van Toor *et al.*, 2017) promotes resilience to anthropogenic perturbations. However, we were unable to measure breeding parameters such as egg volume or chick growth, which may be more sensitive to anthropogenic perturbations (Pons, 1992; Pons and Migot, 1995; Oro, 1996) and therefore cannot rule out the possibility of fitness costs related to landfill closures.

Although demographic responses to changing PAFS availability may be slow (Votier et al., 2004), our results demonstrate rapid behavioural responses (Payo-Payo *et al.*, 2015; Zorrozua *et al.*, 2020). Consequently, when generalist populations switch to alternative resources, it may increase the intensity and alter the spatial-distribution of human-gull interactions, necessitating conservation or management interventions (Bicknell *et al.*, 2013; Sherley *et al.*, 2020). For example, such unforeseen management implications have occurred in South Africa, where populations of great white pelicans (*Pelicanus onocrotalus*) benefitting from PAFS are controlled to reduce predation of endangered seabirds (Mwema, de Ponte Machado and Ryan, 2010).

In our study, increased agricultural foraging by gulls may create conflict with farmers, as they eat crop seeds and livestock food (Patenaude-Monette, Bélisle and Giroux, 2014; van den Bosch *et al.*, 2019) and may transmit disease to livestock (Coulson et al., 1983). Alternatively, more frequent urban foraging could increase nuisance behaviour such as aggressive food-snatching (Goumas *et al.*, 2019). However landfill closures may also provide management benefits, reducing the need for physical and auditory deterrents and lethal management to deter feeding gulls (Rock, 2005; Egunez *et al.*, 2018).

3.7 Conclusion

We found that gulls responded quickly to landfill closures by increased foraging effort and switching to agricultural and urban habitats, but with no effect on adult body condition. The long-term consequences of closures are unclear, but may shift the focus of human-gull interactions to urban and agricultural areas. Accordingly, our study highlights the need to reappraise the term Predictable Anthropogenic Food Subsidies in a changing world.

3.8 References

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Chapter 4 – Urban and coastal breeding gulls segregate by foraging habitat

4.1 Abstract

Despite urbanisation's general erosion of biodiversity, it still provides opportunities for some species. During the 20th century, gulls (*Laridae*) colonised urban areas around the world where they flourished. At the same time, some coastal populations experienced declines. However, little is known about whether ecological differences between urban and non-urban gulls exist. Here we compare foraging and breeding ecology of urban and coastal nesting lesser black-backed gulls (*Larus fuscus*). We first use GPS data to classify the "urbaness" of individual gulls, before using this data, along with diet sampling and nest monitoring to compare breeding ecology, foraging ecology and habitat selection at the colony-level. We found a number of key differences. Urban breeders preferentially foraged in urban areas while coastal breeders foraged in maritime habitats, suggesting a link between nesting and foraging ecology. Coastal breeders also had larger foraging and home ranges than urban breeders. We observed no dietary differences, although coastal breeders laid larger eggs and clutches than urban birds. These findings have important consequences for gull management, highlighting how measures to restrict food availability in urban areas may mitigate human-gull conflict by reducing opportunities for foraging gulls. Moreover, they highlight that conservation measures, such as improved predator management and restoration of coastal and marine ecosystems could help declining coastal populations.

4.2 Introduction

Urbanisation may negatively impact biodiversity (Mcdonald, Kareiva and Forman, 2008; Ortega-Álvarez and MacGregor-Fors, 2009), but can also provide ecological opportunities via habitat creation (Møller, 2009), predictable anthropogenic food subsidies (hereafter PAFS; Oro *et al.*, 2013) and a benign microclimate (Partecke, Van't Hof and Gwinner, 2004). These benevolent conditions have allowed some generalist species to colonise and flourish in towns and cities worldwide (Evans *et al.*, 2010; Lowry, Lill and Wong, 2012).

During the 20th century, several gull species (*Laridae*) began breeding in towns and cities around the world (Smith and Carlile, 1993; Dwyer, Belant and Dolbeer, 1996; Soldatini *et al.*, 2008; Yorio *et al.*, 2016). These generalist foragers exploited abundant PAFS in urban environments (Huig, Buijs and Kleyheeg, 2016) and also benefitted from predator-free breeding habitat and heat island effects (Rock, 2005; Zelenskaya, 2019). Urban breeding thus allowed some gull populations to increase, but this intensified conflict with people via disease transmission (Girdwood *et al.*, 1985; Hatch, 1996), bird-strikes (Neubauer, 1990) and nuisance (e.g. noise, aggression, food-snatching and property damage; Rock, 2005; Calladine and Park, 2006). This in turn instigated efforts to reduce urban gull numbers using lethal and non-lethal control (Rock, 2012; Trotter, 2019). However, increasing urban gull populations contrast with steep declines of some coastal colonies, which instead have become the focus of conservation efforts (Ross-Smith *et al.*, 2014; Blight, Drever and Arcese, 2015; Hario and Rintala, 2016; Nager and O'Hanlon, 2016).

Given the apparent importance of urban colonies, appropriate management and conservation requires detailed information on urban gull movement ecology, habitat selection (Spelt *et al.*, 2019; Méndez *et al.*, 2020), diet (Raven, 1997; Belant, Ickes and Seamans, 1998) and reproductive success (Hooper, 1988; Zelenskaya, 2019) and how they compare with neighbouring natural colonies. Previous comparative studies have focused on single traits, largely breeding parameters, and have found varying trends between breeding habitats among different gull populations (Monaghan, 1979; Hooper, 1988; Vermeer, Power and Smith, 1988; Soldatini *et al.*, 2008; Zelenskaya, 2019). Colony-level comparisons are complicated. For instance, differences may relate to proximity of food (Duhem *et al.*, 2005), density-dependence (Wakefield *et al.*, 2013; Corman *et al.*, 2016) or individual quality, (Ross-Smith, Johnston and Ferns, 2015; Perlut *et al.*, 2016; Kroc, 2018), rather than relating to differences in breeding habitat *per se*.

Here we GPS track adult lesser black-backed gulls (*Larus fuscus graellsii*) breeding at adjacent urban and costal sites and compare movement, foraging and reproduction. We first examine individual foraging movements to quantify urbaness and determine whether any colony-level differences in urban foraging are consistent across individuals. We then compare population-level habitat selection, diet and clutch/chick condition and discuss the implications for gull conservation and management across different breeding habitats. A key advantage of this approach is that gulls from both colonies can access the same foraging habitats, minimising the effect of any differences in resource availability on movement behaviour. Moreover, this study simultaneously compares movement behaviour, diet and breeding performance between neighbouring gull colonies, allowing us to investigate potential mechanisms that may be driving divergent demographic trends between breeding habitats.

4.3 Material and Methods

4.3.1 Study sites

Fieldwork was conducted during April to July, 2014-2018, at neighbouring urban (Barrow-in-Furness; 54°06’N, 3°31’W) and coastal sites (South Walney nature reserve; 54°40’N, 3°14’W) (hereafter ‘urban’ and ‘coastal’). The urban site hosts 80-100 pairs of lesser black-backed gulls plus 1-3 pairs of herring gulls (*Larus* *argentatus*) nesting on the ground amongst rank vegetation surrounded by fencing, walls and deep water. This site is a sub-colony of Barrow-in-Furness which contains a stable population of c. 400 pairs of lesser black-backed and c. 200 pairs of herring gull (Sellers & Shackleton, 2011; UK Seabird Monitoring Programme online database - https://app.bto.org/seabirds/public/data.jsp). The coastal site hosts a large, declining colony of lesser black-backed (2017 = 2,782 pairs, 2018 = 1,981 pairs), and herring gulls (2017 = 1,705 pairs, 2018 = 1,484 pairs) and ~50 pairs of great black-backed gulls (*Larus marinus*) (https://app.bto.org/seabirds/public/data.jsp) in sand dune, shingle and rank vegetation, within electric predator fences.

4.3.2 Movement

We filtered the tracking data for 2017 and 2018, the years when data on diet and breeding parameters were collected, and then extracted data from the period (4-19th June) in both years to correspond to late incubation/early chick-rearing. This resulted in 717 foraging trips from 41 individuals (Table 4.1). Breeding adult lesser black-backed gulls were caught at the nest using wire mesh walk-in traps (Bub, 1991) during late-incubation. Captured birds were fitted with a solar-powered Global Positioning System (GPS) tag (either a University of Amsterdam Bird-Tracking System (UvA-BiTS) device or a Movetech Flyway-18 GPS-GSM device) which collected regular positional fixes (Thaxter *et al.*, 2019). Devices were attached via a Teflon wing-loop harness, to enable long-term deployment without impacting breeding success or over-winter survival (Thaxter *et al.*, 2014, 2016). “Permanent” harnesses were replaced by a “weak-link” design from 2017 allowing the tag to detach without recapture (Table A1). Device and attachment combinations were below the 3% body mass recommended at the time (Phillips, Xavier and Croxall, 2003; Table A2), although recent work suggests such thresholds may be inappropriate (Bodey *et al.*, 2018). All tagging was performed under license, approved by the UK ringing scheme Special Methods Technical Panel (SMTP). All tagged individuals were fitted with uniquely engraved colour rings for subsequent field identification.

Table 4.1. Sample sizes and total foraging trips of tagged gulls by colony and year, following subsampling and removal of incomplete trips. The number of tagged individuals which contributed data in both years are included in parentheses.

Colony	**Year**	**Number of Individuals**	**Number of Foraging Trips**
Urban	2017	14	187
Urban	2018	11 (2)	139
Coastal	2017	18	234
Coastal	2018	9 (9)	157

4.3.3 Diet

During the 2017 and 2018 breeding seasons, we systematically collected all adult prey remains and regurgitated pellets from the territories where we monitored breeding parameters. We also collected all additional regurgitated pellets found away from study territories within the urban colony in 2018. In addition, we opportunistically collected all spontaneous regurgitates produced by chicks from study nests during routine handling in both years.

4.3.4 Breeding parameters

In each year a sample (Urban: 2017 = 82, 2018 = 46; Coastal: 2017 = 64, 2018 = 67) of study nests were marked and visited every 3-5 days. We recorded clutch size, egg volume and hatching success. Where possible, chicks were measured (wing and maximum tarsus length - (mm)), weighed (using a Pesola spring balance to the nearest 1g) and individually marked with sheep spray for subsequent relocation, within four days of hatching. Chicks not located on three successive visits were presumed to have died, while those surviving to 36 days post-hatching were assumed to have fledged. Chick handling and marking was performed under SMTP license.

4.4 Data Analysis

4.4.1 Movement

We resampled tracking data to a one-hour resolution, due to differences in sampling frequency between tags. We defined foraging trips as any positional fix outside the colony boundary (Figs A2 & A3) that had no data gaps greater than four hours.

4.4.2 Quantifying "urbaness"

Individual foraging specialisation is common across animal populations, however, this variation can be masked when examining population-level patterns (Bolnick *et al.*, 2003; Patrick and Weimerskirch, 2017; van den Bosch *et al.*, 2019). In order to better understand differences in foraging ecology between breeding habitats and, determine whether any colony-level differences in habitat use were consistent across individual gulls, we first quantified relative "urbaness" of tracked individuals.

For each foraging trip, we classified the distal point (a proxy for foraging habitat; (Hamer *et al.*, 2009)) as either "urban" or "other" using the 100m resolution Corine European Landcover raster database (CLC2018) (https://land.copernicus.eu/pan-european/corine-land-cover/clc2018) overlaid with active landfill sites (Environment Agency. Permitted Waste Sites - Authorised Landfill Site Boundaries - https://data.gov.uk).

Relative “urbaness” was quantified as the proportion of urban vs. other trips by individual and year. We then modelled urban vs. other trips at the colony-level using a generalised linear mixed effects model (GLMM) with a binomial error structure. The full model contained site, year and the two-way interaction between site and year as fixed effects and individual as a random intercept.

4.4.3 Foraging effort

For each trip we calculated duration (hours), total length (straight-line point to point distance km) and distal point (km) and modelled each variable using GLMMs with a gamma distribution and log link function. In each model we fitted site, year and their interaction as fixed effects, and individual as a random intercept. We also tested the effect of habitat at the distal point (urban vs other) by including trip type, site and their interaction as fixed effects.

4.4.4 Home range

The spatial distribution of individual birds was investigated using kernel density estimation (KDE, Worton, 1989). We first removed birds with <5 foraging trip fixes in a season (minimum required to calculate KDE) and then calculated annual 50% and 95% utilisation distributions of the KDE for each bird, representing the core foraging range and home range respectively (Thaxter *et al.*, 2016), on a 500m grid. The smoothing parameter (h) was determined using the default *ad hoc* method following (Trevail *et al.*, 2019) and (Calenge, 2006).

Core and foraging range area were both log-transformed and modelled with linear mixed effects models (LMMs) which included site, year and the two-way interaction as fixed effects. We also included total number of foraging trip fixes to account for variation in sampling frequency and individual ID as a random effect.

4.4.5 Habitat use

Foraging trip location fixes were classified into seven habitat categories (agriculture, coastal, freshwater, landfill, marine, urban and ‘other’ (unsuitable for foraging); Table A3) using the 100m CLC2018 raster and the Environment Agency data on active landfills.

We then modelled resource selection functions (RSFs) with a use-availability design, which accounts for differences in habitat availability by comparing habitat composition at visited locations to randomly generated pseudoabsences (Aarts *et al.*, 2008). We first removed all birds with <5 location fixes in a given year. For each fix, we generated five pseudo-absences within the 100% minimum convex polygon (MCP) for the colony in that year.

We modelled RSFs for the four main foraging habitats (agriculture, coastal, marine and urban; Fig. C1), fitting separate models for each year. For each foraging habitat, probability of gull utilisation was modelled as a function of habitat type (focal habitat vs. other), breeding site and the two-way interaction using binomial generalised linear models with a logit link. A significant interaction effect supports the hypothesis that habitat selection varies with breeding site. Model fit was assessed by calculating AUC (Zweig and Campbell, 1993), predictive power, sensitivity and specificity (Warwick-evans, Atkinson and Robinson, 2016; Table C7).

4.4.6 Diet

Adult diet pellets and chick regurgitates were dissected in the lab and all prey items were identified to the lowest taxonomic level. Pellets and chick regurgitates were then assigned to one of three foraging habitat types; agricultural (i.e. worms, beetles, small rodents and maize), urban/landfill (i.e. paper, plastic, glass and foil), and marine (i.e. marine molluscs, crustaceans and fish), based on the identity of the prey items found within (Tables C10, C11). For samples which contained prey items from multiple foraging habitats, a single main habitat type was assigned based on the predominant component using visual inspection. We only used pellets collected in June to allow between year comparisons and to overlap with tracking data. Chick regurgitate comparisons were confined to 2018 because so few were collected in 2017. We then compared diet composition between colonies, based on counts of samples assigned to each foraging habitat type, for both adult pellets and chick regurgitates using chi-squared contingency analysis. Due to small sample sizes in some habitat categories for adult pellets, we first collapsed cells into “agricultural” and other” before performing the chi-squared analysis.

4.4.7 Breeding parameters

We calculated egg volume (cm^3) for all eggs following Bolton, (1991; Eq. 1):

$$V = 0.000476 * length(mm) * breadth(mm)^2 \qquad \text{Eq. 1}$$

We also calculated total clutch volume (cm^3) for all nests. For three-egg clutches we calculated intra-clutch variation (difference in volume between the largest and smallest eggs; IESV), a measure of clutch asynchronicity (Royle, 1998). Hatching condition was estimated using scaled mass index (Mi; Peig and Green, 2010), using mass at first measurement and maximum tarsus length as a measure of structural size.

We investigated variation in the four breeding parameters: clutch volume and IESV using linear models and egg volume and chick condition using LMMs to account for nest ID. The maximal models for all breeding parameters models contained site, year and the two-way interaction as fixed effects. In the IESV model, we included volume (cm^3) of the largest egg as a fixed effect, in order to standardise across clutches. For egg volume and chick condition models, measurement date was included to account for seasonal effects. Clutch size was included as a fixed effect in all candidate models for egg and clutch volume. Within clutch volume rank (a proxy for laying order) was included as a fixed effect in all egg volume models to account for clutch asynchrony (Parsons, 1970).

4.4.8 Model selection

We conducted a model selection process based on AIC for all our analyses (Tables C1 – C6 & C12 – C15). Where multiple candidate models had a Δ AIC < 2.0 we selected the model with the fewest parameters (Burnham and Anderson, 2002). Normality plots and visualisation of residuals were used to check assumptions of normality and homogeneity of variance were not violated. For mixed effects models, we calculated both marginal (MR^2) and conditional R^2 (CR^2) values (Nakagawa and Schielzeth, 2013), using the trigamma function where available (Nakagawa, Johnson and Schielzeth, 2017). All statistical analyses were conducted in R (v3.6.2, R Core Team 2019).

4.5 Results

4.5.1 Movement and individual differences in "urbanness"

Analysis of the movement of (n = 41) breeding lesser black-backed gulls revealed that birds generally travelled short distances, frequently inland, with urban birds apparently travelling shorter distances than coastal birds, with similar patterns between years (Fig. 4.1a-d).

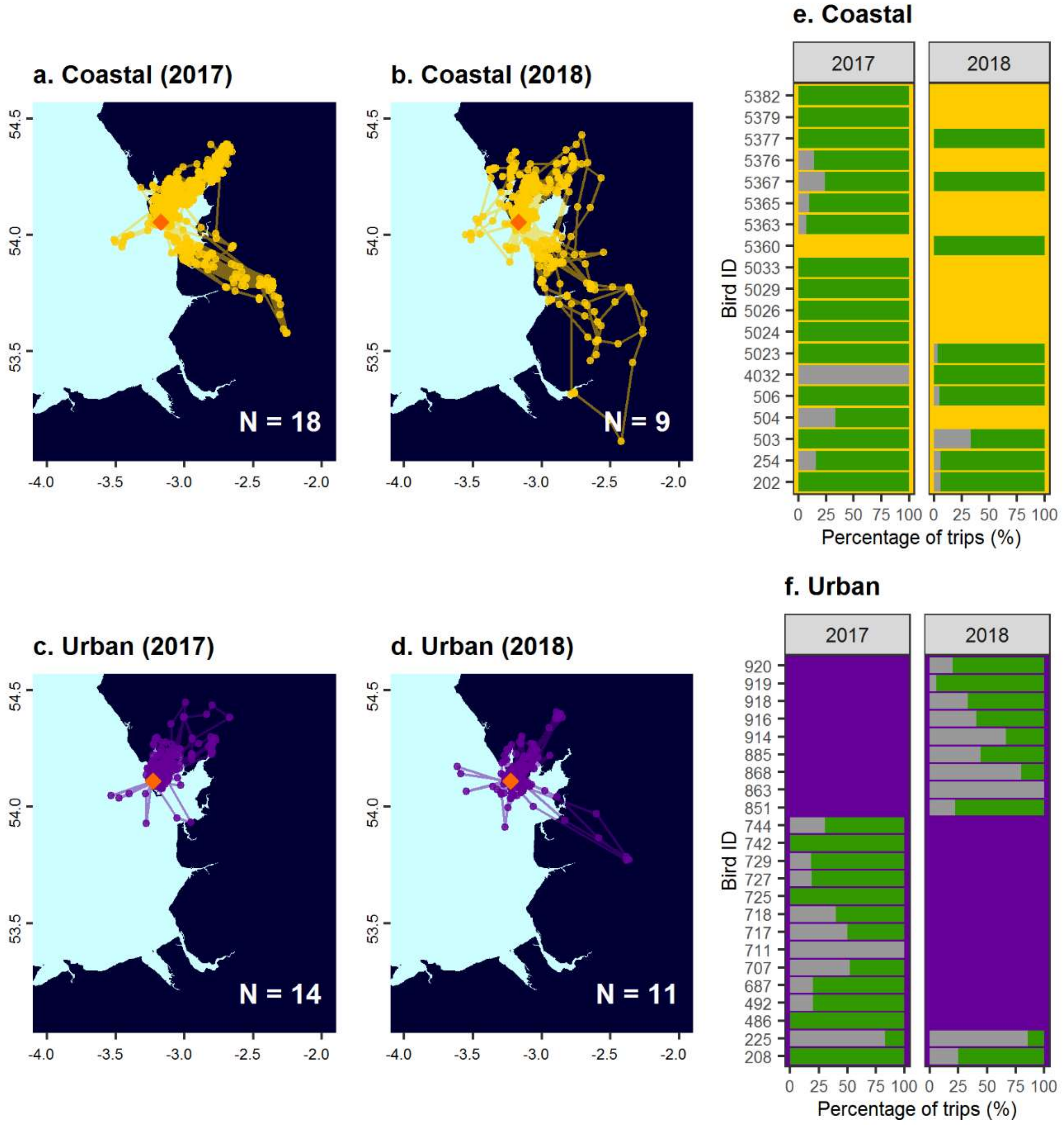

Figure 4.1. Complete foraging trips by 41 tracked lesser black-backed gulls from 4th-19th June from the coastal (a. b.) and urban (c. d.) colonies in 2017 and 2018. Colony locations are marked with navy (coastal) or orange (urban) diamonds. Additionally, we show the proportion of foraging trips to urban (grey) and non-urban (green) foraging sites for each individual breeding at the coastal (e.) and urban (f.) colonies. Urban gulls visited urban habitats more frequently than coastal breeders.

Urban breeders visited urban habitats more frequently than coastal breeders (Table 4.2; Fig. 4.1e-f) with many coastal gulls never foraging in urban habitats (2017 = 61%, 2018 = 44%). At the colony-level, urban breeders were more likely to forage in urban habitats than coastal birds (mean difference ± SE = 2.23 ± 0.46; Fig. 4.2).

Table 4.2. The mean (±SE) and median proportion of trips to urban habitats for individual birds breeding at the urban and coastal colonies in each year

Colony	**Year**	**Mean proportion urban trips (± SE)**	**Median proportion urban trips**	**Number of individuals**
Urban	2017	0.43 (± 0.09)	0.35	14
Urban	2018	0.48 (± 0.09)	0.41	11
Coastal	2017	0.29 (± 0.12)	0.16	18
Coastal	2018	0.11 (± 0.06)	0.06	9

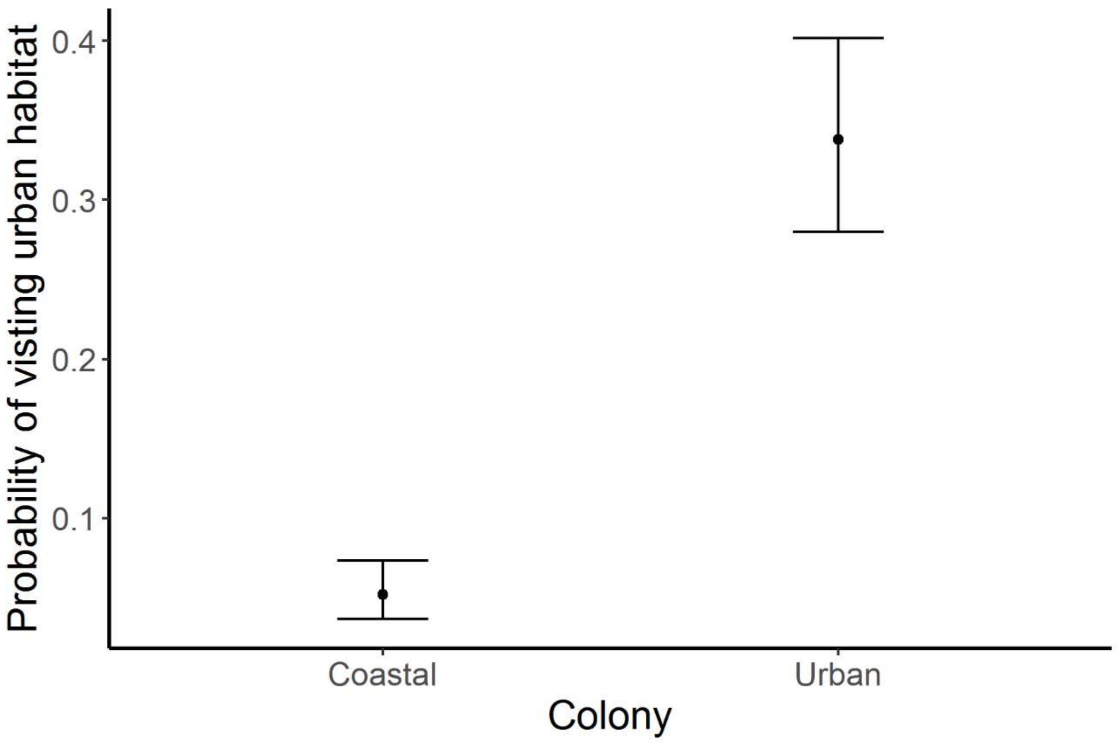

Figure 4.2. Model estimates from a binominal GLMM predicting the probability of making an urban trip for lesser black-backed gulls. Birds breeding at the urban site were more likely to visit urban habitats than birds breeding at the coastal site.

