

Abundance of urban Herring and Lesser black-backed gulls in Liverpool, UK

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1. Abstract

With increasing urbanisation, some wildlife species may face extinction or need to relocate, while others thrive in the urban environment. Urban gulls are a well-studied example of a wildlife that successfully adjusted to life in urban environments. However, their increasing numbers in urbanised spaces can intensify the human-gull conflict, which must be addressed by appropriate management strategies. One of the essential components in conflict mitigation is an understanding of the gull abundance, which was the aim of this study. Between January and December 2022, nine distance-limited count points were established in Liverpool, UK, where counts were conducted monthly. The study focused on the effect of environmental and anthropogenic factors, such as weather conditions, tides, land cover, human density, time of day, and season, on gull abundance. Data were then analysed to identify which factors impacted their numbers the most. The study shows an increase in gull numbers during afternoons coinciding with peak availability of anthropogenic food sources. Juvenile gulls were also more abundant in the evenings, potentially reflecting their adjustment to the times of lower intraspecific competition. It was also revealed that only juvenile Lesser black-backed gulls responded to a greater number of humans, which decreased their count. Higher temperatures also had a significant impact on the number of gulls, increasing their numbers. Overall, this study reveals the presence of species- and age-specific responses to anthropogenic and environmental factors, highlighting the need to recognise these differences and integrate them when planning human-gull conflict mitigation strategies.

2. Declaration

No portion of the work referred to in the thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

3. Acknowledgements

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4. Introduction

Avian abundance patterns are important, as they play a crucial role in understanding bird ecology, population dynamics, conservation status, and environmental changes (Davies et al., 2007; Fiedler et al., 2021; Bart, 2005; Koskimies, 1989). Avian abundance is influenced by a range of factors, including foraging patterns, breeding opportunities, anthropogenic pressures, and climatic factors (Spelt, 2020; Jokimäki et al., 2014; Isaksson et al., 2016). Habitats currently undergo global environmental change, including transformations in land cover and climate (EEA, 2024; Kitaysky and Golubova, 2000). These affect habitat structure, food availability and interactions between species (Arnfield, 2003; Ackerman et al., 2018; Beckerman et al., 2007). Species vary in their ability to adjust to these changes; some thrive in urbanised spaces, while others do not tolerate them and remain in rural areas (Rock, 2005; Blair, 1996). One of the most successful animals increasing in numbers in urban spaces are gulls, especially the Herring (*Larus argentatus*) and Lesser black-backed gull (*Larus fuscus*). With the increase in urbanisation, they began utilising food and nesting resources available in cities, abandoning coastal and marine habitats (Rock, 2005). Their increase in urban areas has heightened the human-gull conflict, putting pressure on local councils to develop effective management strategies to resolve it (Rock, 2005; Belant, 1997). Understanding their patterns of abundance in the changing environment would allow for better mitigation of human-gull conflict. In the following introductory literature review for this thesis, I will explore the impact of key anthropogenic and environmental factors on gull abundance.

4.1 Urbanisation

Urbanisation impacts humans and animals alike. Urbanisation is characterised by a substantial number of people relocating to cities and abandoning rural areas (EEA, 2024). Currently, 58.2% of the world's human population resides in urban areas, and this number is increasing annually (UN, 2014; UN, 2024). This relocation leads to changes in land cover, aiming to accommodate a larger human population in cities and towns. Land cover change alters the natural habitat, affecting both the human population and ecosystems, as well as biodiversity (for example, Joon & Shahrawat, 2016; Wiederkehr et al., 2020). Urbanisation impacts animals positively and negatively alike. Blair (1996) categorised birds in urban areas into those that exploit, avoid, or adjust to the anthropogenic landscape. These responses to environmental changes eventually affect birds' population size, biodiversity, foraging, and breeding behaviours (for example, Prugh et al., 2009; Taylor et al., 2013; Cooke, 1980; Traut & Hostetler, 2003). Urbanisation's impact on birds will be discussed in more depth in the following sections.