4.5.2 Foraging trip characteristics

Trip duration – Breeding colony had no effect on foraging trip duration (mean difference ± SE = -0.04 ± 0.19) across both years. However trip duration was slightly lower in 2018 than 2017 (mean difference ± SE = -0.19 ± 0.08) across both sites. Trips to urban habitats were shorter than trips to other habitats for urban breeders whilst there were only minor differences in trip duration between foraging habitats for coastal breeders due to the two-way interaction between trip type and colony (mean difference ± SE = -0.87 ± 0.18; Fig. 4.3a).

Trip length – Urban breeders had slightly shorter foraging trips than coastal breeders (mean difference ± SE = -0.38 ± 0.21). When accounting for foraging habitat, trips to urban habitats were much shorter than trips to nonurban habitats for urban breeders and the opposite was true for coastal breeders due to the two-way interaction between trip type and colony (mean difference ± SE = -2.47 ± 0.23; Fig. 4.3b).

Distal point – Urban breeders had shorter distal point distances than coastal breeders (mean difference ± SE = -0.33 ± 0.20). Additionally, distal point distance was closer in 2018 than 2017 (mean difference ± SE = -0.18 ± 0.09). Distal points of trips to urban habitats were much closer to the colony for urban breeders than those of trips to other habitats and the reverse was true for coastal breeders (mean difference ± SE = -2.30 ± 0.20; Fig. 4.3c).

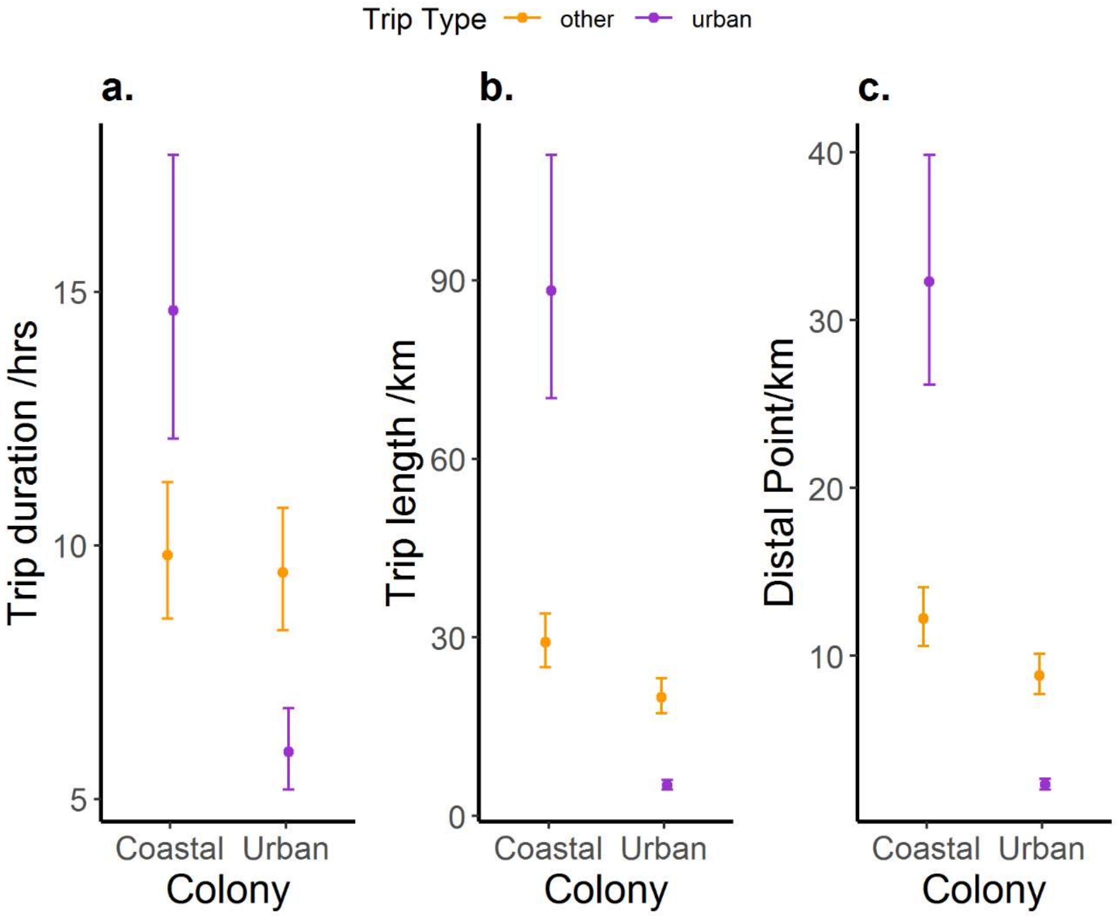

Figure 4.3. Foraging effort and range in breeding lesser black-backed gulls. Back-transformed model estimates and SEs from the best supported model explaining variation in foraging trip characteristics. a. Trip duration (hrs) did not vary with breeding site. b. Trip length (km) was higher for birds at the coastal site than those at the urban site across both years. c. Distal point (km) was higher for coastal breeders than urban breeders across both years. For all trip metrics, trips

to urban habitats were shorter/closer for urban breeders than trips to other habitats and the reverse was true for coastal breeders.

4.5.3 Home range

After controlling for total number of fixes, we found core foraging range area was significantly smaller at the urban site than the coastal site (log mean difference ± SE = -1.11 ± 0.53) across both years (Fig. 4.4a). Controlling for total fixes, home range area was also smaller at the urban site than the coastal site (log mean difference ± SE = -0.94 ± 0.50) across both years (Figure 4.4b).

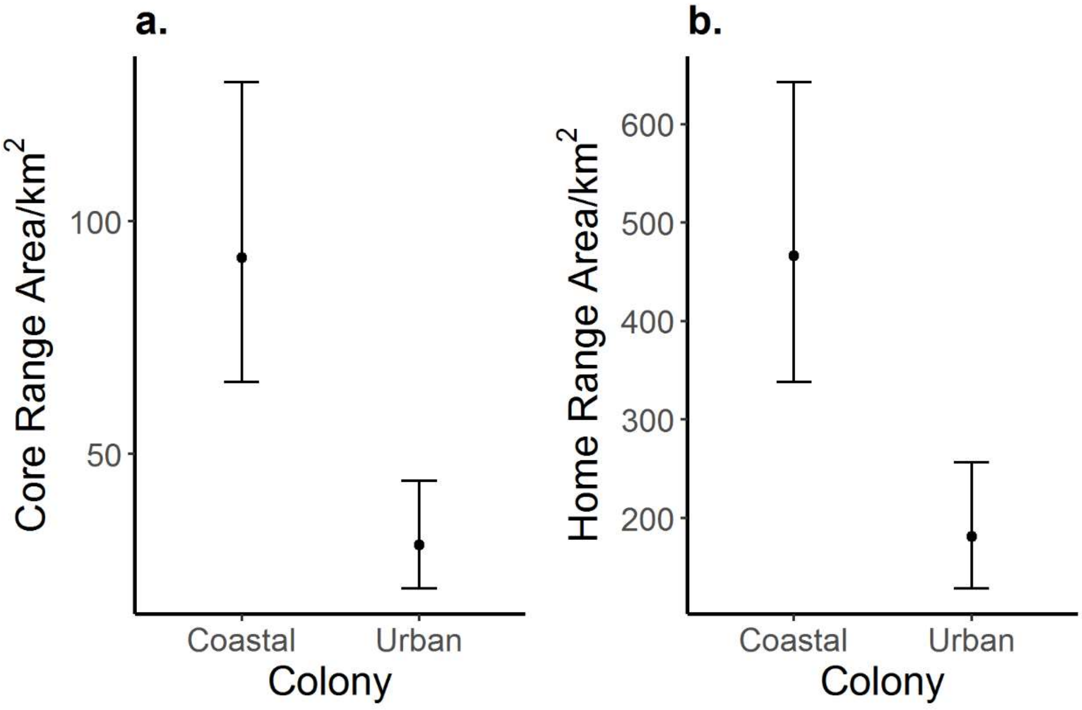

Figure 4.4. Back-transformed model estimates ± SEs for core foraging range and home range areas (km^2). Coastal breeders had a larger average core foraging range (a.) and home range (b.) than urban breeders in both years

4.5.4 Habitat use

Available habitat was dominated by agriculture, with smaller proportions of coastal, marine and urban habitats and differed only slightly between colonies (Fig. C1). However, Coastal breeders selected coastal habitats, visited agricultural habitats proportionately to their availability but used marine and urban habitats less than expected. In contrast, urban breeders selected urban habitats, had weak selection for coastal habitats but utilised agricultural and marine habitats at lower levels relative to their availability (Fig. 4.5; Table 4.3). To test for the possible influence of commuting points on patterns of habitat whether these results were repeated the analysis on a filtered data set containing distal trip locations only, where gulls are assumed to be foraging (Hamer *et al.*, 2009; Fig C2; Table C8). General patterns of habitat selection for the distal points closely match those presented here supporting the assertion that observed differences in habitat selection do not result from the inclusion of commuting points.

Table 4.3. Estimates for the effect of an interaction between the habitat variable and breeding site on the probability of a location being a real gull location or a pseudo-absence for each foraging habitat in each year. Delta (Δ) AIC refers to the change in AIC caused by removing the interaction. Δ AIC values > 2, suggest that the probability of gull utilisation (habitat selection) for that habitat type differs significantly between breeding sites. The coastal colony was the reference level for breeding site, therefore the sign of the estimate represents the difference in habitat selection between coastal and urban colonies. Stars next to p-values represent significance levels (* < 0.05; ** < 0.01; *** < 0.001).

Habitat Variable	**Year**	**Estimate for breeding site interaction**	**p value**	**Δ AIC**
Agriculture	2017	-0.35 (± 0.06)	<0.001***	36.6
Coastal	2017	-1.07 (± 0.08)	<0.001***	186.6
Marine	2017	-1.82 (± 0.18)	<0.001***	143.5
Urban	2017	3.95 (± 0.11)	<0.001***	1937.8
Agriculture	2018	-0.08 (± 0.08)	0.321	-1.0
Coastal	2018	-0.97 (± 0.11)	<0.001***	73.7
Marine	2018	-1.00 (± 0.13)	<0.001***	60.1
Urban	2018	2.75 (± 0.14)	<0.001***	555.9

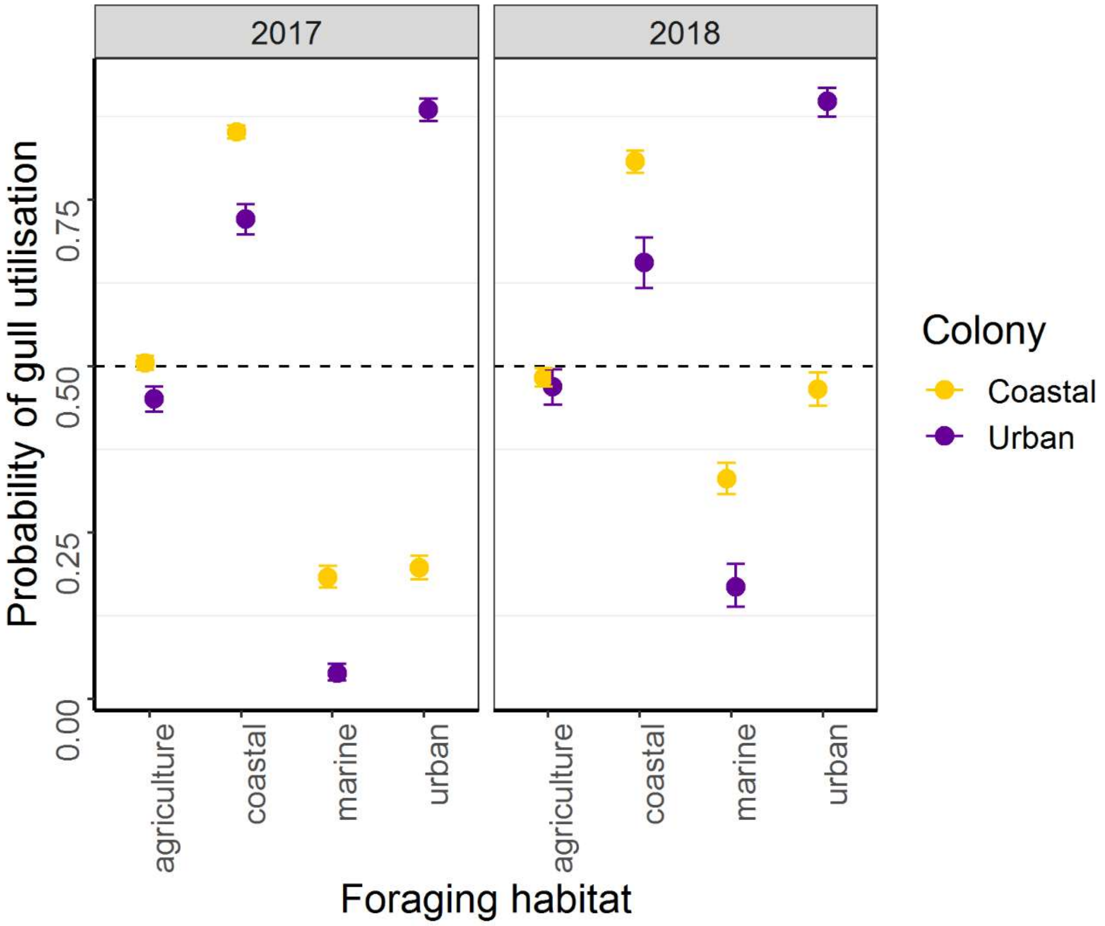

Figure 4.5. Estimates and 95% CIs from resource selection models of the probability of gull utilisation of each of four main foraging habitats (agriculture, coastal, marine, and urban) by coastal (gold) and urban (purple) breeding gulls in each year. A probability of 0.50 indicates that birds are using habitat in proportion to its availability within the foraging range (colony-level minimum convex polygon), whilst values of > 0.50 indicate selection for that habitat type.

4.5.6 Diet

Adult diet - Pellets were dominated by agricultural items. Having collapsed cells into “Agricultural” and “Other”, we found no difference between breeding habitats in 2017 ($X^2_1 < 0.001$, p = n.s.) or 2018 ($X^2_1 < 0.001$, p = n.s.). However, diet varied by year at both the coastal ($X^2 = 6.73$, df = 1, $p < 0.01$) and the urban site ($X^2 = 7.62$, df = 1, $p < 0.01$), driven by increased anthropogenic foods in 2018 (Fig. 4.6a).

Chick diet - During 2018, chicks predominantly regurgitated marine prey (e.g. shrimp, crabs and fish) with a smaller proportion of agricultural foods (e.g. worms (*Lumbricidae*), beetles (*Coleoptera*) and small mammals). This was consistent between breeding habitats ($X^2 < 0.001$, df = 1, p = n.s.; Fig 4.6b).

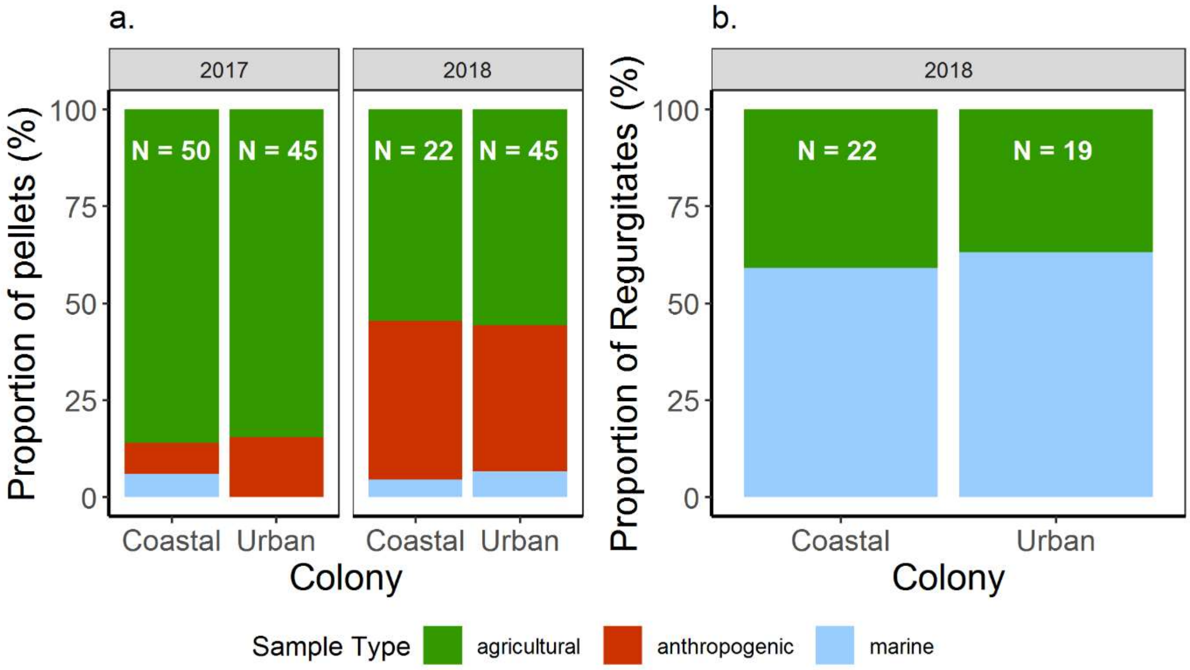

Figure 4.6. The proportion of a. regurgitated pellets and b. chick regurgitates from each main foraging habitat at the urban and coastal sites. There were no significant differences in adult diet between habitats in either year. However there was significant inter-annual variation in pellet composition at both sites, with a reduction in agricultural foraging and an increase in anthropogenic refuse consumption observed in 2018. There were no significant differences in chick diet between breeding sites in 2018.

4.5.7 Breeding parameters

Egg volume – After controlling for clutch size and within clutch volume rank, egg volume was higher in 2018 than 2017 (mean difference ± SE = 2.70 ± 0.92), however, the increase in egg volume between years was smaller at the urban site due to the interaction between site and year (mean difference ± SE = -1.74 ± 1.33; Fig. 4.7a).

Clutch volume – After controlling for clutch size, total clutch volume (cm^3) was significantly lower at the urban site than the coastal site (mean difference ± SE = -4.83 ± 1.91, p = 0.012; Fig. 4.7b). Additionally, clutch volume was significantly higher in 2018 than 2017 (mean difference ± SE = 5.77 ± 1.96, p < 0.01).

Intra-clutch egg size variation – After controlling for volume of the largest egg, IESV did not vary with breeding site but was lower in 2018 than 2017 (mean difference ± SE = -1.30 ± 0.46, p = 0.005; Fig. C5).

Chick condition – Chick condition (Mi) was similar between the urban and coastal sites (mean difference ± SE = 3.73 ± 3.21). However chick condition was lower in 2018 than 2017 (mean difference ± SE = -5.70 ± 2.55). The decrease in chick condition from 2017 to 2018 was greater at the urban site due to the two-way interaction between site and year (mean difference ± SE = -3.90 ± 3.87; Fig. 4.7c).

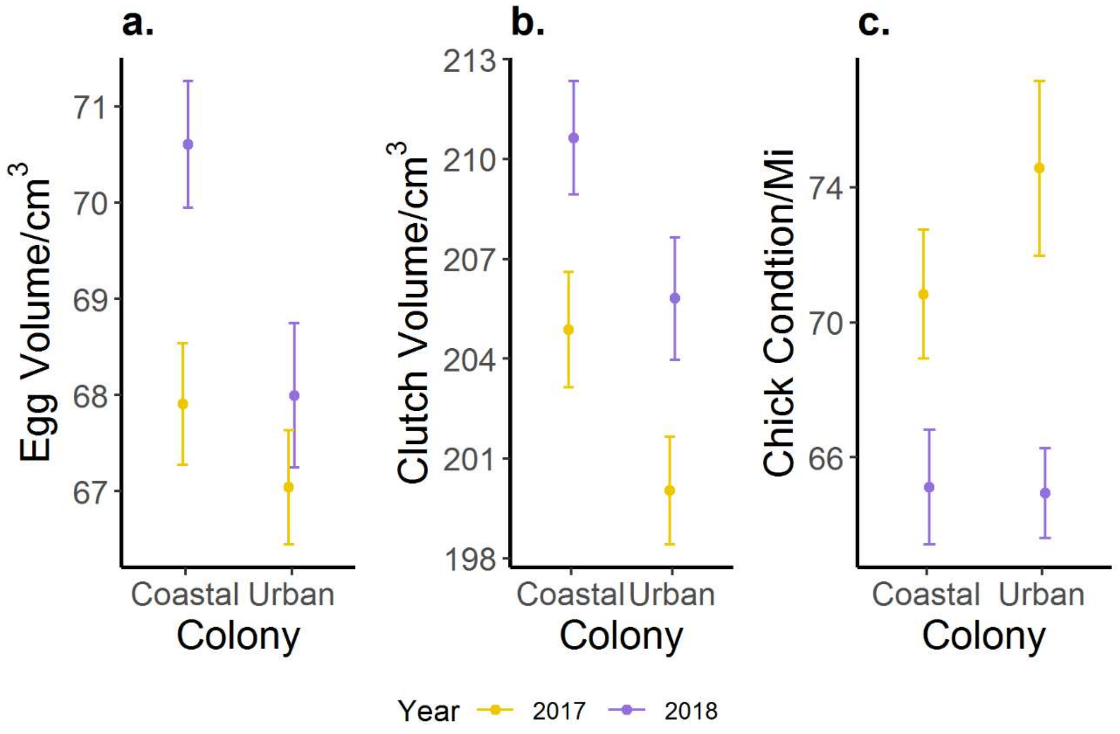

Figure 4.7. Model estimates and standard errors from the best supported models explaining variation in a. egg volume (cm^3), b. total clutch volume (cm^3) for three

egg clutches (median clutch size) and c. chick hatching condition (Mi). Egg volume was higher in 2018 than 2017 and higher at the coastal site than the urban site in 2018. Clutch volume was higher at the coastal and higher in 2018 than 2017. In contrast, chick condition did not vary with breeding colony but was higher in 2017 than 2018.

4.6 Discussion

Overall, our study revealed clear, but not complete, differences in the ecology of urban and coastal nesting lesser black-backed gulls. Urban birds showed a strong tendency for urban foraging while coastal breeders used mostly coastal areas. Importantly, differences in habitat use were consistent at both the individual and population level suggesting the difference is not an artefact of location. Coastal gulls travelled further but spent a similar time away from the colony and laid larger eggs and had larger clutches than urban gulls. Diets were very similar, although sample sizes were small.

4.6.1 Comparing foraging range

While foraging trip duration was similar, coastal breeders travelled further than urban birds (Fig. 4.3), and also had larger home ranges (Fig. 4.5). This difference appears to be driven by frequent short trips of urban birds to urban habitats (Fig. 4.3; but see *Habitat Selection* below). Urbanization also led to lower trip distances in Herring Gulls and such differences likely relate to the quality, quantity and proximity of foraging habitat (Fuirst, Veit, Hahn, Dheilly, & Thorne, 2018). Similar time away from the nest but longer trips of coastal birds may hint at more efficient foraging. However, while urban foods are considered ephemeral in some instances (van Donk *et al.*, 2019), they are highly predictable in others (Spelt *et al.*, 2019).

Differences in foraging range could also be influenced by intra-specific competition (Wakefield *et al.*, 2013) or interspecific competition (Camphuysen, 2013; van Donk *et al.*, 2017).

4.6.2 Habitat selection

Our habitat analysis revealed strong spatial segregation between colonies. Urban breeders were more likely to visit urban foraging habitats than coastal birds at the individual-level (Fig. 4.1e-f; Fig. 4.2) and also selected strongly urban habitats at the population-level, with the same true of coastal gulls and coastal foraging (Fig. 4.5; Fig C1). Habitat use at the urban colony was similar to that of lesser black-backed (Spelt *et al.*, 2019, 2020) and yellow-legged gulls (*Larus michahellis*) (Méndez *et al.*, 2020) tracked at urban breeding colonies in Bristol and Barcelona, which showed high levels of urban foraging. Foraging segregation between colonies has also been observed in GPS-tracked herring gulls in New York state (Fuirst *et al.*, 2018), with urban-foraging observed more frequently across a gradient of increasing urbanisation.

Our coastal birds showed reduced levels of urban foraging compared with some European coastal colonies (Huig, Buijs and Kleyheeg, 2016). Overall however, habitat use of coastal breeders mirrored that at other coastal colonies in Britain and Europe, with birds using a mixture of marine and terrestrial habitats (Camphuysen, 2013; Thaxter *et al.*, 2015; Tyson *et al.*, 2015; Corman *et al.*, 2016; Garthe *et al.*, 2016; Isaksson *et al.*, 2016). Birds in this study foraged at sea less frequently and used intertidal habitats more often than birds from other colonies possibly due to low levels of chick survival (Thaxter *et al.*, 2015), or a lack of fisheries discards in the region (Tyson *et al.*, 2015; Garthe *et al.*, 2016).

Habitat selection of individual gulls may be shaped by a range of trade-offs, which may vary due to extrinsic factors like conspecific density, resource quality or distance from colony (van Donk *et al.*, 2019). In order to quantify the influence of breeding habitat on foraging ecology of gulls breeding in different habitats, analysis of GPS tracking data across multiple colonies of different sizes along the rural-urban gradient is required. Moreover, quantifying the urbaness of individual-level gulls (Figure 4.1e-f) revealed a large amount of variation in urban foraging among individuals at both colonies and the causes and consequences of this individual variation in habitat use require further study.

4.6.3 Diet

Despite differences in habitat use, adult gulls had similar diets at both colonies (Fig. 4.6a). This may be a sampling artefact, as pellets underrepresent soft prey items (Votier *et al.*, 2003) such as urban refuse (e.g. chips and fried chicken), but the sample sizes are also small. Chick regurgitates were also similar between colonies, being dominated by marine prey with fewer agricultural items (Figure 4.6b). The mismatch between habitat selection (Fig. 4.5) and adult diet may also reflect the longer sampling period and greater population coverage compared with movement data. We therefore interpret our diet data cautiously and in future recommend using a range of complimentary techniques including conventional diet, stable isotopes and DNA barcoding (Barrett *et al.*, 2007; Deagle *et al.*, 2007).

4.6.4 Breeding parameters

Overall, coastal birds had better breeding performance than urban birds with larger clutches and eggs than urban breeders (Figure 4.7a-b). This may relate to differences in food quantity/quality (Bolton *et al.*, 1992) or female quality between sites, but we are unable to determine which. Chick condition was similar (Figure 4.7c) although we were unable to measure during the recommended linear growth phase (Bolton, 1991) because fledging success was close to zero at both colonies (due to extreme weather and both mammalian and intra-specific predation).

Recent divergence in population trends between expanding urban (Rock, 2005; Zelenskaya and Khoreva, 2006; Blight, Bertram and Kroc, 2019) and declining coastal gull populations (Ross-Smith *et al.*, 2014; Blight, Drever and Arcese, 2015; Hario and Rintala, 2016) may be driven by differences in reproductive performance; however, this was not reflected in our results, emphasising the need for further work focussing on long-term monitoring across a range of urban and coastal colonies.

4.6.5 Implications for conservation and management

Our observation of strong selection for coastal habitats at the coastal colony suggests that restoring intertidal and marine habitats may aid the recovery of struggling gull populations in "natural" habitats. However, monitoring breeding parameters revealed that mammalian predation contributed to poor reproductive success at the coastal site, and this has also been an issue at other colonies (Camphuysen, 2013; Davis *et al.*, 2018). Conservation organisations should therefore prioritise predator control or investment into improved non-lethal deterrents in order to boost breeding success at protected area gull colonies (Davis *et al.*, 2018). However, observations of chick mortality in response to extreme weather events suggests long-term vulnerability to climate change effects at these colonies.

Although we observed spatial and habitat segregation between colonies, we were unable to detect any consequences in terms of diet or reproductive performance. However, we demonstrated marked individual variation in habitat use at both colonies (Fig. 4.1e-f), suggesting that individual-level monitoring, linking movement with survival and reproductive performance may be required to understand the mechanisms driving divergent trends in abundance between urban and rural gulls (Ross-Smith *et al.*, 2014).

Population-level foraging habitat segregation, with urban foraging performed mostly by urban breeders (Fig. 4.5; Fig C1), also has important implications for gull management. Measures to reduce refuse availability, such as secure waste disposal and public education programmes, may be an important tool to mititgate some types of human-gull conflict (e.g. aggressive food snatching (Goumas *et al.*, 2019), littering) in Barrow and other urban areas without reducing food availability for declining "natural" populations. Reducing food availability caused a rapid reduction in abundance of a human-associated red fox (*Vulpes vulpes*) population (Bino *et al.*, 2010), however is the ability to switch to forage in alternative habitats (Fig. 5) is likely to buffer the demographic impacts for the urban colony.

4.7 Conclusion

To conclude, we found urban and coastal nesting gulls segregated by foraging habitat. However this did not result in substantial differences in diet and breeding parameters between colonies, emphasising the need for further work to fully elucidate links between breeding habitat, foraging ecology and reproductive success. Despite this, colony-level differences in foraging ecology are important from an applied perspective, suggesting management could lead to habitat-specific outcomes – specifically, interventions aimed at urban foragers, such as public education programmes to prevent gull-feeding and improved waste management, may mitigate some human-gull conflict whilst being less likely to negatively impact non-urban populations. Additionally, restoration of coastal and marine ecosystems could be an important way to aid the recovery of struggling coastal populations. Nevertheless, segregation between colonies was not absolute, highlighting the importance of understanding individual variation in habitat use and movement ecology.

4.8 References

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Chapter 5 – Foraging site fidelity in the lesser black-backed gull: generalist populations conceal a range of individual strategies

5.1 Abstract

There is emerging interest in how population generalisation is manifest. The composition of generalised populations in terms of generalist and specialist individuals has important implications for our understanding of foraging ecology and for conservation and management. Individual foraging specialisations may be expressed in terms of Individual Foraging Site Fidelity (IFSF), where individuals repeatedly utilise a subset of the population-level home range. IFSF can be quantified by calculating population-level repeatability of foraging behaviours. However, in generalist populations, these values may conceal the degree of individual differences in foraging behaviour. Moreover, it is unclear how population size or resource availability may influence the degree of IFSF within and among generalist populations. Here we examined the incidence and extent of IFSF in adult lesser black-backed gulls (*Larus fuscus graelsii*) from three colonies (two coastal, one urban) by calculating the population and individual-level repeatability of foraging variables. We then examined the composition of each population in terms of site faithful individuals vs. those foraging at multiple sites. Finally, we compare the degree of individual site fidelity among colonies, which differed with respect to conspecific density and habitat use. Comparing across the three populations we found evidence of individual specialisation, with several behavioural variables showing moderate repeatability, although this varied between colonies and breeding seasons. Comparing among individuals, we found a large amount of variation in the degree of IFSF within all three colonies. Individual birds lay on a continuum in this respect, from very high to very low IFSF. We also found a higher incidence of site fidelity in the colony (Barrow),

where individuals relied most on predictable anthropogenic resources. Understanding the composition of generalist populations in terms of spatially variable vs. consistent individuals and how this might vary under different competitive and environmental influences is key to our understanding of foraging ecology and also has implications for predicting responses to management interventions and future changes in resource availability.

5.2 Introduction

Individual foraging specialisations, where some individuals utilise only a subset of the resources available to the population, are ubiquitous across a range of taxa (Bolnick *et al.*, 2003; Araújo, Bolnick and Layman, 2011). As such, many apparently generalised species and populations are composed of individuals which consistently differ relative to each other in their foraging behaviour and resource use (Bearhop *et al.*, 2006; Bell, Hankison and Laskowski, 2009; Ceia and Ramos, 2015). Initially, studies of individual foraging specialisation focussed largely on diet (Bearhop *et al.*, 2004; Araújo, Bolnick and Layman, 2011); however, bio-logging has allowed researchers to quantify spatial specialisation in terms of site fidelity, habitat specialisation and overlap in area use between individuals (Wakefield *et al.*, 2015; Carneiro *et al.*, 2017; Navarro *et al.*, 2017; Kerches-Rogeri *et al.*, 2020).

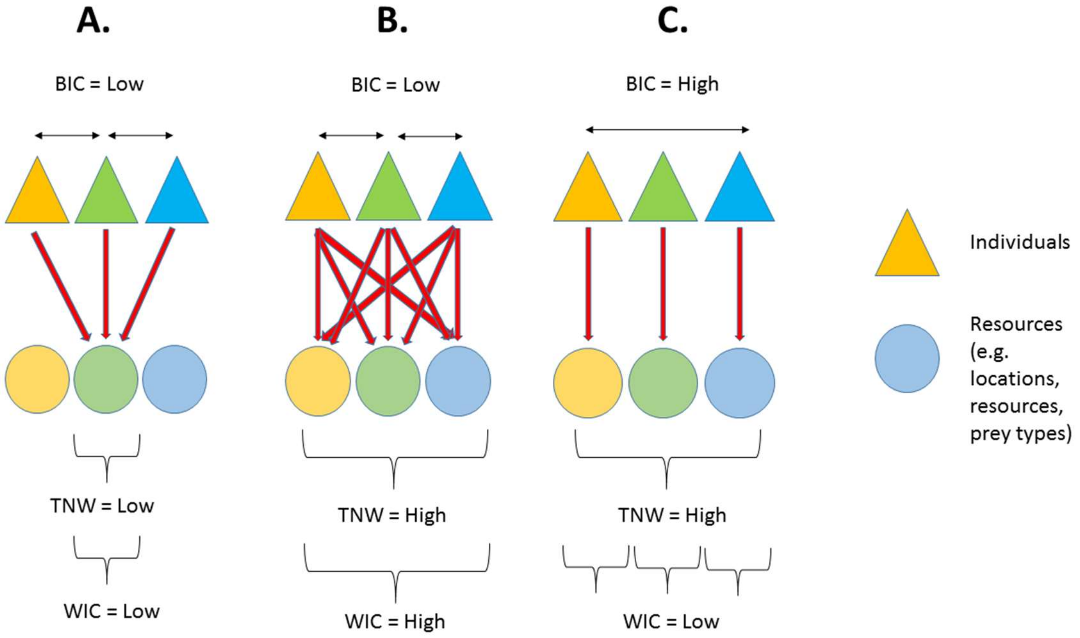

Figure 5.1. A conceptual framework showing how Roughgarden's (1972) niche metrics vary between three hypothetical populations in terms of total niche width (TNW; the variance of total resource use across individuals), within individual component (WIC; mean of individual niche widths) and between individual component (BIC; variance in average resource use among individuals). Specialist populations (A) are characterised by a low TNW whilst generalist populations (B and C) are characterised by a high TNW. Moreover, generalist populations may either contain generalist individuals all using a range of resources (Low BIC, high WIC; B) or multiple individuals which each use a subset of the population niche (High BIC, low WIC, C).

There is an emerging interest in how population generalisation is manifest in terms of the coexistence of specialist and generalist individuals. Figure 5.1 illustrates how generalist populations with a broad niche width may either consist of generalist individuals all exploiting a range of resources (B) or individuals that specialise on different resources (C) (Roughgarden, 1972; Bolnick *et al.*, 2003; Bearhop *et al.*, 2004; Vander Zanden *et al.*, 2010; Kerches-Rogeri *et al.*, 2020). In reality, generalist populations often lie on a continuum from B to C, containing a mix of generalist and specialist individuals (Potier *et al.*, 2015; Wakefield *et al.*, 2015; Patrick and Weimerskirch, 2017; van Donk *et al.*, 2018). The balance of specialists and generalists within these populations is maintained, at least in part, by variation in the cost-benefit trade-offs associated with individual specialisation (Svanbäck and Persson, 2004)

Individual foraging specialisations can link to fitness (Patrick and Weimerskirch, 2017; van den Bosch *et al.*, 2019) with subsequent consequences for population dynamics, (Annett and Pierotti, 1999; Patrick and Weimerskirch, 2014; Ceia and Ramos, 2015). Therefore, understanding how individuals vary in their degree of individual specialisation is likely important in revealing the drivers of expansive population dynamics in successful generalist species (Navarro *et al.*, 2017).

Individual Foraging Site Fidelity (IFSF), where individuals repeatedly utilise a small area within the population-level home range, is a common form of individual specialisation (Switzer, 1993; Baylis *et al.*, 2012; Cleasby *et al.*, 2015; van Donk *et al.*, 2018; Kerches-Rogeri *et al.*, 2020). Seabird populations frequently show a high incidence of individual foraging specialisation (Ceia and Ramos, 2015; Phillips et al. 2017), likely because high intraspecific competition drives ecological diversification (Bolnick *et al.*, 2003; Araújo, Bolnick and Layman, 2011) and spatio-temporal predictability of ocean habitats favours foraging site fidelity (Courbin *et al.*, 2018). Importantly, IFSF has been linked to differences in habitat use and diet (Baylis *et al.*, 2012; van Donk *et al.*, 2018; van den Bosch *et al.*, 2019) and as such are potentially excellent indicators of between-individual variation in resource use and in turn are likely to feedback into population dynamics and inform management decisions

IFSF leads to highly consistent foraging trips, and, as such, multiple studies have calculated the repeatability of foraging trip metrics as a way to characterise IFSF in seabirds (Wakefield *et al.*, 2015; Votier *et al.*, 2017; Borrmann *et al.*, 2019). In most such studies, repeatability is expressed as the fraction of behavioural variation resulting from differences between individuals (Bell, Hankison and Laskowski, 2009; Ceia and Ramos, 2015). Calculated this way, repeatability is akin to BIC (Fig 5.1), and provides information on how different individuals are relative to each other. However, this population-level measure provides no indication of how consistent individuals are in their foraging behaviour over time (Bell, Hankison and Laskowski, 2009; Potier *et al.*, 2015). By calculating repeatability values for each individual, variation among individuals in the extent to which they are repeatable (i.e. WIC; Fig. 5.1) can be quantified (Potier *et al.*, 2015; Wakefield *et al.*, 2015).

Gulls (*Laridae*) are traditionally considered to be population-level generalists, foraging in both terrestrial and marine environments on a range of natural and anthropogenic resources (Annett and Pierotti, 1999; Duhem *et al.*, 2008; Tyson *et al.*, 2015; Isaksson *et al.*, 2016; van Donk *et al.*, 2017; Spelt *et al.*, 2019). A number of studies have investigated individual foraging specialisation in terms of diet, habitat selection, repeatability of foraging behaviour and site fidelity in several gull populations (Ceia *et al.*, 2014; Navarro *et al.*, 2017; Borrmann *et al.*, 2019; van den Bosch *et al.*, 2019; Jakubas *et al.*, 2020). However, the degree of variation in site fidelity between individuals and the extent to which this might vary between populations requires further study.

Here, we investigated IFSF in breeding adult lesser black-backed gulls (*Larus fuscus graelsii*) from three colonies (two coastal, one urban) in northwest England where birds had access to a diverse resource landscape. We first calculated population-level repeatability to determine the extent to which these different populations can be considered generalists in terms of foraging movements. We then calculated individual-level repeatability to test the hypothesis that these populations are comprised of relatively specialised individuals. Finally, we investigated how IFSF varied among different sized colonies and reliance on predictable anthropogenic resources. If population size (a proxy for the intensity of intra-specific competition) is the most important driver of site fidelity in breeding lesser black-backed gulls, then we expect to observe the highest levels of IFSF at Ribble, followed by Walney and then Barrow. Conversely, if resource predictability is driving site fidelity, then we expect birds from Barrow, where urban foraging is most common, to exhibit the highest levels of IFSF, followed by Ribble and then Walney.

5.2. Material and Methods

5.2.1 Study colonies

Fieldwork was conducted during the breeding seasons (May-July) from 2014 to 2018 at three lesser black-backed gull colonies in northwest England: Ribble Marshes in Lancashire (53°42’N, 2°59’W) and South Walney nature reserve (54°40’N, 3°14’W) and Barrow-in-Furness in Cumbria (54°06’N, 3°31’W; hereafter “Ribble” and “Walney” and “Barrow” respectively). Ribble and Walney are coastal colonies within Special Protection Areas (SPAs; EC Birds Directive 2009/147/EC) where breeding lesser black-backed gulls are a designation feature whilst Barrow is an urban population.

Ribble is a stable mixed colony of herring (*Larus argentatus*) and lesser black-backed gulls, with 6554-7022 actively occupied nests (AONs) of the latter when the colony was last surveyed in 2016. Walney contains herring, great black-backed (*Larus marinus*) and lesser black-backed gulls, the latter having declined from an estimated 19,487 AONs during 1998-2002 to 1,981 AONs in 2018. The sub-colony studied at Barrow hosted 80-100 pairs of lesser black-backed gulls plus 1-3 pairs of herring gulls in 2018 and is part of a larger stable urban population of c. 400 pairs of lesser black-backed and c. 200 pairs of herring gull (figures from UK Seabird Monitoring Programme online database - "https://app.bto.org/seabirds/public/data.jsp").

5.2.2. Tagging protocol

Adult lesser black-backed gulls were caught at the nest using wire mesh walk-in traps (Bub, 1991) during late-incubation and fitted with a solar-powered Global Positioning System (GPS) tag (either a University of Amsterdam Bird-Tracking System (UvA-BiTS) device or a Movetech Flyway-18 GPS-GSM device) which collected regular positional fixes (Thaxter *et al.*, 2019). Devices were attached via a Teflon wing-loop harness, to enable long-term deployment with negligible fitness impacts (Thaxter *et al.*, 2014, 2016). “Permanent” harnesses were replaced by a “weak-link” design from 2017 allowing the tag to detach without recapture (Table A1). Device and attachment combinations were below the 3% body mass recommended at the time (Phillips, Xavier and Croxall, 2003; Table A2), however, recent work suggests such thresholds may be inappropriate (Bodey *et al.*, 2018). All tagging was performed under license, approved by the UK Ringing Scheme Special Methods Technical Panel (SMTP). All tagged individuals were fitted with uniquely engraved colour rings for subsequent field identification.

5.3 Data analysis

5.3.1 Movement behaviour

We extracted GPS data for the period (4-19th June) during 2017 and 2018 which corresponds to late incubation/early chick-rearing. This was the period where the maximum number of birds were tagged at all colonies before high levels of reproductive failure removed the constraint of central place foraging for many individuals. Due to differences in sampling frequency between tags, we resampled all tracks to a one hour resolution. As we were unable to infer behavioural states from the tag data and given the frequency of fixes, we defined foraging trips as any positional fix outside the colony boundary (Figs A1-A3) with no data gaps greater than four hours (i.e. with good satellite coverage), with all colonial absences assumed to represent foraging trips. We then filtered the dataset to retain only individuals with at least two foraging trips, the minimum required to calculated individual-level repeatability. This resulted in a data set with 1,118 foraging trips from 60 individuals. The number of foraging trips in a given breeding season varied considerably among individual birds from a minimum of two to a maximum of 36 (Fig. 5.2).

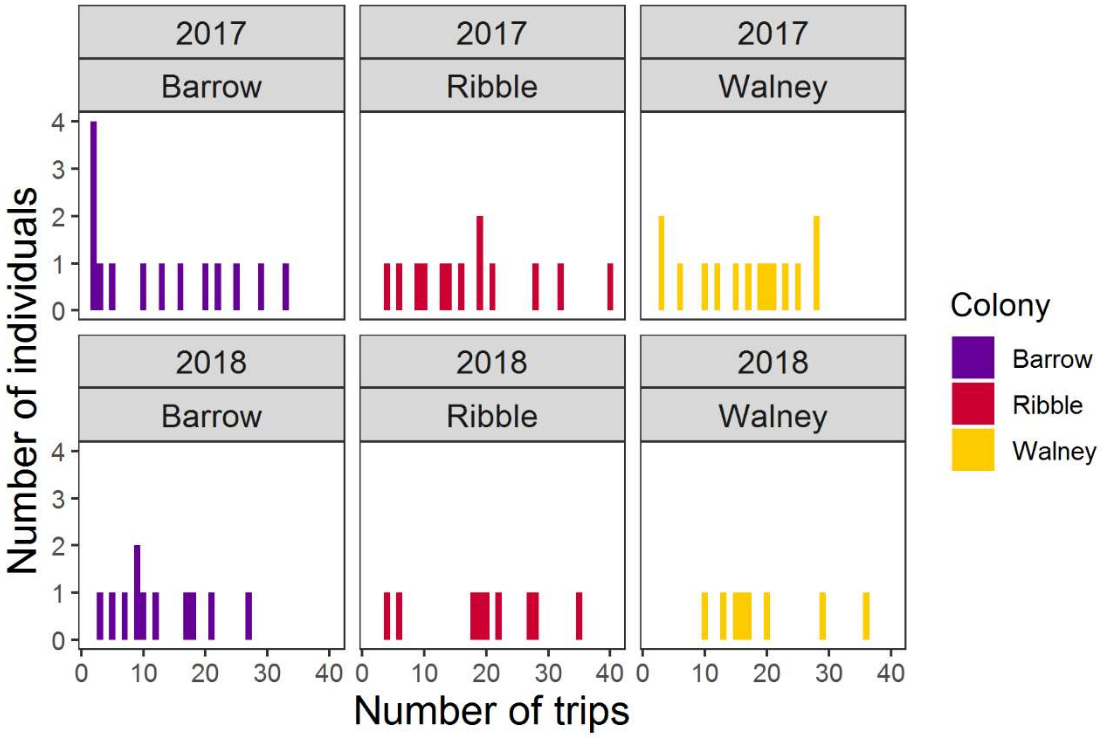

Figure 5.2. Breakdown of the number of foraging trips for each individual bird in each breeding season. There was considerable variation in the number of foraging trips per individual at all colonies. The minimum required for inclusion in this study was two foraging trips whilst the maximum number of trips observed within the study period was 36.

5.3.2 Population-level repeatability (BIC)

For each trip we calculated five variables which relate to different components of foraging site fidelity: trip duration (hrs), cumulative trip length (km), distal point distance from the colony (km), distal point latitude and distal point longitude. Here we assume that the latter two variables relate to the location of the foraging site (Hamer *et al.*, 2009) and provide an indication of foraging site fidelity, whilst trip duration, trip length and distal point distance relate, at least in part, to constraints involved in the economics of foraging. Due to the presence of a small number of very long trips (n = 3% of all trips), trip duration, trip length and distal point distance were log-transformed to meet assumptions of normality.

In order to calculate repeatability, we first fitted linear mixed effects models (LMMs) with a Gaussian error distribution for each behavioural variable. We estimated population-level repeatability separately for each colony in each breeding season (2017, 2018) and therefore created separate models for each colony/year combination. In all models, number of trips was included as a fixed effect to control for variance in the response variable resulting from differences in the number of observations per individual, and individual identity was fitted as a random intercept. We then used these models to estimate adjusted population-level repeatability (r) using the *rptr* package in R (Stoffel, Nakagawa and Schielzeth, 2017)*;* r is a ratio of the within-individual to between-individual variance and provides an index of repeatability that ranges from 0 (low BIC, high WIC; e.g. populations A and B, Fig. 5.1) to 1 (high BIC, low WIC, e.g. population C, Fig. 5.1), that is not influenced by the absolute value of the behavioural trait (Potier *et al.*, 2015). Following Potier *et al.* (2015), we classified behaviours as highly repeatable ($r > 0.50$), moderately repeatable ($0.25 < r < 0.50$) and poorly repeatable ($r < 0.25$) at the level of colony/year.

5.3.3. Individual-level repeatability (WIC)

In addition to population-level repeatability, we also calculated the individual repeatability (r_{ind}) of each behavioural trait following Potier *et al.* (2015) expressed as:

Eq. 1

$$r_{ind} = \frac{S_A^2}{(S_{ind}^2 + S_A^2)}$$

In this equation S_A^2 represents the between-individual variance whilst S_{ind}^2 represents the within-individual variance over time, obtained by partitioning the residual variance in the model over each level of the individual random effect as follows:

Eq. 2

$$S_{ind}^2 = E(X_{ind} - E(X_{ind}))^2$$

Here X_{ind} represents each residual value of a given behavioural observation and $E(X_{ind})$ is the mean of residual values for a given behaviour for each individual. To calculate S_{ind}^2 we therefore extracted the residual value for each observation from the LMM, subtracted the mean of all of the residuals for that individual and squared the resulting value. We then took the mean of these squared differences as our measure of within-individual variance (S_{ind}^2) for Eq. 1.

Calculating r_{ind} allows us to understand the composition of individual-level repeatability values for each population. Therefore, for populations with low population-level repeatability, we can distinguish between those comprised of individuals which use similar resources consistently (Fig. 5.1, population A) and those comprised of individuals which use multiple resources (Fig. 5.1, population B).

We then tested for colony and year effects by modelling the individual repeatability of each of the five foraging behaviours separately using binomial generalised linear models (GLMs) with a logit link function. We created maximal models containing colony, year and the two-way interaction as fixed effects. Where individuals were tracked across multiple years, we had multiple measurements of specialisation. However, because this was the case for only nine of 60 individuals and because of singularity issues when attempting to fit generalised linear mixed effects models, we did not include individual as a random effect.

5.3.4 Model selection

Model selection was based on AICc due to small sample sizes (Tables D2 – D6). Where multiple candidate models had a Δ AICc < 2.0 we selected the model with the fewest parameters (Burnham and Anderson, 2002). Model fit was assessed via visualisation of the simulated scaled residuals using functions in the *DHARMa* package. All statistical analyses were conducted in R (v3.6.2, R Core Team 2019).

5.4 Results

5.4.1 Population-level repeatability (BIC)

Generally, breeding adult lesser black-backed gulls (n = 60) from all three colonies travelled inland to forage and largely avoided adjacent marine habitats (Fig. 5.3). Foraging trips were broadly similar in terms of distance travelled and spatial distribution in both years of the study (Fig 5.3). Importantly, all three populations showed a generalist pattern of space use, with individual gulls from all colonies foraging across a range of different locations indicating a broad TNW (Fig. 5.1 – population B or C).

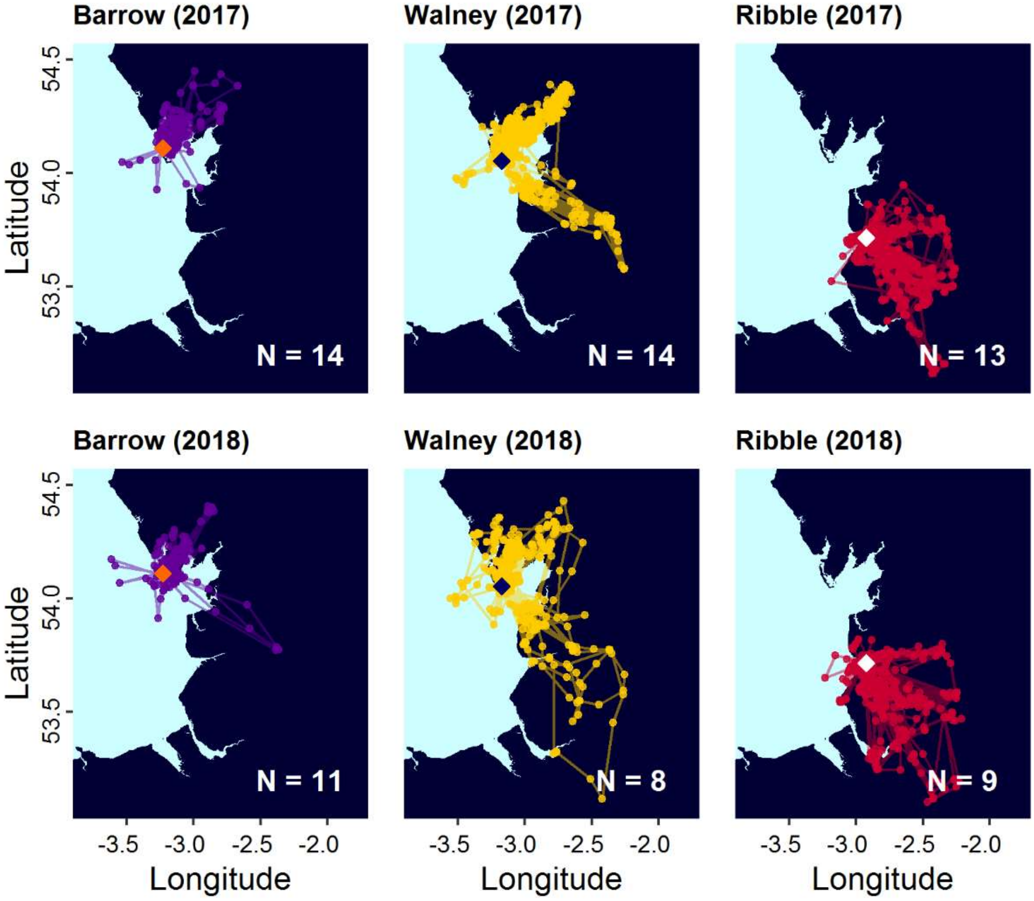

Figure 5.3. Complete foraging trips of all tracked birds from Barrow (purple), Walney (yellow) and Ribble (red) in each year of the study. Colony locations are marked with orange (Barrow), navy (Walney) and white (Ribble) diamonds. N denotes the number of birds tracked in each year.

At the population-level, gull foraging site fidelity varied from being moderately to weakly specialised, among colonies and between years (Fig. 5.3; Table 5.1). There were no highly repeatable foraging behaviours, with all *r* values lying in the range $0.04 < r < 0.43$. For birds from Ribble and Barrow, repeatability was consistently lower across behavioural variables in 2018; however, this was not the case for birds from Walney (Figure 5.3; Table 5.1).

Table 5.1 Population-level repeatability (r) of five different variables related to foraging behaviour in lesser black-backed gulls. Behavioural variables were classified as either moderately repeatable (0.25 < r < 0.50; *) or poorly repeatable (r < 0.25). Overall, behavioural repeatability was highest for birds from Walney.

Colony	**Behaviour**	**r ± se (2017)**	**r ± se (2018)**
Ribble	Trip duration	0.40* ± 0.12	0.04 ± 0.04
	Trip length	0.09 ± 0.06	0.05 ± 0.05
	Distal point	0.11 ± 0.06	0.06 ± 0.06
	Distal latitude	0.33* ± 0.11	0.20 ± 0.10
	Distal longitude	0.21 ± 0.09	0.43* ± 0.15
Walney	Trip duration	0.27* ± 0.10	0.29* ± 0.13
	Trip length	0.31* ± 0.10	0.29* ± 0.13
	Distal point	0.36* ± 0.11	0.34* ± 0.14
	Distal latitude	0.35* ± 0.11	0.23 ± 0.11
	Distal longitude	0.22 ± 0.09	0.08 ± 0.06
Barrow	Trip duration	0.32* ± 0.12	0.13 ± 0.09
	Trip length	0.34* ± 0.12	0.14 ± 0.08
	Distal point	0.29* ± 0.11	0.14 ± 0.09
	Distal latitude	0.37* ± 0.12	0.07 ± 0.07
	Distal longitude	0.36* ± 0.12	0.20 ± 0.10

5.4.2 Individual-level repeatability (WIC)

Visualising the foraging trips of individual tracked gulls revealed a range of foraging strategies, from birds which visited a range of foraging sites to those which were generally loyal to a single site (Fig. 5.1). The nature of the locations visited varied between birds, highlighting the fact that colony-level spatial niches were partitioned between individuals.

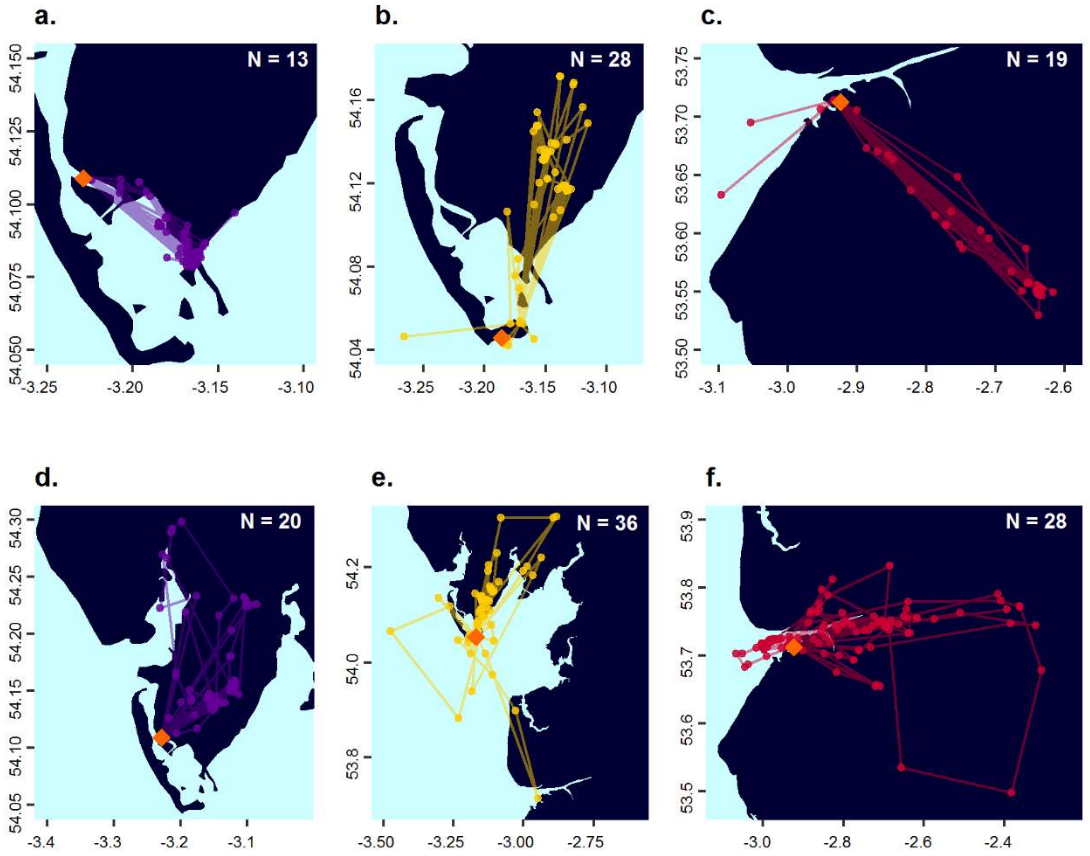

Figure 5.4. All foraging trips by an example data set of 6 tracked birds breeding at Barrow (purple), Walney (yellow) and Ribble (red). Colony locations are marked with orange diamonds. Some individuals (a, b, c), were highly site faithful, mostly foraging within a spatially restricted area. In contrast other birds (d, e, f) were highly variable in their choice of foraging location. The examples presented here represent extremes at either end of a continuum from variable to site faithful foraging behaviour.

Although we found only moderate levels of site fidelity at the population-level, individual-level repeatability values ranged from high to low. Trip duration showed the lowest degree of individual-repeatability, with very few consistent individuals. This matched our expectations as trip duration encompasses time searching for prey and is likely to vary between trips even in highly site faithful individuals. Whilst the degree of individual-repeatability varied between years and among colonies and foraging trip metrics, the general patterns mirrored those observed from the foraging tracks (Fig. 5.4), with all colonies containing a mixture of repeatable site faithful individuals and variable birds which utilised multiple foraging sites (Fig. 5.5).

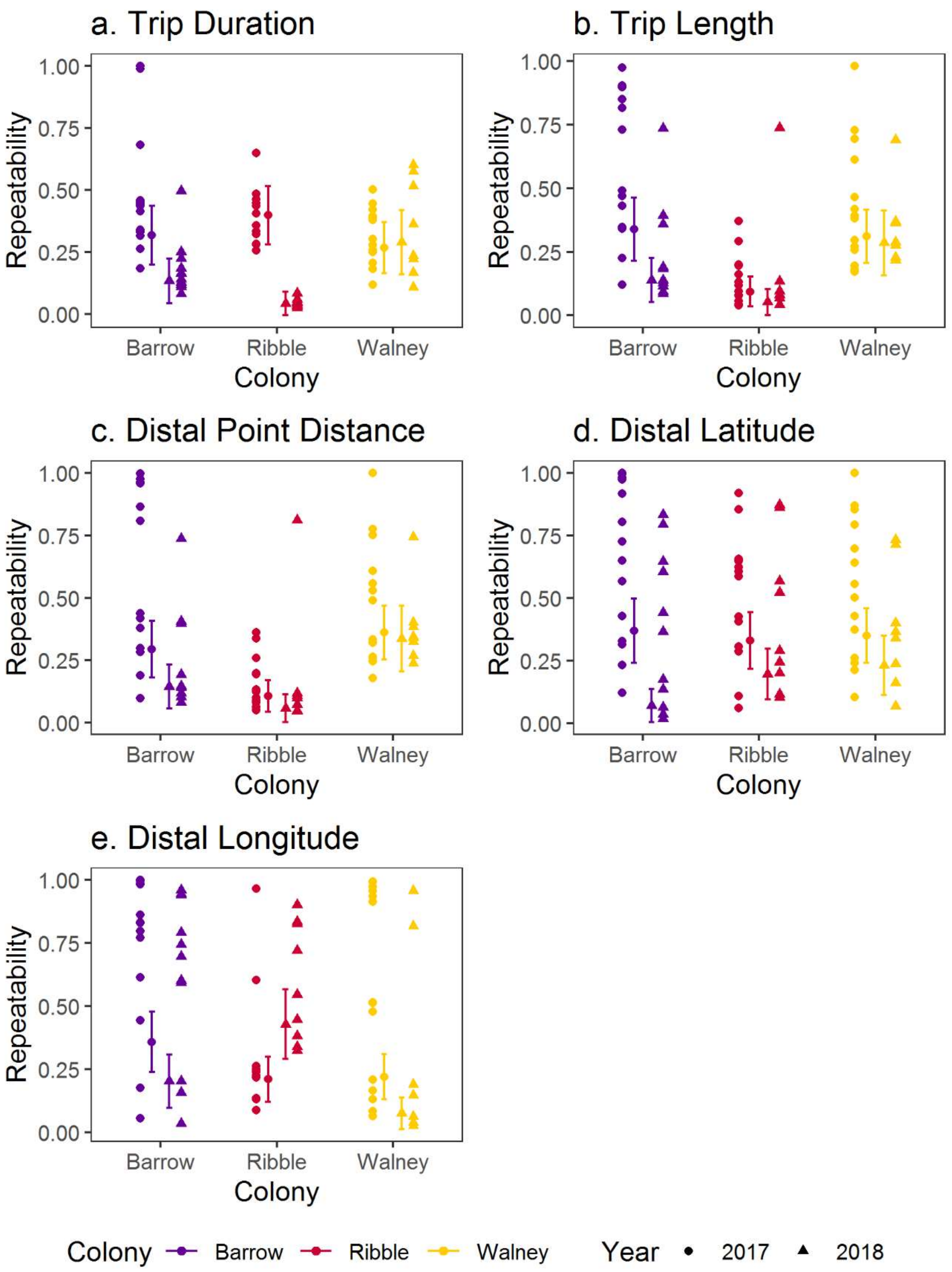

Figure 5.5 Population-level (r) and individual-level (r_{ind}) repeatability values for five different lesser black-backed gull foraging behaviours at measured in birds

breeding at Barrow (purple), Ribble (red) and Walney (yellow) during 2017 (circles) and 2018 (triangles). r values are depicted as points with ± 1 standard error bars whilst values for r_{ind} are presented as individual shapes.

5.4.3 Colony differences in individual-level repeatability (WIC)

There were no among colony differences in individual-level repeatability (WIC) for trip duration, trip length, or distal latitude (Tables D2, D3, D5). Individual repeatability of distal point distance was lower at Ribble than Barrow (mean difference ± SE = -1.50 ± 0.61); however, there was no difference between Barrow and Walney (mean difference ± SE = -0.06 ± 0.59; Figure 5.6). Additionally, individual-level repeatability of distal longitude was significantly higher at Barrow than Ribble (mean difference ± SE = -1.11 ± 0.61) or Walney (mean difference ± SE = - 0.99 ± 0.61; Fig. 5.6).

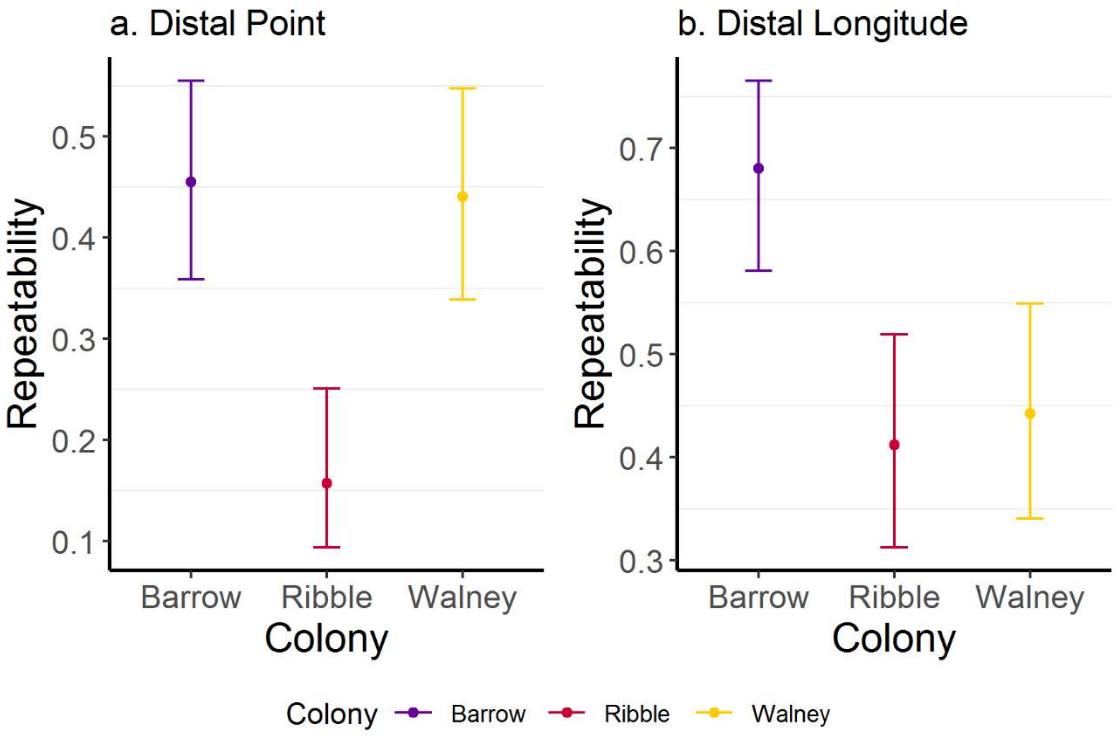

Figure 5.6. Back-transformed model estimates and standard errors from the best supported model explaining variation in individual-level repeatability of a. distal point distance and b. distal longitude. Individual repeatability of distal point distance was lower at Ribble than Barrow or Walney. Additionally individual repeatability of distal longitude was higher for birds from Barrow than for those

from Ribble or Walney. These results suggest high levels of IFSF at Barrow, a small urban colony.

5.5 Discussion

At the population-level lesser black-backed gulls foraged in a range of different locations such that they might be considered generalists at some colonies and in some years, although some spatial foraging metrics were repeatable (Table 5.1). However, these population-level values masked the true extent of variation in individual variation in site fidelity, with these largely generalist populations consisting of a mixture of birds which foraged at multiple locations and site faithful individuals (Fig. 5.3; Fig. 5.5). Combining results from the population-level (BIC) and individual-level (WIC) analyses with the observation of broad TNWs (Fig. 5.3) suggests all three colonies lay somewhere between theoretical populations B and C (Fig. 5.1). Although the colonies varied in terms of their population density and population-level resource use, we found little evidence of differences in individual behavioural consistency between birds from these colonies. However, we observed lower repeatability of distal point distance at Ribble and higher individual repeatability of distal longitude, at Barrow (Fig. 5.6). The higher levels of IFSF at Barrow may be due to birds relying on predictable anthropogenic subsidies (Chapter 4).

5.5.1. Population-level repeatability of foraging behaviour (BIC)

We found some evidence of IFSF at the population-level with moderate repeatability (BIC) observed in all foraging behaviours for at least one of the colonies (i.e. between populations B and C; Fig. 5.1). Similar levels of population-level repeatability of different foraging trip metrics have been observed in breeding great black-backed gulls (*Larus marinus*) (Borrmann *et al.*, 2019), incubating black-headed gulls (*Chroicocephalus ridibundus*) (Jakubas *et al.*, 2020) and breeding great cormorants (*Phalacrocorax carbo*) (Potier *et al.*, 2015).

At the population-level, IFSF in lesser black-backed gulls is likely driven by a combination of suitable ecological opportunities, with birds able to forage on a range of resources in different habitats, and intraspecific resource competition leading to spatial niche partitioning in this colonial breeder (Bolnick *et al.*, 2003; Martin and Pfennig, 2010; Araújo, Bolnick and Layman, 2011; Borrmann *et al.*, 2019; Balme *et al.*, 2020). Additionally, local enhancement may play a role in site fidelity (Wakefield *et al.*, 2013). However, none of the foraging variables studied were highly repeatable and most were below the average level of behavioural repeatability (0.37) revealed by a meta-analysis across multiple studies (Bell, Hankison and Laskowski, 2009). This suggests that lesser black-backed gulls exhibit a largely generalist foraging ecology at the population-level.

One factor which may have reduced IFSF was the timing of the study period, which encompassed late incubation and early chick rearing. During chick-rearing, birds may adjust their foraging behaviour in order to provision their growing chicks, with dietary-switches following chick-hatching (Annett and Pierotti, 1989; Duhem *et al.*, 2005; Davis, Elliott and Williams, 2015). Habitat switches during the study period will inevitably reduce individual site fidelity causing a reduction in population-level repeatability. Furthermore, a study of IFSF in breeding Kittiwakes (*Risa tridactyla*) found increases in the repeatability of trip metrics including distance duration and range following chick hatching (Harris *et al.*, 2020). Similar shifts in foraging behaviour following chick-hatching in this study could have contributed to low overall population-level repeatability values for these trip metrics.

Although we did not investigate inter-annual variation in IFSF, we observed reduced population-level repeatability values across foraging variables in 2018 for birds from Ribble and Barrow. During 2018, dry weather likely reduced resource availability in frequently visited agricultural habitats (Kruuk, 1978; Isaksson *et al.*, 2016). Reduced foraging success may increase the variability of behaviours relating to prey-searching such as trip duration and cumulative trip length. Moreover, individuals following a win-stay-lose-switch approach (Wakefield *et al.*, 2015) may switch sites due to poor foraging success, reducing site fidelity. Conversely, the reduction in population-level repeatability may be due to tracking different birds at Ribble and Barrow in 2018 (Table A1), which may have included more generalist individuals by chance.

5.5.2. Individual-level repeatability of foraging behaviour (WIC)

Calculating individual-level repeatability values across different foraging variables revealed how population-level metrics may conceal the true extent of variation in the degree of IFSF within populations (Potier *et al.*, 2015). Our results revealed a range of individual strategies, from repeatable site faithful individuals to variable birds which use a range of foraging sites, providing further evidence for the coexistence of specialist, intermediate and generalist individuals within populations of gulls (Navarro *et al.*, 2017; van Donk *et al.*, 2018; van den Bosch *et al.*, 2019) and other generalist species (Baylis *et al.*, 2012; Arthur *et al.*, 2015; Potier *et al.*, 2015; Votier *et al.*, 2017). However, despite increasing evidence for the existence of such intra-population differences in foraging behaviour, the proximate causes of site fidelity at the individual-level remain poorly understood (Piper, 2011).

Intrinsic factors such as morphology, physiology or personality may drive differences in site fidelity between individuals (Bearhop *et al.*, 2004; Camprasse *et al.*, 2017; van Donk *et al.*, 2018; Harris *et al.*, 2020). Alternatively, differences in site fidelity may be a consequence of individual preferences in diet (Woo *et al.*, 2008) or foraging habitat (van den Bosch *et al.*, 2019), with higher levels of site fidelity often resulting from specialisation on sites or prey items which are more predictable (Switzer, 1993; Baylis *et al.*, 2012). Gulls from these three colonies foraged in a range of different habitats including urban areas characterised by predictable anthropogenic resources (Spelt *et al.*, 2019, 2020), agricultural areas with more ephemeral resource availability (Kruuk, 1978; Isaksson *et al.*, 2016) and intertidal habitats where prey is cyclically available (van Donk *et al.*, 2018). Multiple drivers may contribute to the observed individual variation in site fidelity within colonies, which is likely maintained by long-term variation in the cost-benefit trade-offs associated with fidelity to different foraging sites (Svanbäck and Persson, 2004).

5.5.3. Inter-colony differences in individual site fidelity (WIC)

We did not detect any differences in the individual-level repeatability for most foraging trip metrics. However, individual-level repeatability of distal longitude, which represents foraging location, was higher at Barrow (low WIC), indicating a higher degree of site fidelity at this small urban colony. Additionally, individual-level repeatability of distal point distance was lower at Ribble, a large coastal colony. Density-dependent resource competition between conspecific individuals is a key structuring force on movement and foraging behaviour in gulls and other seabirds (Wakefield *et al.*, 2013; Corman *et al.*, 2016; Lamb, Satgé and Jodice, 2017). Moreover, high levels of intraspecific competition have been shown to favour the evolution of individual specialisation, leading to increased dietary differentiation and an expansion of total niche width, in both experimental and field studies (Svanbäck and Bolnick, 2007; Araújo, Bolnick and Layman, 2011). The observation of higher site fidelity at Barrow, the smallest colony in our study, suggests that density-dependent competition is not playing a key role in driving IFSF in these populations.

Differences in IFSF between sites may also result from colony-level differences in intrinsic factors (Camprasse *et al.*, 2017; van Donk *et al.*, 2018; Harris *et al.*, 2020). For example, IFSF was higher in larger individual herring gulls (*Larus argentatus*) breeding in the Netherlands (van Donk *et al.*, 2018). We did not test for a relationship between IFSF and morphology here, however, our sample of tagged gulls may have been larger at the urban colony by chance, contributing to colony-level differences in site fidelity. Observed differences between sites may also be due to differences in personality, with a study on Kittiwakes finding that bolder individuals are more site faithful (Harris *et al.*, 2020). Boldness is a beneficial trait for animals breeding and foraging in urban areas, reducing potential impacts of human disturbance (Møller, 2009), and urban-breeding may have selected for bolder individuals at Barrow, contributing to higher site fidelity at this colony.

Site fidelity may also be driven by habitat preferences and individuals foraging in locations characterised by predictable resources often show higher site fidelity (Switzer, 1993; Baylis *et al.*, 2012; Arthur *et al.*, 2015; van Donk *et al.*, 2018). We observed variation in population-level resource use between colonies, with **chapter 4** demonstrating segregation between urban foragers from Barrow and coastal foragers from Walney. Gulls forage in urban areas for predictable resources such as anthropogenic refuse which may favour site fidelity (Spelt *et al.*, 2019, 2020; van Donk *et al.*, 2019). In contrast, coastal habitats are cyclically available with the tide, causing birds to spend time in other areas when they are unavailable (van Donk *et al.*, 2018). **Chapter 3** showed that birds from Ribble also utilised urban foraging habitats extensively following landfill closures. However, Ribble breeders could visit several different urban areas, which may have reduced site fidelity, whilst those from Barrow largely relied on Barrow-in-

Furness for urban foraging. This variety of urban foraging options may have contributed to our finding of lower individual-level repeatability of distal point distance (high WIC) at Ribble (Figure 5.6a).

As such, inter-colony differences in individual-level IFSF (WIC) could at least partly be driven by the location of the nesting site, both in relation to the resource landscape and other colonies (Wakefield *et al.*, 2013; Corman *et al.*, 2016). Further work, linking IFSF to individual habitat choice, is therefore key to understanding the drivers of observed differences in site fidelity between colonies. Moreover, modelling IFSF (spatial specialisation) as a function of habitat specialisation would provide insights into whether individual gulls specialise on specific foraging locations which have been learned over time (Wakefield *et al.*, 2015; Votier *et al.*, 2017) or whether they possess habitat or dietary preferences that lead to specialisation on the same habitat type across multiple sites (van den Bosch *et al.*, 2019).

5.5.4 Implications for conservation and management

Site faithful individuals may benefit from improved familiarity with their foraging site, leading to improved foraging success and increased energy intake rates (Irons, 1998). Although fitness benefits of site fidelity have only rarely been quantified (Piper, 2011), site fidelity has been shown to reduce foraging effort and improve reproductive success in gulls and other seabirds (Patrick and Weimerskirch, 2017; van den Bosch *et al.*, 2019). IFSF may also influence population dynamics in these successful species, reducing competition and facilitating population growth (Bolnick *et al.*, 2003; Araújo, Bolnick and Layman, 2011; Navarro *et al.*, 2017). Observation of a higher degree of foraging site fidelity at Barrow, an urban colony, suggests that differences in site fidelity may be contributing to divergent population trends between breeding habitats in lesser black-backed gulls (Ross-Smith *et al.*, 2014). Future studies, linking site fidelity and individual habitat use with reproductive performance across a range of urban and rural colonies may help to determine the drivers of population trajectories in this species.

IFSF can also have costs as site faithful individuals may have relatively poor knowledge of the wider environment compared with individuals which use a range of sites, making them vulnerable to environmental change (Wilson and Yoshimura, 1994; Kotzerka, Hatch and Garthe, 2011). Ongoing policy changes are altering the resource landscape for many gull populations, reducing the availability of anthropogenic subsidies such as landfill refuse and fisheries discards (Bicknell *et al.*, 2013; Tyson *et al.*, 2015; Zorrozua *et al.*, 2020). Understanding the degree of individual site fidelity within populations, the location of foraging sites and the nature of resources at these sites is key to understanding how generalist populations will respond to environmental change. The presence of generalist individuals across our study colonies suggests that habitat-switching may limit the population-level impacts of policy changes, however, they may select for generalist individuals within populations (Wakefield *et al.*, 2015; Dehnhard *et al.*, 2016). Future studies combining tracking data with monitoring of breeding parameters in tagged individuals could link site fidelity, resource specialisation and reproductive performance and identify the mechanisms underpinning demographic responses to anthropogenic change.

Understanding the prevalence of site faithful individuals is also important when designing measures to mitigate human-gull conflict. In populations with a high prevalence of site faithful individuals and a low WIC (Fig. 5.1, population C), measures to restrict resource availability at these foraging sites may result in a reduction in population density (Bino *et al.*, 2010). Similarly, if site faithful individuals are common (Fig. 5.1, population C), then forced colony relocations which increase the effort required to access preferred sites may reduce reproductive performance and ultimately lead to reductions in population density (Kavelaars *et al.*, 2020). The presence of site faithful individuals at Barrow suggest that measures to restrict resource availability may be a useful tool to mitigate conflict with individuals loyal to urban foraging sites. However, the presence of multiple generalists (high WIC; Fig. 5.1), suggest such approaches are unlikely to reduce population density at this colony.

5.6 Conclusion

By investigating foraging site fidelity at both the population and individual level, this study provides further evidence that apparent generalist populations often consist of a mixture of flexible generalists and site faithful specialists. We also demonstrated that the degree of IFSF varies between colonies. This variation may be due to intrinsic differences between birds or differences in the nature and predictability of foraging habitats between colonies. Further work linking foraging site fidelity to habitat choice at the individual-level is therefore key to understanding the drivers of inter-colony differences, and provide insights into the importance of spatial specialisation vs. habitat specialisation in these generalist populations. Additionally, investigating the consequences of site fidelity and habitat specialisation in terms of reproductive performance may help to determine the mechanisms underpinning divergent demographic trends between breeding habitats and population responses to future environmental change.

5.7 References

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Chapter 6 – General Discussion

6.1 Revisiting thesis aims

In this thesis, I investigated the influence of human activities on the ecology and demography of gulls (*Laridae*), focussing on the lesser black-backed gull as an example of an opportunistic species that has responded strongly to anthropogenic change. Gulls are successful beneficiaries of anthropogenic change, however, they have also been harmed by human activities. Moreover relatively little is known about their ecology in urban areas.

Therefore in **chapter 2**, I synthesised the peer-reviewed literature on global changes in gull demography, summarising trends in abundance and distribution and the role of human activities in driving these trends. I then reviewed the impacts of changing gull abundance on both ecosystems and human activities before discussing the responses of conservation and management, and drawing together a research agenda aimed at balancing mitigation with conservation.

The research agenda in **chapter 2**, along with the work of Ross Smith et al. (2014), highlighted 10 key knowledge gaps which hinder our ability to effectively manage and conserve gulls. I used a multi-year GPS tracking dataset from adult lesser black-backed gulls breeding at three colonies in northwest England, supplemented with data collected in the field on diet, breeding parameters and biometrics to help fill some of these research gaps. The resulting chapters focus particularly on ecological responses to habitat modification and changing anthropogenic subsidies.

In **chapter 3**, I used telemetry data to investigate changes in the foraging ecology of gulls from two coastal colonies following landfill closures, highlighting the value of bio-logging as a tool to monitor behavioural responses to anthropogenic perturbations. I also tested for an effect of landfill closures on adult body condition.

In **chapter 4**, I combined GPS-tracking with traditional diet analyses and breeding parameters to provide the first insights into population-level differences in movement and breeding ecology between neighbouring urban and rural colonies.

Finally, in **chapter 5**, by calculating both population and individual-level measures of individual foraging site fidelity, I provided insights into the extent to which this important component of intra-population variation differed among three colonies (two coastal, one urban) and between years, and in relation to the use of Predictable Anthropogenic Food Subsidies (PAFS).

6.1 Summary of findings

Chapter 2 summarised global trends in gull demography, revealing a general pattern of increased abundance and range expansions (including into urban areas) across a number of species during the 20th century. These patterns were driven by changing human activities including reduced persecution and improved legal protection, habitat creation, and the provision of PAFS. More recently, a number of populations have stabilised or declined, linked to a range of anthropogenic and natural drivers. Synthesising the peer-reviewed literature revealed geographic biases, with a dearth of published data on demographic trends away from Europe and North America and few population estimates from urban areas. Expanding gull populations have been subjected to a range of management interventions, however, assessing the efficacy of different approaches is hindered by a lack of demographic monitoring, information on economic costs and properly controlled studies. Moreover, management is largely reactive, particularly in urban areas, with limited dialogue between different stakeholders. Finally, recent declines suggest a lack of resilience in some gull populations and dependence on human activities, highlighting a need to balance mitigation with conservation.

Chapter 3 found that adult lesser black-backed gulls breeding at two colonies increased their foraging effort in response to landfill closures and altered their habitat selection, switching to forage in either agricultural or urban habitats dependent on the colony. However, a landfill closure effect on body condition was not detected.

Chapter 4 revealed that urban and rural breeders segregated by foraging habitat, with urban breeders selecting strongly for urban habitats and coastal breeders selecting for intertidal habitats. However, no dietary differences and only minor differences in breeding parameters were found between colonies.

Finally, **Chapter 5** found moderate evidence for Individual Foraging Site Fidelity (IFSF) at the population-level, although this varied between years and among behavioural metrics and colonies. These population-level metrics concealed a range of individual strategies, from highly site faithful through to generalist individuals. Additionally, individual repeatability of distal longitude was higher at an urban colony, Barrow, suggesting increased IFSF might be driven by reliance on PAFS.

6.3 Implications and directions for future research

6.3.1 Quantifying gull abundance and assessing drivers of change

Chapter 2 revealed geographic biases in the peer-reviewed literature, highlighting the urgent need to generate accurate estimates for gull populations globally, particularly in less well-surveyed regions and urban habitats. Drones have recently gained prominence as a useful tool for monitoring both natural and urban colonies (Rush *et al.*, 2018; Blight, Bertram and Kroc, 2019), however such approaches face legal barriers, particularly in some urban areas.

Our review of population trends was also restricted to the peer-reviewed literature. Much additional information on trends in gull abundance is available in the grey literature such as national and international atlases and monitoring databases while more is found in non-English language publications. Building on the review in **chapter 2**, a global synthesis of the drivers of trends in gull abundance and distribution across regions, species and populations which draws from the entire breadth of available data sources would be timely.

6.3.2 Are control measures effective?

Chapter 2 also revealed a lack of published information on the efficacy of control measures. Existing studies have focussed on culls at large natural colonies, and found limited success in terms of reducing gull population size due to density-dependent effects and the longevity and dispersal ability of adults (Coulson, Duncan and Thomas, 1982; Wanless *et al.*, 1996; Bosch *et al.*, 2000; Payo-Payo *et al.*, 2015). However, such studies were generally opportunistic in response to management activities, and the implementation of properly controlled studies, using a Before-After-Control-Impact framework, for example, would help quantify the impacts of lethal control on gull demography, and disentangle the effects of other demographic drivers such as changing resource availability (Henden *et al.*, 2020).

Studies attempting to quantify the efficacy of urban gull management in a controlled way were also lacking. In urban areas, management generally involves non-lethal approaches (Rock, 2005); however, assessing the costs and benefits of different approaches is hindered by a lack of information on economic costs and reporting of outcomes (Trotter, 2019). Moreover, there appears to be a lack of connectedness among different stakeholders. A national review of the extent and economic costs of urban gull control activities, using data from local authorities, would be useful in quantifying the scale and costs of urban gull management. Additionally, developing links between researchers and management organisations would allow the design and implementation of studies to quantify the efficacy of different control measures and the consequences for urban gull ecology and demography. Such local partnerships could provide the ecological evidence to develop integrated gull management approaches which function at the landscape-level (Belant, 1997).

6.3.3 Quantifying public perception of gulls

Finally, **chapter 2** found that gulls currently suffer from poor public perception, particularly in urban areas where they are often considered a problem (Rock, 2005; Goumas *et al.*, 2019). Observations of habitat-switching to urban and agricultural habitats following landfill closures in **Chapter 3**, suggest ongoing changes in resource availability will shift foraging gulls from different breeding habitats into closer proximity with humans. This will increase the likelihood of human-gull conflict and may impact public perceptions of gulls, leading to increased calls for management (Trotter, 2019). However, encounters with urban gulls may have benefits to public health and well-being (Keniger *et al.*, 2013) and urban gulls may provide ecosystem services in the form of refuse and roadkill scavenging (Huig, Buijs and Kleyheeg, 2016; Schwartz *et al.*, 2018) and controlling invasive species (Méndez *et al.*, 2020). Social science approaches have been used to quantify public opinions regarding several problematic urban species (Hill, Carbery and Deane, 2007; Delahay and Heydon, 2009; Nardi *et al.*, 2020). Similar approaches could be applied to gulls to engage with stakeholders who value having gulls in towns and cities and inform the development of public education programmes to reduce human-gull conflict.

6.3.4 Fitness consequences of anthropogenic perturbations

Chapter 3 demonstrated increased foraging effort of birds from two coastal colonies following landfill closures and it was expected that this would negatively impact breeding gulls (van den Bosch *et al.*, 2019; Kavelaars *et al.*, 2020). However, no effect was found on adult body condition. This was most likely due to a type II error, although rapid habitat switches or an inability to quantify individual-level effects may also have contributed. Alternatively, in a year of low food availability following landfill closure, birds may prioritise self-maintenance in favour of investing in reproduction (Bolton *et al.*, 1992; Payo-Payo *et al.*, 2015). Previous studies have shown negative fitness effects of anthropogenic perturbations on gulls including reductions in egg and chick production (Pons, 1992; Pons and Migot, 1995; Oro, 1996; Oro, Jover and Ruiz, 1996). Combining telemetry data with population-level monitoring of breeding parameters could help determine the demographic impacts of changes in foraging behaviour following landfill closure. Moreover, this chapter only focussed on short-term behavioural responses to anthropogenic perturbations, however, gulls may show initial strong behavioural or demographic responses before adjusting to new conditions (Payo-Payo *et al.*, 2015). Monitoring of movement behaviour and breeding parameters over multiple breeding seasons following is therefore key to determining whether gull populations show long-term resilience to changes in PAFS availability.

The nature of the compensatory foraging habitats also varied between colonies with birds from Ribble switching to urban habitats following landfill closure and birds breeding at Walney switching to agricultural areas. Compensatory habitat choice may influence demographic responses to landfill closures. For example, whilst urban resources may be equivalent to landfill refuse (van Donk *et al.*, 2019), agricultural areas may represent low value foraging habitats due to the small size and low calorific value of prey items (Patenaude-Monette, Bélisle and Giroux, 2014; van den Bosch *et al.*, 2019) and ephemeral nature of prey availability (Isaksson *et al.*, 2016). The use of agricultural areas as compensatory foraging habitat may have contributed to recent rapid declines at Walney from 2,831 AONs in 2016 (the year prior to landfill closure) to 389 in 2019 (https://app.bto.org/seabirds/public/data.jsp), although mammalian predators are also an issue at this site (Davis *et al.*, 2018). Combining telemetry data with monitoring of diet and breeding parameters at the population-level would provide insights into the fitness consequences of changing foraging effort and habitat switching in response to anthropogenic perturbations.

6.3.5 Ecological segregation

Chapter 4 adds to our knowledge of the ecology of urban and rural gulls. A major finding was that urban and coastal breeders segregated by foraging habitat, with urban breeders selecting for urban habitats and coastal breeders selecting for intertidal habitats. This has promising management applications, as it suggests that management interventions targeting urban breeders, such as restriction of refuse availability (Bino *et al.*, 2010), should not impact birds form the coastal colony where the species is a designated feature of a Special Protection Area (SPA). However, the results from **chapter 3** demonstrate that birds from other SPA colonies forage extensively in urban habitats, as do coastal breeders in the Netherlands (Huig, Buijs and Kleyheeg, 2016), questioning the generality of these findings.

Habitat selection in population-level generalists such as gulls is the result of complex cost-benefit trade-offs informed by a range of intrinsic and extrinsic factors (van Donk *et al.*, 2019). Urban foraging may be costly for birds from

Walney, as birds may be excluded from the closest urban area, Barrow-in-Furness, due to density-dependent competition from urban breeders (Wakefield *et al.*, 2013; Corman *et al.*, 2016). In contrast, urban foraging may be less costly for birds from Ribble which have several towns and cities within close proximity of the colony to choose from. In order to quantify the impact of urbanisation on the foraging ecology of lesser black-backed gulls breeding in different habitats, analysis of GPS tracking data across multiple colonies along the rural-urban gradient, from remote island colonies to large urban areas, is required. Such an analysis could utilise existing tracking data sets from urban (Spelt *et al.*, 2019) and rural (Thaxter *et al.*, 2015, 2019) lesser black-backed gull colonies in Britain and in Europe (Camphuysen, 2013; Corman *et al.*, 2016; Isaksson *et al.*, 2016; Kavelaars, Lens and Müller, 2019), although more data may be required from urban colonies.

Although there were clear differences in habitat selection by breeding adult gulls, no population-level differences were detected in diet. This may be due to biases in diet sampling techniques, which often underrepresent soft prey items such as carbohydrates and cooked meats found in urban refuse (Votier *et al.*, 2003; Barrett *et al.*, 2007). Alternatively, dietary similarities may have resulted from prey-switching to feed growing chicks on a marine or agricultural diet (Annett and Pierotti, 1989; Zorrozua *et al.*, 2020). Future studies could refine the dietary analysis by combining conventional approaches with techniques such as stable isotopes (Bearhop *et al.*, 2004; Corman *et al.*, 2016; Lopezosa *et al.*, 2019) and DNA fingerprinting (Deagle *et al.*, 2007). This would reduce bias and increase taxonomic resolution (Barrett *et al.*, 2007; Ronconi *et al.*, 2014), and may provide further insights into dietary differences between breeding habitats.

Slight differences were detected in breeding parameters between colonies, with higher egg and clutch volumes at the coastal site although chick condition was similar. This result ran counter to our expectations, given the divergent demographic trends between declining coastal colonies and increasing urban populations in this species (Marques *et al.*, 2009; Ross-Smith *et al.*, 2014). However, overall reproductive success was low across both colonies due to predation impacts and severe weather. Additionally, the urban colony was not a traditional roof-top colony and many pairs were forcibly relocated from a neighbouring site, which can reduce reproductive investment (Salas *et al.*, 2020). These uncertain results highlight the need for long-term demographic monitoring across a range of colonies, in order to determine the drivers of divergent demographic trends between breeding habitats.

6.3.6 Individual foraging site fidelity

Chapter 5 demonstrated that across colonies, lesser black-backed gulls showed moderate evidence of site fidelity, although by calculating individual repeatability metrics, it was evident that populations comprised a mix of some birds that used variable foraging locations and others loyal to a specific location. This study only considered individual foraging specialisation in terms of site foraging site fidelity, however, other studies have shown that individual gulls may also specialise on particular foraging habitats rather than specific foraging sites (Navarro *et al.*, 2017; van den Bosch *et al.*, 2019; Jakubas *et al.*, 2020). Modelling IFSF (spatial specialisation) as a function of habitat specialisation would provide insights into whether individual gulls specialise on specific foraging areas which have been learned over time (Wakefield *et al.*, 2015; Votier *et al.*, 2017) or whether they possess dietary preferences or particular foraging skills that lead to specialisation on the same habitat type across multiple sites (van den Bosch *et al.*, 2019).

Understanding the prevalence of site faithful individuals within populations and the habitats they use is important to informing conservation and management interventions targeted at foraging birds, for example, removal of urban refuse (Bino *et al.*, 2010), as such approaches will have minimal impacts on demography if individuals can use a range of foraging sites. Moreover, forced colony relocations may be effective in managing populations containing site faithful individuals, as they may be unwilling to switch foraging sites resulting in negative fitness consequences (Kavelaars *et al.*, 2020).

6.3.7 Individual responses to anthropogenic perturbations

Chapter 3 demonstrated population-level responses to landfill closures, as breeding gulls increased their foraging effort and switched to forage in either urban or agricultural habitats. However, **chapter 5** revealed marked variation in the degree of IFSF at these colonies and landfill utilisation varied markedly among individuals prior to closures, with many never visiting the focal landfills. The strength of individual responses to closures was expected to depend on the extent of landfill utilisation, however, our sample sizes of tagged birds were too small to investigate these responses. The extent of individual behavioural flexibility in gulls is an open question. Individual gulls can switch to forage on alternative resources when translocated to a new area (van Toor *et al.*, 2017) and can adjust their foraging behaviour in response to human behavioural cycles (Tyson *et al.*, 2015; Spelt *et al.*, 2020). However, such flexibility is not universal (Kavelaars *et al.*, 2020). By tracking large samples of birds over multiple years, future studies could quantify individual behavioural responses to anthropogenic perturbations, and relate this to specialisation on specific foraging sites or resources. Moreover, monitoring the breeding parameters of tagged birds would allow studies to quantify the consequences of different behavioural responses to anthropogenic change and control for other drivers such as reproductive failure, which add noise to population-level patterns. This would allow the identification of the mechanisms underpinning demographic responses to anthropogenic change.

6.3.8 Individual-level responses to urbanisation

In addition to revealing strong foraging segregation at the population-level, **chapter 4** also revealed variation in individual-level habitat use, with birds from both colonies utilising urban foraging habitats to varying extents. This evidence of individuality was reinforced by **chapter 5**, which demonstrated a high degree of inter-individual variation in IFSF at both colonies. Unfortunately, the sensitive nature of both colonies prevented investigation of the consequences of individual foraging decisions by monitoring the diet and breeding performance of tagged individuals. Future work combining telemetry data with information on diet and breeding parameters from tagged adults or even breeding pairs (Kavelaars, Lens and Müller, 2019; Kavelaars *et al.*, 2020) could and examine the consequences of differences in habitat selection within and between colonies in terms of foraging effort, diet and ultimately, reproductive performance. Furthermore, combining GPS tags with tri-axial accelerometers could allow behavioural reconstructions and investigation of the energetic costs and benefits of different foraging decisions (van Donk *et al.*, 2019). Such individual-level approaches could begin to tease apart the ecological mechanisms driving divergent demographic trends between urban and coastal breeding habitats in this species (Ross-Smith *et al.*, 2014).

6.3.9 Long-term foraging site fidelity

Chapter 5 revealed marked inter-annual variation in IFSF at the population-level which varied among colonies and behavioural metrics. This is an interesting result, however, there were insufficient individuals sampled over multiple breeding seasons to investigate the long-term consistency of IFSF at the individual-level. Studies of pelagic seabirds have shown long-term IFSF which appears largely robust to changes in local environmental conditions or breeding state (Wakefield *et al.*, 2015; Zango *et al.*, 2020). The evidence for site fidelity in gulls is mixed, with short-term prey switches observed in response to translocation (van Toor *et al.*, 2017) or cyclic resource availability (Tyson *et al.*, 2015; Spelt *et al.*, 2020) contrasting with observations of long-term site fidelity from other studies (Kavelaars *et al.*, 2020). Further studies could use existing and newly collected telemetry datasets to investigate the long-term consistency of IFSF in lesser black-backed gulls from multiple colonies across their European range which vary in conspecific population density and resource availability. Additionally, such analyses could investigate long-term individual consistency of IFSF in response to human-induced changes in the availability of PAFS (Bicknell *et al.*, 2013; Zorrozua *et al.*, 2020).

6.3.10 Ontogeny of foraging behaviour

A related question concerns the ontogeny of foraging behaviour and the development of individual specialisation in these population-level generalists. Evidence from pelagic seabirds suggests long term site fidelity may result from a phase of initial exploratory behaviour with foraging strategies becoming refined and canalised over time (Votier *et al.*, 2017). Gulls represent a more complex system as individuals can potentially forage across different sites and in multiple habitats (van den Bosch *et al.*, 2019; Jakubas *et al.*, 2020). Data from bio-logging devices is starting to provide insights into the foraging behaviour of juvenile and immature seabirds (Votier *et al.*, 2011, 2017; Péron and Grémillet, 2013; Riotte-Lambert and Weimerskirch, 2013) and tracking studies of juvenile and immature lesser black-backed gulls could provide similar insights into the ontogeny of foraging behaviour and the development of IFSF in this population-level generalist in a complex and changing resource landscape.

6.3.11 Gull conservation

The results presented in this thesis may also be used to inform gull conservation. In **chapter 4**, we observed low fledging success at the coastal colony of South Walney NR – part of the South Walney and Piel Channel Flats SSSI and Morecambe Bay and Duddon Estuary SPA, where the lesser black-backed gull is a feature, largely as a result of predation by mammalian predators including badgers (*Meles meles)* and red foxes (*Vulpes vulpes*). Mammalian predation has also been implicated as a key driver of declines at other coastal SPA colonies where the species is a feature (Davis *et al.*, 2018), and systematic investment into predator control and deterrents such as predator-proof fencing are likely the most practical conservation solution to boost reproductive performance and bolster these declining natural gull colonies.

Our analysis of foraging habitat selection in **chapter 4** and **chapter 5** also revealed that gulls breeding at the SPA colonies of Ribble and South Walney relied on anthropogenic resources far outside protected area boundaries including landfill refuse and human-modified agricultural and urban habitats. The availability of PAFS from both landfills and urban refuse may decline in the future due to ongoing policy changes (Zorrozua *et al.*, 2020) and possible management interventions (Coccon and Fano, 2020) respectively, leaving these colonies facing additional resource stress. This highlights that in addition to conserving breeding sites, careful consideration of functional linkages with foraging habitats in management decisions may be required to maintain favorable conservation status for mobile species such as gulls that forage widely from their colonies

(Thaxter *et al.*, 2012). This is also true of gulls foraging in ‘natural’ habitats, which again will often lie outside protected site boundaries.

For lesser black-backed gulls breeding in northwest England, low levels of marine foraging compared with other colonies (Thaxter *et al.*, 2015; Garthe *et al.*, 2016) suggests a lack of suitable marine prey. This highlights ecosystem restoration as a potential tool to improve the conservation status of these colonies. Policy drivers in the UK Marine Strategy and 25 Year Environment Plan (https://www.gov.uk/government/publications) for clean, healthy and biodiverse marine ecosystems could support such recovery, and in turn allow more gulls to adopt a more ‘natural’ foraging strategy within well managed, functioning, marine ecosystems. In instances where human actions rapidly reduce resource availability for protected area colonies, such as following landfill closures, short-term supplementary feeding could be used to address resource deficits. A similar approach was used to conserve breeding brown skuas (*Stercorarius antarcticus*) on Macquarie Island following removal of their invasive rabbit prey during ecosystem restoration (Travers *et al.*, 2020). However, where colonies are highly reliant on unsustainable anthropogenic subsidies and alternative foraging habitats are unavailable, as this thesis shows, gulls may forage in human locations that increase conflicts with people. Additionally, the more gulls compete for these increasingly scarce resources, the more likely declines at colonies (including protected sites) become.

Finally, my results demonstrate that the foraging ecology of lesser black-backed gulls varies between individuals, years and colonies due to differences in individual preferences, the availability and distribution of resources within the foraging range and extrinsic factors such as population density and the presence of other gull species. A combination of long-term GPS-tracking and demographic monitoring at SPA colonies where the species is a feature is therefore a key conservation priority, in order to detect colony-specific specific threats such as changes in food availability and predation, identify the likely drivers of demographic change and inform conservation action at the landscape-level.

6.4 Conclusions

This thesis provides the first synthesis of the peer-reviewed literature on changes in the global abundance and distribution of gulls, revealing a general pattern of population and range expansions in response to human activities, with more recent declines in some areas. Additionally, this review revealed issues with current gull management approaches and outlined a number of avenues for future research. By combining data from a range of approaches, this thesis also provides new insights into the influence of anthropogenic change on the ecology of lesser black-backed gulls. In particular, the availability of anthropogenic subsidies and human-modified habitats can strongly influence the population-level movement and foraging behaviour of this opportunistic species. Overall, these results suggest an uncertain future for the UK lesser black-backed gull population and gulls more generally, with their future as long-term “winners” of the Anthropocene in doubt. The observed reliance of individuals and populations on a range of anthropogenic habitats reveals a lack of resilience and suggests a lack of sufficient “natural” prey in coastal and marine ecosystems. Ongoing changes in PAFS availability therefore present a threat to protected area colonies and could cause individuals from different breeding colonies to forage more frequently in urban areas, increasing the potential for human-gull interactions that could lead to conflict. This highlights the management of refuse as an important tool for mitigating human-gull conflict in urban areas in the short-term. Moving forward, there is an urgent need to quantify public perceptions of gulls and design public education programmes and policies to minimise conflicts and encourage people to embrace urban gulls. Importantly, however, gull responses to human activities varied among individuals, breeding colonies and years. This suggests gull responses to further anthropogenic change may depend on the resource landscape within the foraging range and demonstrates the need to develop local strategies for gull conservation and management involving a range of stakeholders. Overall, this thesis emphasises the need for long-term monitoring of ecological and demographic responses to human activities at both the individual and population-levels using a range of approaches. Such monitoring programmes are required to generate sufficient ecological evidence to inform the conservation and management of opportunistic species in the Anthropocene.

6.5 References

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Appendix A. General supplementary information

Additional tagging information

Captured birds were fitted with a solar-powered GPS tag (either a University of Amsterdam Bird-Tracking System (UvA-BiTS) device or a Movetech Flyway-18 GPS-GSM device) attached via a Teflon wing-loop harness. “Permanent” harnesses were replaced by a “weak-link” design from 2017 allowing the tag to detach without recapture (Table A1).

Table A1. A summary of number of tags deployed, device type and attachment method in each year across all three colonies.

Site	Year	Birds Tagged	Tag type	Attachment
Ribble	2016	11	Movetech	Permanent harness
Ribble	2017	2	Movetech	Weak-link harness
Ribble	2017	8	UvA-BiTS	Weak-link harness
Ribble	2018	10	Movetech	Weak-link harness
Barrow	2016	7	Movetech	Permanent harness
Barrow	2017	13	Movetech	Weak-link harness
Barrow	2018	9	Movetech	Weak-link harness
Walney	2014	24	UvA BiTS	Permanent harness
Walney	2016	20	UvA BiTS	Permanent harness
Walney	2016	5	Movetech	Permanent harness

During tagging potential device effects were carefully considered. Although the accepted body mass threshold of 3% (Phillips, Xavier and Croxall, 2003) is now debated, all tags fitted on gulls were below this threshold (Table A2).

Table A2. Tag and harness mass as a percentage of body mass for all birds tagged across all three sites between 2014 and 2018. Tag and harness mass includes 3g for a colour-ring. For birds some birds tagged with Movetech devices in 2018 (*) the exact tag masses are missing and therefore values represent closest assumed tag masses of 24.5g based on known masses of tags from that year. This value of total tag and harness mass includes 3g for colour ring and 3.5 for harness.

Bird ID	Tag Type	Site	Year	Tag and harness mass (g)	Bird weight (g)	Percentage of body mass (%)
179	Movetech	Ribble	2016	25.25	920	2.74
205	Movetech	Ribble	2016	24.92	920	2.71
242	Movetech	Ribble	2016	25	920	2.72
243	Movetech	Ribble	2016	25.86	1010	2.56
446	Movetech	Ribble	2016	21.03	790	2.66
450	Movetech	Ribble	2016	21.43	800	2.68
464	Movetech	Ribble	2016	21.42	820	2.61
465	Movetech	Ribble	2016	21.01	780	2.69
467	Movetech	Ribble	2016	21.46	840	2.55
469	Movetech	Ribble	2016	21	890	2.36
484	Movetech	Ribble	2016	21	860	2.44
734	Movetech	Ribble	2017	19.26	980	1.97
743	Movetech	Ribble	2017	19.8	920	2.15
5454	UvA S	Ribble	2017	13.53	920	1.47
5456	UvA S	Ribble	2017	13.42	910	1.47
5458	UvA S	Ribble	2017	13.51	860	1.57
5459	UvA S	Ribble	2017	13.5	740	1.82
5460	UvA S	Ribble	2017	13.5	960	1.41
5461	UvA S	Ribble	2017	13.45	750	1.79
5462	UvA S	Ribble	2017	13.55	800	1.69
5463	UvA S	Ribble	2017	13.68	765	1.79
852	Movetech	Ribble	2018	17.8	880	2.02
853	Movetech	Ribble	2018	18.28	865	2.11
854	Movetech	Ribble	2018	17.96	845	2.13
862	Movetech	Ribble	2018	17.96	960	1.87
879	Movetech	Ribble	2018	18.1	970	1.87
880	Movetech	Ribble	2018	17.69	820	2.16
881	Movetech	Ribble	2018	17.76	920	1.93
882	Movetech	Ribble	2018	18.25	840	2.17
911*	Movetech	Ribble	2018	24.5	1030	2.37
915*	Movetech	Ribble	2018	24.5	955	2.56
204	Movetech	Barrow	2016	24.82	910	2.73
208	Movetech	Barrow	2016	24.56	900	2.73
225	Movetech	Barrow	2016	25.33	990	2.56
276	Movetech	Barrow	2016	25.17	930	2.71
456	Movetech	Barrow	2016	21.05	810	2.60
471	Movetech	Barrow	2016	21.51	800	2.69
472	Movetech	Barrow	2016	21.00	870	2.41

486	Movetech	Barrow	2016	18.28	770	2.37
488	Movetech	Barrow	2016	18.19	780	2.33
492	Movetech	Barrow	2016	21.28	790	2.69
687	Movetech	Barrow	2017	18.54	980	1.89
707	Movetech	Barrow	2017	19.78	920	2.15
708	Movetech	Barrow	2017	18.82	855	2.20
711	Movetech	Barrow	2017	19.23	980	1.96
715	Movetech	Barrow	2017	18.51	845	2.19
717	Movetech	Barrow	2017	19.64	930	2.11
718	Movetech	Barrow	2017	18.44	835	2.21
725	Movetech	Barrow	2017	19.24	900	2.14
727	Movetech	Barrow	2017	18.74	840	2.23
729	Movetech	Barrow	2017	19.26	950	2.03
742	Movetech	Barrow	2017	18.92	890	2.13
744	Movetech	Barrow	2017	18.99	935	2.03
777	Movetech	Barrow	2017	18.38	830	2.21
920*	Movetech	Barrow	2018	24.5	940	2.61
919*	Movetech	Barrow	2018	24.5	865	2.83
918*	Movetech	Barrow	2018	24.5	900	2.72
916*	Movetech	Barrow	2018	24.5	825	2.97
914*	Movetech	Barrow	2018	24.5	875	2.8
885*	Movetech	Barrow	2018	25.34	980	2.59
868	Movetech	Barrow	2018	24.5	840	2.92
863*	Movetech	Barrow	2018	24.5	970	2.53
851	Movetech	Barrow	2018	24.46	1010	2.42
494	UvA L	Walney	2014	18.50	870	2.13
496	UvA L	Walney	2014	18.50	720	2.57
497	UvA L	Walney	2014	18.50	780	2.37
499	UvA L	Walney	2014	18.50	860	2.15
501	UvA L	Walney	2014	18.50	990	1.87
502	UvA L	Walney	2014	18.50	710	2.61
503	UvA L	Walney	2014	18.50	660	2.80
504	UvA L	Walney	2014	18.50	730	2.53
506	UvA L	Walney	2014	18.50	720	2.57
4031	UvA M	Walney	2014	15.50	920	1.68
4032	UvA M	Walney	2014	15.50	710	2.18
4033	UvA M	Walney	2014	15.50	820	1.89
4034	UvA M	Walney	2014	15.50	940	1.65
4035	UvA M	Walney	2014	15.50	770	2.01
5023	UvA S	Walney	2014	13.50	680	1.99
5024	UvA S	Walney	2014	13.50	910	1.48
5025	UvA S	Walney	2014	13.50	930	1.45
5026	UvA S	Walney	2014	13.50	880	1.53
5027	UvA S	Walney	2014	13.50	760	1.78
5029	UvA S	Walney	2014	13.50	730	1.85
5030	UvA S	Walney	2014	13.50	900	1.50
5032	UvA S	Walney	2014	13.50	750	1.80
5033	UvA S	Walney	2014	13.50	790	1.71
5034	UvA S	Walney	2014	13.50	970	1.39
202	Movetech	Walney	2016	25.00	980	2.55
220	Movetech	Walney	2016	25.00	1100	2.27
253	Movetech	Walney	2016	25.00	980	2.55

254	Movetech	Walney	2016	25.00	900	2.78
278	Movetech	Walney	2016	25.00	960	2.60
5358	UvA S	Walney	2016	13.50	950	1.42
5360	UvA S	Walney	2016	13.50	790	1.71
5362	UvA S	Walney	2016	13.50	940	1.44
5363	UvA S	Walney	2016	13.50	780	1.73
5365	UvA S	Walney	2016	13.50	920	1.47
5366	UvA S	Walney	2016	13.50	980	1.38
5367	UvA S	Walney	2016	13.50	940	1.44
5368	UvA S	Walney	2016	13.50	895	1.51
5371	UvA S	Walney	2016	13.50	860	1.57
5375	UvA S	Walney	2016	13.50	810	1.67
5376	UvA S	Walney	2016	13.50	880	1.53
5377	UvA S	Walney	2016	13.50	880	1.53
5378	UvA S	Walney	2016	13.50	940	1.44
5379	UvA S	Walney	2016	13.50	770	1.75
5380	UvA S	Walney	2016	13.50	900	1.50
5381	UvA S	Walney	2016	13.50	940	1.44
5382	UvA S	Walney	2016	13.50	770	1.75
5383	UvA S	Walney	2016	13.50	850	1.59
5385	UvA S	Walney	2016	13.50	930	1.45
5386	UvA S	Walney	2016	13.50	810	1.67

Colony boundaries

Foraging trips were defined as any positional fix outside the colony area for Ribble (Fig. A1), Walney (Fig. A2) and Barrow (Fig. A3).

Figure A1. Colony area used to define foraging trips for Ribble birds (red polygon). Any GPS fixes outside the colony boundary were defined as a foraging trip

Figure A2. Colony area used to define foraging trips for Walney birds (blue polygon). Any GPS fixes outside the colony boundary were defined as a foraging trip

Figure A3. Colony area used to define foraging trips for Barrow birds (blue polygon). Any GPS fixes outside the colony boundary were defined as a foraging trip.

Habitat classifications

When conducting habitat analyses in **chapter 3** and **chapter 4**, location points were assigned to one of seven main habitat categories (agriculture, coastal, freshwater, landfill, marine, other, urban) by grouping codes from the Corine European Landcover seamless vector database (Table A3).

Table A3. Habitat classifications from the Corine European Landcover database grouped into main foraging habitats types used for habitat selection modelling.

CLC Code	Habitat Classification	Main Habitat Classification
111	Continuous urban fabric	Urban
112	Discontinuous urban fabric	Urban
121	Industrial or commercial units	Urban
122	Road and rail networks and associated land	Urban
123	Port areas	Urban
124	Airports	Urban
131	Mineral extraction sites	Urban
133	Construction sites	Urban
141	Green urban area	Urban
142	Sport and leisure facilities	Urban
132	Dump	Landfill
211	Non-irrigated arable land	Agriculture
212	Permanently irrigated land	Agriculture
213	Rice fields	Agriculture
221	Vineyards	Agriculture
222	Fruit trees and berry plantations	Agriculture
223	Olive groves	Agriculture
231	Pastures	Agriculture
241	Annual crops associated with permanent crops	Agriculture
242	Complex cultivation patterns	Agriculture
243	Land principally occupied by agriculture with significant areas of natural vegetation	Agriculture
331	Beaches dunes sands	Coastal
421	Salt marshes	Coastal
422	Salines	Coastal
423	Intertidal flats	Coastal
521	Coastal lagoons	Coastal
522	Estuaries	Coastal
523	Sea and ocean	Marine
411	Inland marshes	Freshwater
412	Peat bogs	Freshwater

511	Water courses	Freshwater
512	Water bodies	Freshwater
244	Agro-forestry areas	Other
311	Broad-leaved forest	Other
312	Coniferous forest	Other
313	Mixed forest	Other
321	Natural grasslands	Other
322	Moors and heathland	Other
323	Sclerophyllous vegetation	Other
324	Traditional woodland-shrub	Other
332	Bare rocks	Other
333	Sparsely vegetated areas	Other
334	Burnt areas	Other
335	Glaciers and perpetual snow	Other

Appendix B. Supplementary material for chapter 3

Foraging effort

Model selection for movement data was undertaken via AIC selection using the *ICtab* function from the “bbmle” package in R. Where multiple equivalent candidate models were within ΔAIC < 2.0, the simplest model was chosen as the minimum adequate model (**Bold**; Tables B1 – B4).

Table B1. Top five candidate models to explain probability of visiting any landfill at the colony-level ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.0399$, $CR^2 = 0.328$.

Model	AIC	dAIC	df	Weight
Landfill ~ lf_status + (1|ID)	**470.2**	**0.0**	**3**	**0.49**
Landfill ~ lf_status + colony (1|ID)	471.1	0.9	4	0.31
Landfill ~ lf_status + colony + colony*lf_status (1|ID)	472.0	1.7	5	0.20
Landfill ~ 1 + (1|ID)	492.3	22.1	2	<0.001
Landfill ~ colony + (1|ID)	494.3	24.1	3	<0.001

Table B2. Top five candidate models to explain trip duration (hrs) at the colony-level ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.0833$, $CR^2 = 0.299$.

Model	AIC	dAIC	df	Weight
Trip duration ~ lf_status + colony + (1|ID)	**7017.1**	**0.0**	**5**	**0.659**
Trip duration ~ lf_status + colony + colony*lf_status + (1|ID)	7018.6	1.5	6	0.309
Trip duration ~ lf_status + (1|ID)	7023.1	6.1	4	0.032
Trip duration ~ 1 + (1|ID)	7216.2	199.1	3	<0.001
Trip duration ~ colony + (1|ID)	7217.5	200.4	4	<0.001

Table B3. Top five candidate models to explain trip length (km) at the colony-level ranked by AIC weight. Pseudo-R^2 values for the selected model - MR^2 = 0.0441 CR^2 = 0.251.

Model	**AIC**	**dAIC**	**df**	**Weight**
Trip length ~ lf_status + colony + colony*lf_status + (1|ID)	1392.5	0.0	6	0.43
Trip length ~ lf_status + (1|ID)	**1392.8**	**0.3**	**4**	**0.37**
Trip length ~ lf_status + colony + (1|ID)	1394.0	1.5	5	0.20
Trip length ~ colony + (1|ID)	1450.1	57.6	4	<0.001
Trip length ~ 1 + (1|ID)	1454.1	61.6	3	<0.001

Table B4. Top five candidate models to explain distal point (km) at the colony-level ranked by AIC weight. Pseudo-R^2 values for the selected model - MR^2 = 0.0764, CR^2 = 0.269.

Model	AIC	dAIC	df	Weight
Distal point ~ lf_status + colony + colony*lf_status + (1|ID)	**9025.4**	**0.0**	**6**	**0.58**
Distal point ~ lf_status + colony + (1|ID)	9027.4	2.0	5	0.22
Distal point ~ lf_status + (1|ID)	9027.5	2.1	4	0.20
Distal point ~ colony + (1|ID)	9088.3	62.9	4	< 0.001
Distal point ~ 1 + (1|ID)	9094.6	69.1	3	< 0.001

Resource selection functions

Habitat availability

Available habitat varied around the Ribble and Walney colonies, being dominated by agricultural and urban habitats at Ribble and agricultural and marine habitats at Walney (Fig. B1).

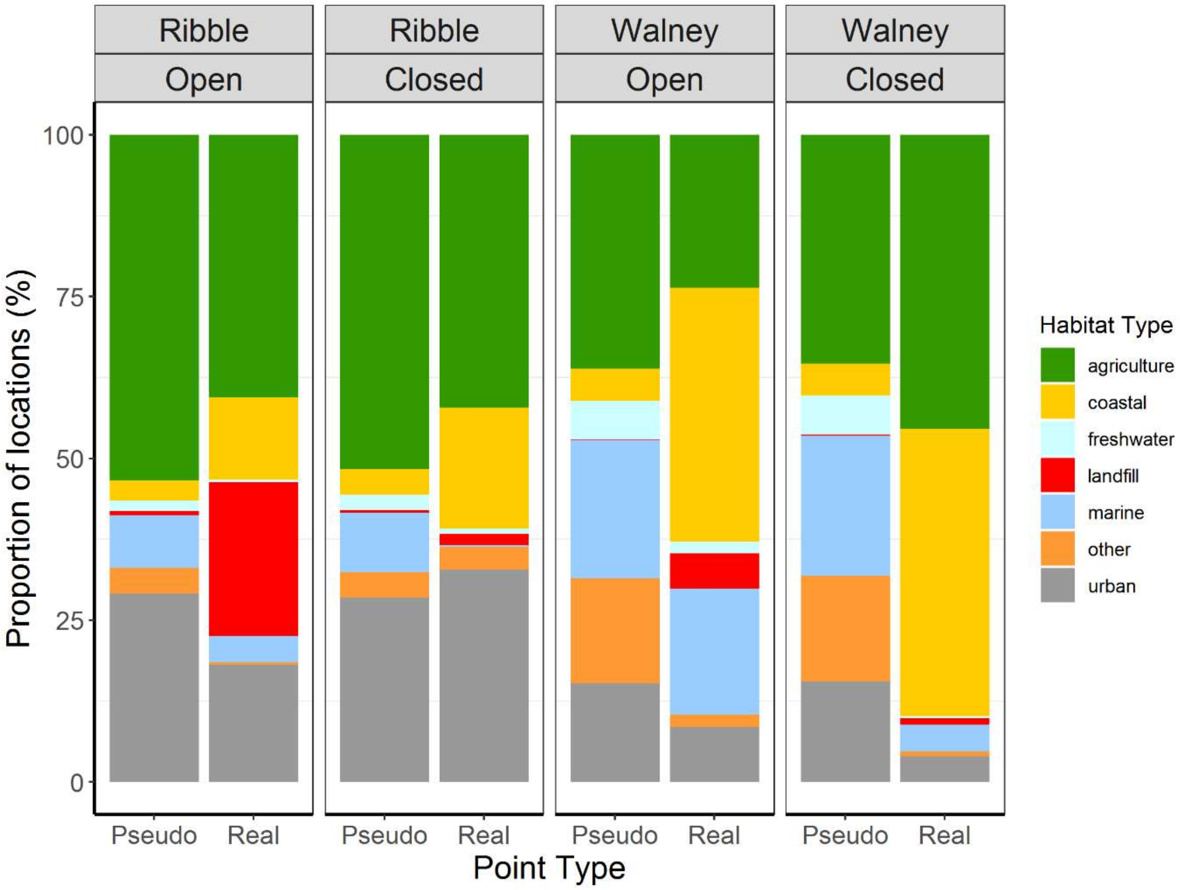

Figure B1. Proportion of real gull location fixes vs. randomised pseudoabsences (Pseudo) assigned to each of seven main habitat classes – agricultural, coastal, freshwater, landfill, marine, urban and other (scrub woodland and other non-foraging habitats) – for gulls breeding at Ribble and Walney in the years before and after landfill closure. Available habitat at Ribble was dominated by agricultural and urban environments whilst marine and freshwater habitats constituted a greater proportion of the pseudoabsence locations for Walney.

<u>Model fit</u>

We assessed model fit for binomial GLMMS of the probability of a location being a real gull location or a pseudo-absence by calculating the area under the receiving operator characteristic curve, predictive power, sensitivity and specificity (Table B5).

Table B5. Assessment of habitat selection models containing a habitat variable, site and the site*habitat interaction for all tagged birds (Table 4.1). All metrics are derived from a confusion matrix based on the original data. AUC (area under the receiver operating curve) ranges from 0 to 1, where 0.5 is random, and higher values indicate better model performance. CC = Correct Classification, PPP = Positive Predictive Power, NPP = Negative Predictive Power, Sen. = Sensitivity, Spec, = Specificity.

Model	**Site**	**CC (%)**	**PPP (%)**	**NPP (%)**	**Sen.**	**Spec.**	**AUC**
Agriculture	Ribble	53.09	19.54	86.16	0.582	0.521	0.5513
Coastal	Ribble	83.10	48.09	85.35	0.174	0.962	0.5682
Landfill	Ribble	84.04	74.75	84.18	0.064	0.996	0.5299
Marine	Ribble	24.01	17.87	97.75	0.990	0.0902	0.5399
Urban	Ribble	59.32	18.75	84.63	0.432	0.625	0.5287
Agriculture	Walney	48.95	19.55	87.07	0.662	0.455	0.5586
Coastal	Walney	86.07	62.53	88.95	0.409	0.951	0.6801
Landfill	Walney	83.89	85.77	83.87	0.040	0.999	0.5192
Marine	Walney	31.10	17.88	88.13	0.856	0.214	0.5349
Urban	Walney	28.29	18.01	91.64	0.930	0.154	0.5417

Distal points analysis

We repeated the analysis on a filtered data set containing only distal foraging trip locations, where gulls were assumed to be foraging, to account for the potential inclusion of commuting points in the main analysis. Patterns of habitat selection based on distal trip locations (Table B6; Fig. B1) were similar to those based on all foraging trip locations (Table 3.5; Fig. 3.5).

Table B6. Estimates for the effect of an interaction between the habitat variable and landfill status on the probability of a location being a real gull location or a pseudo-absence based on distal foraging trip locations only. Delta (Δ) AIC refers to the change in AIC caused by removing the interaction. If Δ AIC > 2, the interaction is not significant meaning we found no evidence for an effect of breeding habitat on selection for that habitat type. If the interaction effect is significant, habitat selection varied with landfill status. Models were run separately for each site. Stars next to p-values represent significance levels (* < 0.05; ** < 0.01; *** < 0.001).

Habitat Variable	**Site**	**Estimate for landfill status interaction**	**p value**	**Δ AIC**
Agriculture	Ribble	0.0374	0.833	-2.0
Coastal	Ribble	0.375	0.250	-0.7
Landfill	Ribble	-3.15	<0.001***	18.3
Marine	Ribble	-3.34	<0.001***	47.4
Urban	Ribble	1.58	<0.001***	49
Agriculture	Walney	1.23	<0.001***	154.0
Coastal	Walney	0.180	0.300	-0.9
Landfill	Walney	-2.31	0.0141*	2.6
Marine	Walney	-2.14	<0.001***	225.4
Urban	Walney	0.152	0.325	-1.0

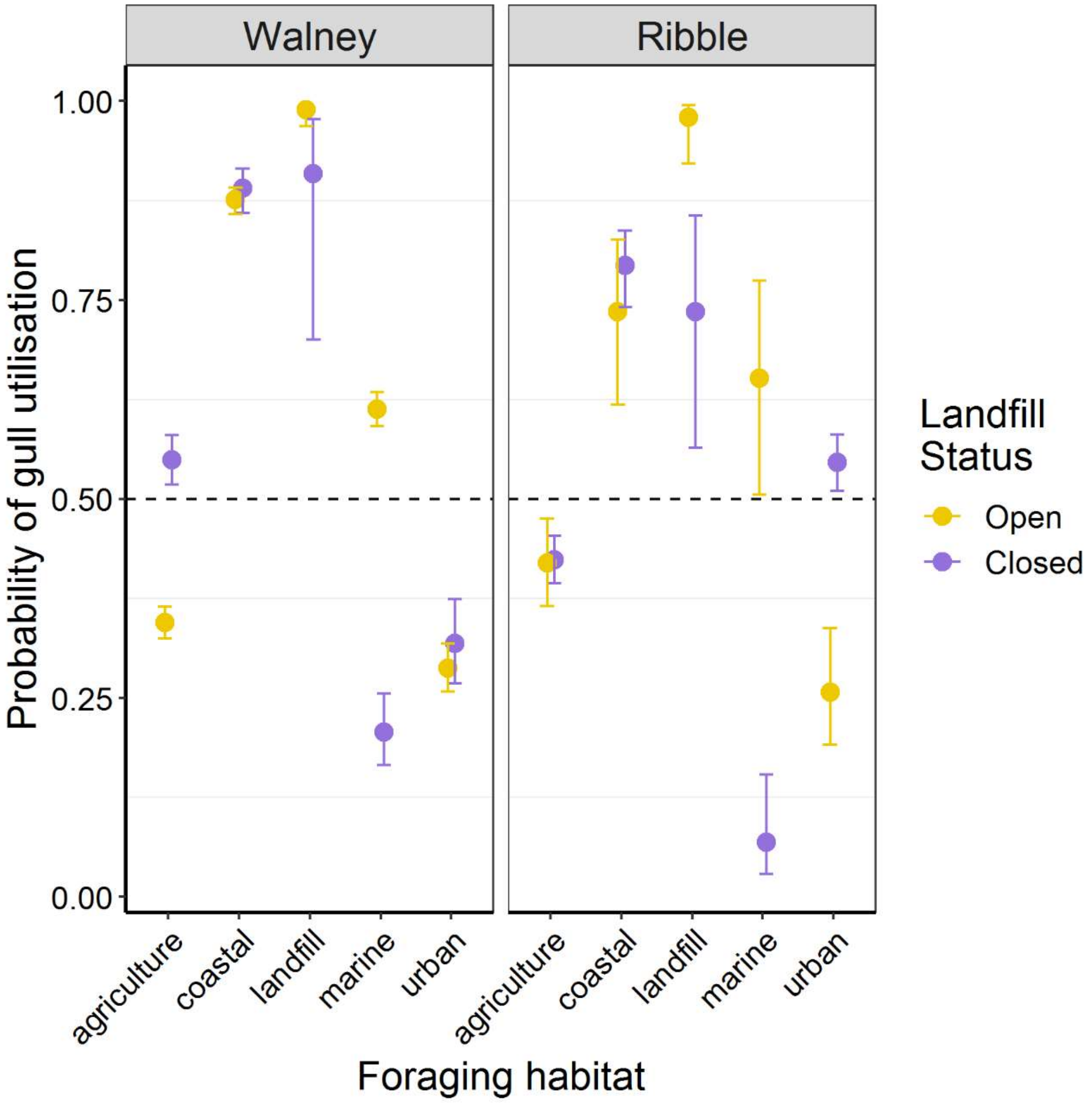

Figure B2. Estimates and 95% confidence intervals from resource selection models for all GPS-tagged lesser black-backed gulls breeding at Ribble and Walney before (gold) and after (purple) closure of the focal landfill site based on distal trip locations. Models estimate the probability of a given location point being a real gull location rather than a pseudo-absence in response to five main foraging habitat categories (agriculture, coastal, landfill, marine, urban). A probability of 0.50 indicates that birds used habitat in proportion to its availability whilst values of > 0.50 indicate selection for that habitat type at the colony-level.

Table B7. Assessment of habitat selection models for distal foraging trip locations containing a habitat variable, site and the site*habitat interaction (Table S15). All metrics are derived from a confusion matrix based on the original data. AUC (area under the receiver operating curve) ranges from 0 to 1, where 0.5 is random, and higher values indicate better model performance. CC = Correct Classification, PPP = Positive Predictive Power, NPP = Negative Predictive Power, Sen. = Sensitivity, Spec, = Specificity.

Model	**Site**	**CC (%)**	**PPP (%)**	**NPP (%)**	**Sen.**	**Spec.**	**AUC**
Agriculture	Ribble	53.73	20.53	87.23	0.619	0.521	0.5699
Coastal	Ribble	82.16	41.73	85.24	0.177	0.951	0.5639
Landfill	Ribble	84.06	68.57	84.37	0.0803	0.993	0.5365
Marine	Ribble	35.01	17.63	86.15	0.789	0.262	0.5258
Urban	Ribble	58.81	19.78	85.46	0.482	0.609	0.5455
Agriculture	Walney	47.87	20.26	88.65	0.725	0.429	0.5772
Coastal	Walney	85.16	59.32	87.98	0.350	0.952	0.6508
Landfill	Walney	84.27	92.42	84.18	0.0614	0.999	0.5302
Marine	Walney	63.04	21.53	86.02	0.460	0.665	0.5623
Urban	Walney	29.14	18.21	92.26	0.932	0.163	0.5474

Appendix C. Supplementary material for chapter 4

Movement data model selection

Model selection for movement data was undertaken via AIC selection using the *ICtab* function from the “bbmle” package in R. Where multiple equivalent candidate models were within ΔAIC of 2.0, the simplest model was chosen as the minimum adequate model (**Bold**; Tables C1 – C6). For trip length, one of the 13 candidate models failed to converge (trip length ~ trip_type + year + (1|ID)).

Table C1. Top five candidate models to explain the probability of visiting an urban habitat ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.158$, $CR^2 = 0.294$.

Model Structure	AIC	ΔAIC	DF	Weight
Trip type ~ site + (1|bird ID)	580.5	0.0	3	0.50
Trip type ~ site + year + site:year + (1|bird ID)	**581.6**	**1.1**	**5**	**0.28**
Trip type ~ site + year + (1|bird ID)	582.2	1.7	4	0.21
Trip type ~ 1 + (1|bird ID)	598.7	18.3	2	<0.001
Trip type ~ year + (1|bird ID)	600.3	19.8	3	<0.001

Table C2. Top five candidate models to explain trip duration (hrs) ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.0358$, $CR^2 = 0.202$.

Model Structure	AIC	ΔAIC	DF	Weight
Trip duration ~ trip_type + site + year + trip_type:site + site:year + (1|bird ID)	4333.8	0.0	8	0.642
Trip duration ~ trip_type + site + year + trip_type:site + (1|bird ID)	**4335.3**	**1.5**	**7**	**0.302**
Trip duration ~ trip_type + site + year + (1|bird ID)	4338.7	4.9	6	0.056
Trip duration ~ trip_type + site + year + site:year + (1|bird ID)	4357.7	23.9	7	<0.001
Trip duration ~ trip_type + year + (1|bird ID)	4358.3	24.5	5	<0.001

Table C3. Top five candidate models to explain trip length (km) ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.197$, $CR^2 = 0.338$.

Model Structure	**AIC**	**ΔAIC**	**DF**	**Weight**
Trip length ~ trip_type + site + year + trip_type:site + (1|bird ID)	5730.3	0.0	7	0.44
Trip length ~ trip_type + site + trip_type:site + (1|bird ID)	**5730.9**	**0.6**	**6**	**0.32**
Trip length ~ trip_type + site + year + trip_type:site + site:year + (1|bird ID)	5731.5	1.2	8	0.24
Trip length ~ trip_type + site + year + (1|bird ID)	5861.6	131.3	6	<0.001
Trip length ~ trip_type + site + year + site:year (1|bird ID)	5862.6	132.3	7	<0.001

Table C4. Top five candidate models to explain distal point distance (km) ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.241$, $CR^2 = 0.375$.

Model Structure	**AIC**	**ΔAIC**	**DF**	**Weight**
Distal point ~ trip_type + site + year + trip_type:site + site:year + (1|bird ID)	4474.4	0.0	8	0.52
Distal point ~ trip_type + site + year + trip_type:site + (1|bird ID)	**4475.3**	**0.8**	**7**	**0.34**
Distal point ~ trip_type + site + (1|bird ID)	4477.1	2.7	6	0.14
Distal point ~ trip_type + site + year + site:year + (1|bird ID)	4619.2	144.8	7	<0.001
Distal point ~ trip_type + site + year + (1|bird ID)	4620.4	145.9	6	<0.001

Table C5. Top five candidate models to explain core foraging range area (km^2) ranked by AIC weight. Pseudo-R^2 values for the selected model - $MR^2 = 0.161$, $CR^2 = 0.286$.

Model Structure	**AIC**	**ΔAIC**	**DF**	**Weight**
Core range area ~ site + year + total_fixes + (1|birdID)	199.4	0.0	6	0.338
Core range area ~ site + total_fixes +(1|birdID)	**199.9**	**0.5**	**5**	**0.258**

Core range area ~ site + year + total_fixes + year:site + (1|birdID)	200.2	0.8	7	0.225
Core range area ~ total_fixes + (1|bird ID)	201.9	2.5	4	0.099
Core range area ~ year + total_fixes (1|bird ID)	202.3	2.9	5	0.080

Table C6. Top five candidate models to explain core home range area (km^2) ranked by AIC weight. Pseudo-R^2 values for the selected model – MR^2 = 0.180, CR^2 = 0.333

Model Structure	AIC	ΔAIC	DF	Weight
Home range area ~ site + year + total_fixes + (1|birdID)	192.3	0.0	6	0.35
Home range area ~ site + year + total_fixes + year:site +(1|birdID)	193.3	1.0	7	0.21
Home range area ~ site + year + total_fixes + (1|birdID)	**193.3**	**1.0**	**5**	**0.21**
Home range area ~ total_fixes + (1|bird ID)	194.5	2.2	4	0.11
Home range area ~ year + total_fixes (1|bird ID)	194.6	2.3	5	0.11

Resource selection functions

Habitat availability

Available habitat was largely similar between the urban and coastal colonies, being dominated by agricultural habitats. However the availability of urban foraging habitats for coastal breeders was significantly higher than it was for urban breeders (Fig. C1).

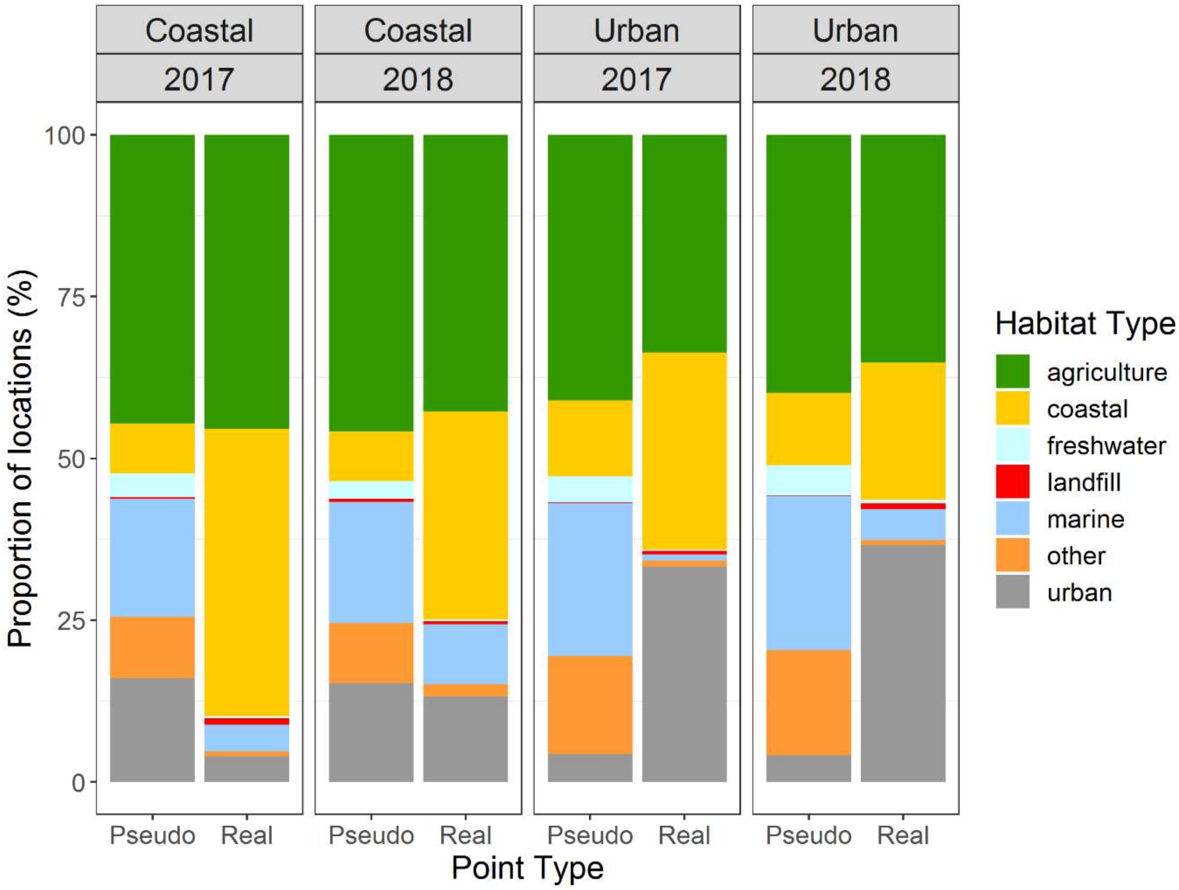

Figure C1. Proportion of real gull location fixes (Real) vs. randomised pseudoabsences (Pseudo) assigned to each of seven main habitat classes – agricultural, coastal, freshwater, landfill, marine, urban and other (scrub, woodland and other non-foraging habitats) – for gulls breeding at the coastal and urban sites in both years. Pseudoabsence locations were defined at the level of the colony home range (minimum convex polygon).

Model fit – Resource selection functions

We assessed model fit for binomial GLMMS of the probability of a location being a real gull location or a pseudo-absence by calculating the area under the receiving operator characteristic curve, predictive power, sensitivity and specificity (Table C7).

Table C7. Assessment of habitat selection models containing a habitat variable, site and the site*habitat interaction (Table 3). All metrics are derived from a confusion matrix based on the original data. AUC (area under the receiver operating curve) ranges from 0 to 1, where 0.5 is random, and higher values indicate better model performance. CC = Correct Classification, PPP = Positive Predictive Power, NPP = Negative Predictive Power, Sen. = Sensitivity, Spec, = Specificity.

Model	**Year**	**CC (%)**	**PPP (%)**	**NPP (%)**	**Sen.**	**Spec.**	**AUC**
Agriculture	2017	51.36	17.43	84.07	0.513	0.514	0.513
Coastal	2017	82.71	47.79	88.44	0.405	0.912	0.658
Marine	2017	32.56	19.43	96.85	0.968	0.197	0.583
Urban	2017	45.06	20.29	89.89	0.784	0.384	0.584
Agriculture	2018	46.80	17.52	84.42	0.591	0.443	0.517
Coastal	2018	81.11	40.76	86.62	0.293	0.915	0.604
Marine	2018	32.02	18.68	92.48	0.919	0.201	0.560
Urban	2018	42.03	18.70	87.28	0.741	0.356	0.548

Habitat selection – Distal points

One main analysis of habitat selection included all foraging trip points due to low data resolution (1 hr fixes), which risks including commuting locations where birds are not foraging. We therefore repeated the analysis on a filtered data set containing distal trip locations, where gulls were assumed to be foraging. Patterns of habitat selection based on distal trip locations were similar to those based on all foraging trip locations (Table 4.8; Fig 4.5). One exception was a lack of breeding habitat differences in the selection for agricultural habitats. Otherwise, coastal and marine breeders differed in their selection for all other habitats.

Additionally, the analysis of distal points resulted in coastal breeders showing selection for marine habitats in 2018, possibly due to a number of short foraging trips to this habitat.

Table C8. Estimates for the effect of an interaction between the habitat variable and breeding site on the probability of a location being a real gull location or a pseudo-absence for each foraging habitat in each year based on distal locations only. Delta (Δ) AIC refers to the change in AIC caused by removing the interaction. Δ AIC values > 2, suggest that the probability of gull utilisation (habitat selection) for that habitat type differs significantly between breeding sites. The coastal colony was the reference level for breeding site, therefore the sign of the estimate represents the difference in habitat selection between coastal and urban colonies. Stars next to p-values represent significance levels (* < 0.05; ** < 0.01; *** < 0.001).

Habitat Variable	**Year**	**Estimate for breeding site interaction**	**p value**	**Δ AIC**
Agriculture	2017	-0.130 (± 0.128)	0.310	-1.0
Coastal	2017	-1.07 (± 0.177)	<0.001***	35.1
Marine	2017	-1.70 (± 0.309)	<0.001***	34.8
Urban	2017	2.95 (± 0.213)	<0.001***	226.9
Agriculture	2018	-0.0428 (± 0.152)	0.779	-1.9
Coastal	2018	-0.762 (± 0.221)	<0.001***	9.9
Marine	2018	-1.85 (± 0.222)	<0.001***	74.4
Urban	2018	3.28 (± 0.264)	<0.001***	181.9

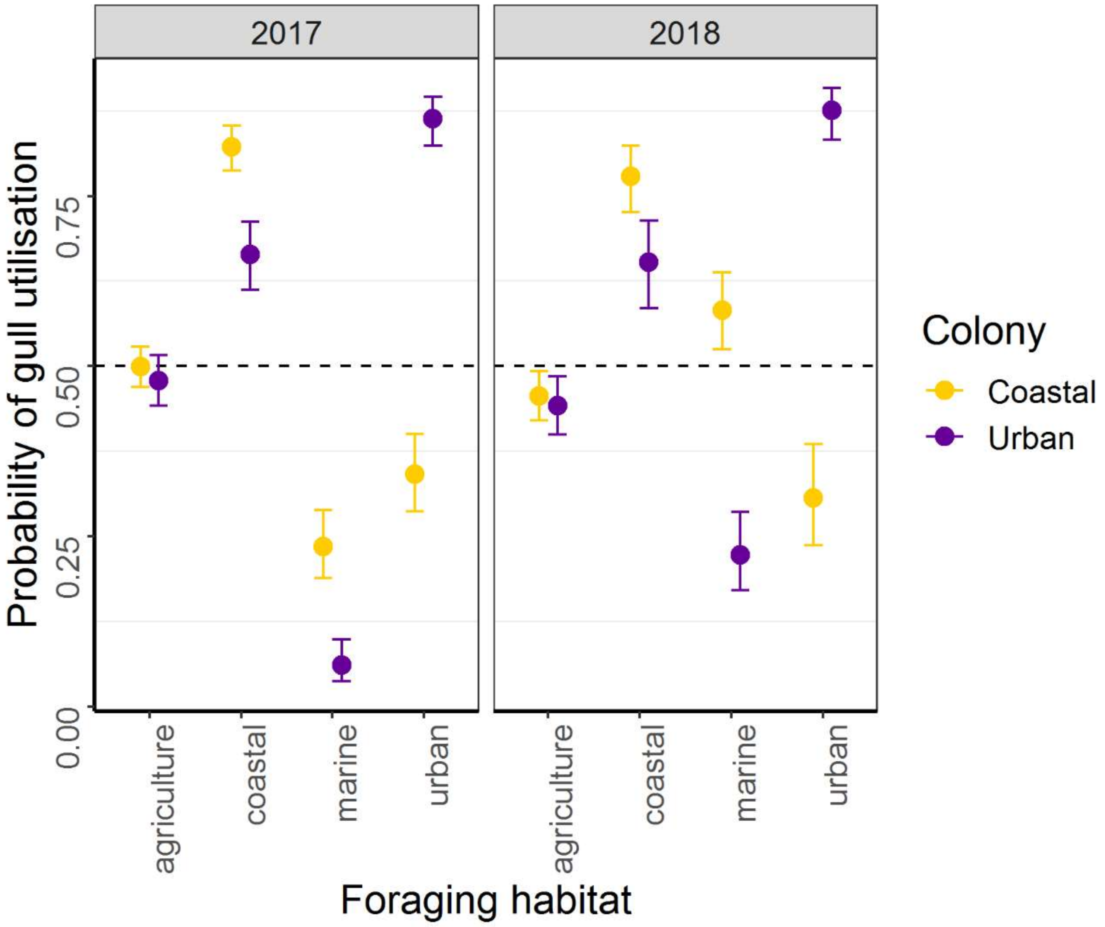

Figure C2. Estimates and 95% CIs from resource selection models of the probability of gull utilisation of each of four main foraging habitats (agriculture, coastal, marine, urban) by coastal (gold) and urban (purple) breeding gulls in each year based on distal foraging trip locations only. A probability of 0.50 indicates that birds are using habitat in proportion to its availability within the foraging range (colony-level minimum convex polygon), whilst values of > 0.50 indicate selection for that habitat type.

Table C9. Assessment of habitat selection models for distal foraging trip locations containing a habitat variable, site and the site*habitat interaction (Table S15). All metrics are derived from a confusion matrix based on the original data. AUC (area under the receiver operating curve) ranges from 0 to 1, where 0.5 is random, and higher values indicate better model performance. CC = Correct Classification, PPP = Positive Predictive Power, NPP = Negative Predictive Power, Sen. = Sensitivity, Spec, = Specificity.

Model	**Year**	**CC (%)**	**PPP (%)**	**NPP (%)**	**Sen.**	**Spec.**	**AUC**
Agriculture	2017	46.26	17.04	83.81	0.575	0.440	0.508
Coastal	2017	80.27	38.76	86.81	0.316	0.900	0.608
Marine	2017	33.90	19.66	96.52	0.961	0.215	0.588

Urban	2017	52.46	21.01	88.29	0.672	0.495	0.583
Agriculture	2018	49.14	18.81	85.93	0.619	0.466	0.542
Coastal	2018	79.73	34.48	85.68	0.241	0.909	0.575
Marine	2018	55.84	20.00	86.15	0.550	0.560	0.555
Urban	2018	53.78	21.77	88.94	0.683	0.509	0.596

Diet sampling

Due to variation in sample sizes across years and months at the urban and coastal sites we only analysed diet pellet data from June in each year (Fig. C3).

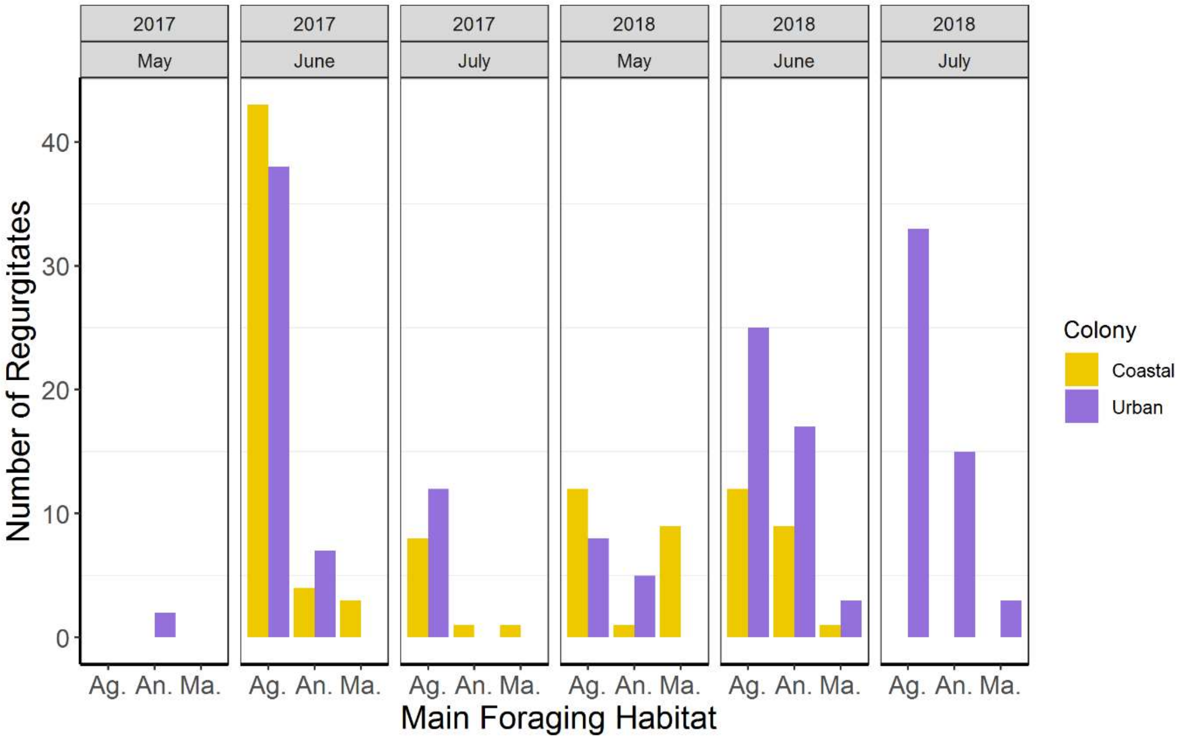

Figure C3. Diet pellet data broken down by main foraging habitat for each month during the 2017 and 2018 breeding seasons across the urban and rural sites. Due to variation in sample sizes, we only analysed pellet data from June in each year. Main foraging habitats are abbreviated as follows: Ag. = Agricultural, An. = Anthropogenic, Ma. = Marine.

In 2017, there were very high levels of egg and chick mortality at the urban site. This meant that we were only able to compare chick diet composition between breeding habitats for the 2018 breeding season (Fig. C4).

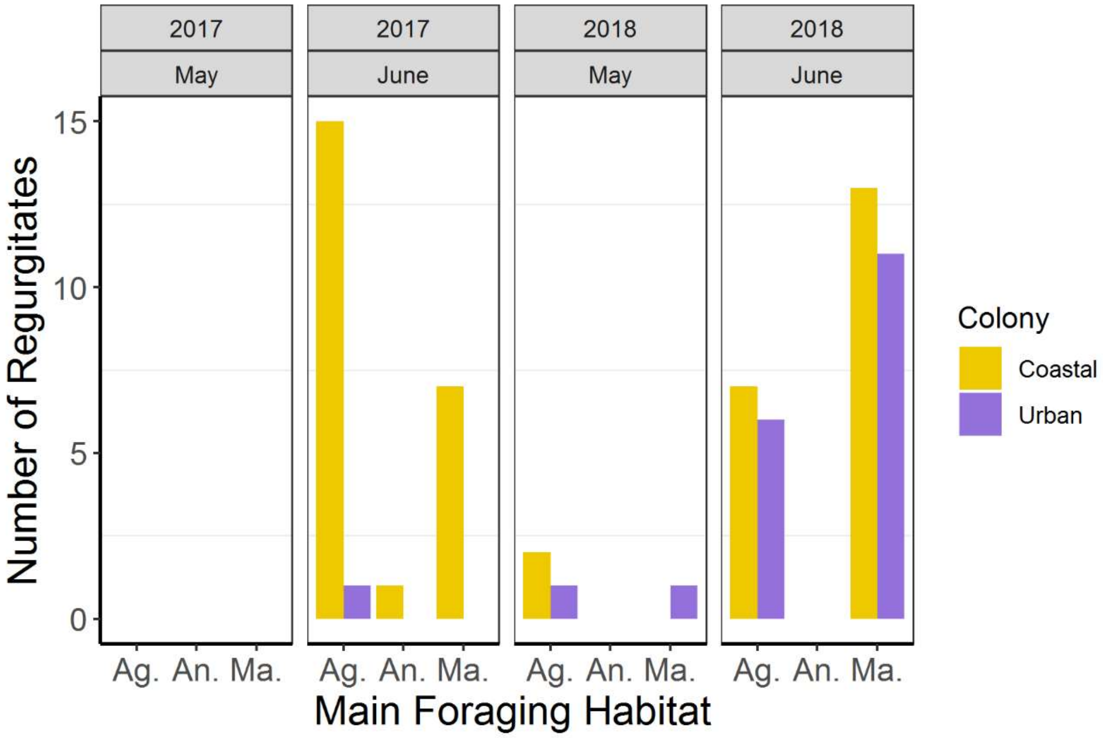

Figure C4. Chick regurgitate samples broken down by main foraging habitat for each colony across the two field seasons, A lack of urban samples in 2017 meant that breeding habitat differences in chick diet composition were only investigated for 2018. Main foraging habitats are abbreviated as follows: Ag. = Agricultural, An. = Anthropogenic, Ma. = Marine.

Prey classification

Prey items from regurgitated pellets and spontaneous regurgitates were classified into one of three main foraging habitats (Agricultural, Anthropogenic and Marine) based on the prey items they contained. Here we provide a breakdown of how prey items were classified into foraging habitats for pellets (Table C10) and spontaneous regurgitates (Table C11)

Table C10. All prey items found in regurgitated pellets from the 2017 and 2018 breeding seasons classified into three main gull foraging habitats – agricultural, anthropogenic and marine.

Foraging Habitat	**Prey Item**
Agricultural	Beetle (*Coleoptera spp.*) Rodent (*Rodentia spp.)*

	Maize Grain fragments Terrestrial vegetation (Grass) Unidentified fly larvae (*Diptera spp.*) Snail (*Mollusca spp.*)
Anthropogenic	Chicken bone Plastic Cardboard/paper Glass Tinfoil Polystyrene Wood
Marine/Intertidal	Crab (*Portunidae spp.)* Mussel (*Mytilus spp.)* Unidentified intertidal mollusc (*Mollusca spp.)*

Table C11. All prey items found in chick regurgitates during the 2018 breeding season classified by main gull foraging habitat. Note that only agricultural and marine prey items were found in our samples.

Foraging Habitat	**Prey Item**
Agricultural	Earthworm (*Annelida spp.*) Slug (*Mollusca spp.*) Leatherjacket (*Tipulidae spp.*) Dung Beetle (*Scarabidae*) Ground Beetle (*Carabidae*) Grain fragments Terrestrial vegetation (Grass)
Marine/Intertidal	Crab (*Portunidae spp.)* Shrimp (*Crangonidae spp.*) Fish sp.

Breeding parameters

Model selection

Model selection for movement data was undertaken via AIC selection using the *ICtab* function from the "bbmle" package in R. Where multiple equivalent candidate models were within ΔAIC of 2.0, the simplest model was chosen as the minimum adequate model (**Bold**; Tables C12 – C15).

Table C12. Top five candidate models to explain egg volume ranked by AIC weight. MCS = maximum clutch size; WCVR = Within clutch volume rank; nestID

= unique nest ID. Pseudo-R^2 values for the selected model - $MR^2 = 0.247$, $CR^2 = 0.879$.

Model	AIC	dAIC	df	Weight
~ site + year + site*year + MCS + WCVR + (1|nestID)	**3625.7**	**0.0**	**10**	**0.5670**
~ site + year + MCS + WCVR + (1|nestID)	3627.8	2.1	9	0.1964
~ site + year + site*year + day_marked + MCS + WCVR + (1|nestID)	3627.8	2.1	11	0.1956
~ year + day_marked MCS + WCVR + (1|nestID)	3632.9	7.2	8	0.0158
~ site + year + day_marked + MCS + WCVR + (1|nestID)	3633.3	7.6	10	0.0127

Table C13. Top five candidate models for total clutch volume ranked by AIC weight. MCS = maximum clutch size. Selected model - Adjusted $R^2 = 0.8686$, $F = 409.2_{4,243}$, $p < 0.001$.

Model	AIC	dAIC	df	Weight
~ Site + year + MCS	**2048.5**	**0.0**	**6**	**0.569**
~ Site + year + MCS + site*year	2049.5	1.0	7	0.348
~ year + MCS	2052.9	4.4	5	0.062
~ Site + MCS	2055.2	6.7	5	0.020
~ MCS	2061.1	12.7	4	0.001

Table C14. Top five candidate models for IESV (cm^3) ranked by AIC weight. Selected model - Adjusted $R^2 = 0.06715$, $F = 8.198_{2, 198}$, $p < 0.001$.

Model	AIC	dAIC	df	Weight
~ year + Egg1_volume	**1042.6**	**0.0**	**4**	**0.622**
~ site + year + Egg1_volume	1044.5	1.9	5	0.242
~ site + year + site:year + Egg1_volume	1046.4	3.9	6	0.090
~ Egg1_volume	1048.5	5.9	3	0.032
~ site + Egg1_volume	1050.3	7.7	4	0.013

Table C15. The top five candidate models for chick hatching condition ranked by AIC weight. Day relates to the day of the year chicks were first measured. Pseudo-R^2 values for selected model - MR^2 = 0.110, CR^2 = 0.523.

Model	AIC	dAIC	df	Weight
~ site + year + site*year + 1|nestID	**1317.4**	**0.0**	**6**	**0.464**
~ site + year + site*year + day 1|nestID	1317.8	0.5	7	0.367
~ site + year + 1|nestID +	1320.9	3.6	5	0.078
~ year + 1|nestID	1322.2	4.9	4	0.040
~ site + year + day + 1|nestID	1322.6	5.3	6	0.033

IESV model estimates

Clutch asynchrony did not vary between breeding habitats but was higher in 2017 than 2018 at both sites (Fig. C5).

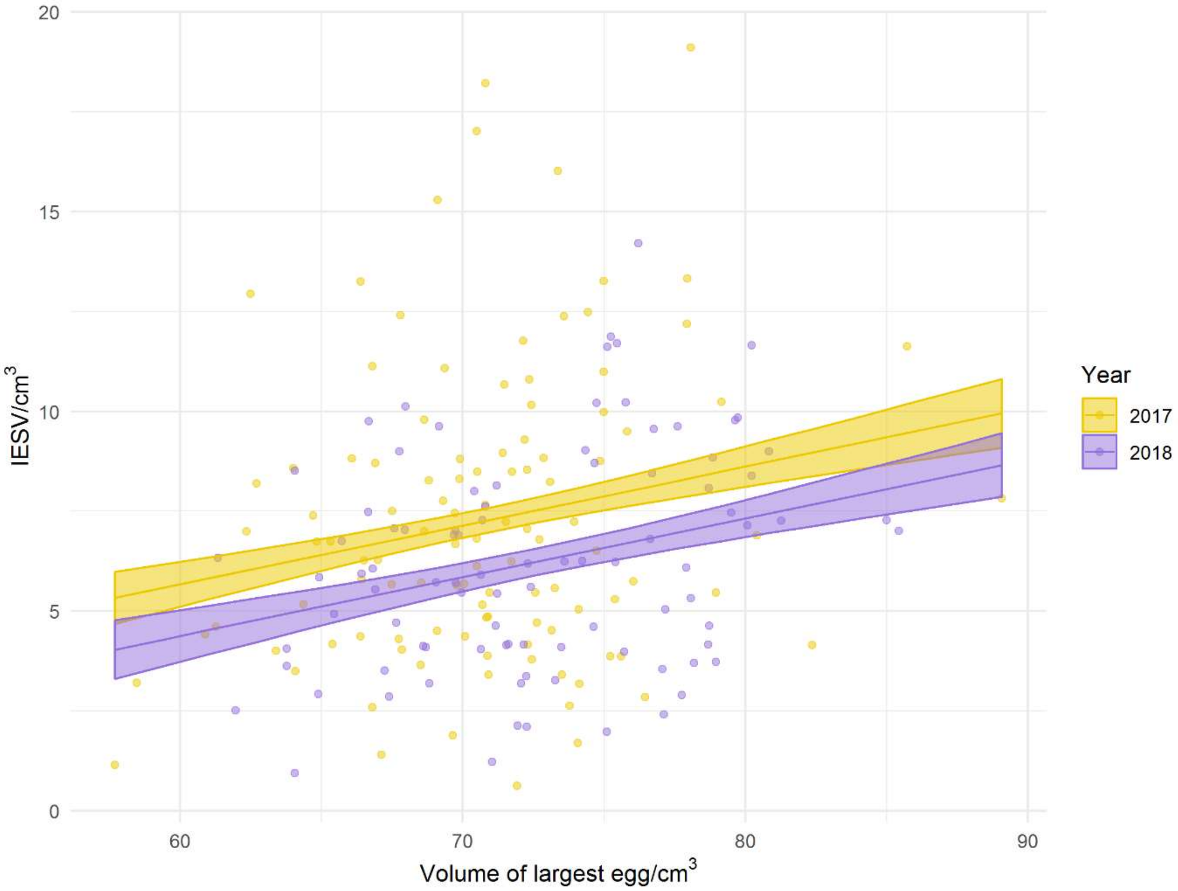

Figure C5. Fitted estimates ± SEs for IESV (cm^3) across all values of largest egg volume (cm^3) in both years. Points represent the raw data. IESV was higher in 2017 than 2018 revealing higher levels of within-clutch asymmetry.

Appendix D. Supplementary material for chapter 5

Colony-level trip metrics

Population-level summary statistics for five foraging trip metrics (trip duration, trip length, distal point distance, distal latitude and distal longitude) and sample sizes are presented for each colony in 2017 and 2018 (Table D1).

Table D1. Population-level means and standard errors for foraging trip metrics across all tracked birds at each colony in each year. N represents the number of individual gulls tracked at each colony in each year.

Colony	Behaviour	Mean ± se (2017)	Mean ± se (2018)
Ribble	Trip duration	7.40 ± 0.39	8.94 ± 0.57
	Trip length	45.49 ± 2.67	43.59 ± 3.46
2017 (n = 13)	Distal point	20.70 ± 1.14	19.67 ± 1.40
2018 (n = 9)	Distal latitude	53.61 ± 0.009	53.62 ± 0.011
	Distal longitude	-2.74 ± 0.014	-2.78 ± 0.017
Walney	Trip duration	10.76 ± 0.76	9.57 ± 1.22
	Trip length	37.37 ± 2.74	33.17 ± 4.48
2017 (n = 14)	Distal point	16.21 ± 1.09	12.26 ± 1.18
2018 (n = 8)	Distal latitude	54.10 ± 0.009	54.10 ± 0.011
	Distal longitude	-3.04 ± 0.014	-3.10 ± 0.012
Barrow	Trip duration	8.48 ± 0.66	7.84 ± 0.56
	Trip length	15.57 ± 1.58	17.23 ± 1.93
2017 (n = 14)	Distal point	6.49 ± 0.50	7.78 ± 0.89
2018 (n = 11)	Distal latitude	54.14 ± 0.004	54.13 ± 0.007
	Distal longitude	-3.19 ± 0.006	-3.17 ± 0.001

Individual repeatability – Model selection

Model selection for individual repeatability values was based on AICc values using the *ICtab* function from the “bbmle” package in R. Where multiple equivalent candidate models were within ΔAIC of 2.0, the simplest model was chosen as the minimum adequate model (**Bold**; Tables D2 – D6).

Table D2. Top five candidate models to explain individual repeatability of trip duration ranked by AICc weight.

Model	**AICc**	**dAICc**	**df**	**Weight**
R trip duration ~ 1	**66.3**	**0.0**	**1**	**0.740**
R trip duration ~ colony	69.9	3.5	3	0.126
R trip duration ~ year	70.2	3.9	2	0.105
R trip duration ~ colony + year	74.1	7.7	4	0.015
R trip duration ~ colony + year + colony*year	74.3	7.9	6	0.014

Table D3. Top five candidate models to explain individual repeatability of cumulative trip length ranked by AICc weight.

Model	**AICc**	**dAICc**	**df**	**Weight**
R trip length ~ colony + year	75.8	0.0	4	0.333
R trip length ~ colony	76.3	0.5	3	0.263
R trip length ~ year	77.2	1.4	2	0.164
R trip length ~ 1	**77.5**	**1.7**	**1**	**0.141**
R trip length ~ colony + year + colony*year	78.2	2.4	6	0.099

Table D4. Top five candidate models to explain individual repeatability of distal point distance ranked by AICc weight.

Model	**AICc**	**dAICc**	**df**	**Weight**
R distal point distance ~ colony + year	77.8	0.0	4	0.473
R distal point distance ~ colony	**79.4**	**1.6**	**3**	**0.217**
R distal point distance ~ year	80.3	2.5	2	0.136
R distal point distance ~ colony + year + colony*year	80.8	3.0	6	0.106
R distal point distance ~ 1	81.7	3.9	1	0.068

Table D5. Top five candidate models to explain individual repeatability of distal latitude ranked by AICc weight.

Model	**AICc**	**dAICc**	**df**	**Weight**
R distal latitude ~ year	96.5	0.0	2	0.5695
R distal latitude ~ 1	**97.7**	**1.2**	**1**	**0.3179**
R distal latitude ~ colony + year	100.8	4.3	4	0.0674
R distal latitude ~ colony	102.0	5.4	3	0.0378
R distal latitude ~ colony + year + colony*year	105.2	8.7	6	0.0074

Table D6. Top five candidate models to explain individual repeatability of distal longitude ranked by AICc weight.

Model	**AICc**	**dAICc**	**df**	**Weight**
R distal latitude ~ colony	**93.4**	**0.0**	**3**	**0.510**
R distal latitude ~ colony + year + colony*year	94.8	1.4	6	0.250
R distal latitude ~ colony + year	95.7	2.3	4	0.158
R distal latitude ~ 1	97.6	4.2	1	0.062
R distal latitude ~ year	99.8	6.4	2	0.021