4.1.1 Foraging

The high availability of anthropogenic food in urban areas can have both negative and positive effects on bird populations (for example, Shochat et al., 2010; Smith & Carlile, 1993). Living near humans provides animals with easy access to intentionally supplied food, for example through bird feeders used by species such as Blue tits *Cyanistes caeruleus* (Contesse et al., 2004; Støstad et al., 2017). Food access can also become available unintentionally through access to refuse tips or fisheries waste, which may provide more predictable food sources than natural ones (Huig et al., 2016; Bicknell et al., 2013). Streetlights in cities enable birds such as the Feral pigeon *Columba livia domestica* to forage for longer even after sunset, which is not possible in rural areas (Leveau, 2020). Animals living in cities can advance their breeding dates due to increased food availability, which can enhance their breeding performance (for example, O'Leary & Jones, 2006; Kettel et al., 2018). Certain species, including Silver gulls *Chroicocephalus novaehollandiae*, can shift their diet to predominantly anthropogenic food sources (Smith & Carlile, 1992; 1993). Increased and predictable food availability in urban spaces may increase the chances of survival and thus productivity, leading to increased population size and changes in the abundance of certain species such as Wood stork *Mycteria americana* (Seress and Liker, 2015; Evans and Gawlik, 2020; Kettel et al., 2018). By contrast, increased food availability in cities may also have a negative impact on wildlife. For example, supplementary feeding can facilitate pathogen transmission within House finch *Haemorrhous mexicanus* populations because of their increased aggregation at feeders and exposure to contaminated surfaces (Schaper et al., 2021; Jones and Reynolds, 2008). Supplementary feeding can also increase the abundance of introduced species such as the House sparrow *Passer domesticus* and the Spotted dove *Streptopelia chinensis* within urban environments in New Zealand (Galbraith et al., 2015).

There is evidence that in some species, such as the American Crow *Corvus brachyrhynchos*, juveniles fed anthropogenic food can be smaller than their rural counterparts, due to the poor nutritional value of the food, rather than its quantity (Heiss et al., 2009). In species such as Blue tits *Cyanistes caeruleus*, fat-rich food supplementation negatively affected breeding performance in the following year (Plummer et al. 2013; Harrison et al., 2010). Another consequence of urbanisation is that insects and fish may accumulate heavy metals in their bodies, and when consumed by birds such as the Great egret *Ardea alba*, may impact their health (Pandiyan et al., 2025). Birds can also learn to choose anthropogenic foods over natural ones. White storks *Ciconia Ciconia*, for example, travel further to landfill sites to obtain anthropogenic food, which is more energy efficient, but in the event of landfill closures, birds can face a drastic, unexpected reduction of food resources, which will impact their breeding outcomes (Soriano-Redondo et al., 2021; Marcelino et al., 2023). These hazards and potential threats impact population density and ultimately affect the abundance of the species (Seress and Liker, 2015).

4.1.2 Breeding and Population

Understanding the effect of urbanisation on avian breeding is important for recognising the advantages and disadvantages of life in urban areas. Firstly, it may be more difficult to find a mate in cities due to habitat fragmentation and noise pollution, which interfere with the songbird mating process (Slabbekoorn and Peet, 2003; Dale, 2001). Artificial light pollution in cities can disrupt the circadian rhythms of birds, affecting the timing of their courtship singing and, consequently, the mating process (Miller, 2006). For example, species such as the American robin *Turdus migratorius* were affected by artificial light pollution, and they commence their morning songs during the true night, indicating a change in behaviour (Miller, 2006). Mating is followed by nesting, which may also differ in urban spaces. Birds can find many suitable replacements for their natural nesting habitats in the form of chimneys, roofs and buildings (Tomiałojć, 1970; Emlen, 1974; Jokimäki et al., 2014). For example, the House sparrow *Passer domesticus* nests on the clips of the gutter-spouts or in park lamp casings, replacing natural nesting sites (Indykiewicz, 1990). A good example of a bird that has increased in abundance in urban areas, due to greater availability of breeding sites, is the Lesser black-backed gull *Larus fuscus*, which colonised flat rooftops across the UK, replacing open, flat ground, typically used for nesting in natural habitats (Rock, 2005; Raven and Coulson, 1997; Calladine, 1997).

Studies on productivity in urban environments have yielded contradictory results; in some urban species, productivity increased, while in others, it decreased (for example, Boal and Mannan, 1999; Kettel et al., 2018; Tella et al., 1996; Frey et al., 2011). For example, in Crested goshawks *Accipiter trivirgatus*, reduced predation in urban areas compared to rural spaces resulted in increased survival of fledglings (Lin et al., 2015). Bird populations inhabiting urban spaces are usually denser than those in rural areas, because of more reliable access to foraging material and reduced predation (for example, Evans et al., 2011; Fuller et al., 2008; Eötvös et al., 2018; Møller et al., 2012). Higher population density might affect breeding performance through density-dependent processes. For example, in colonial species, such as Cliff swallows *Petrochelidon pyrrhonota*, increased density can enhance productivity through improved information transfer, which leads to increased foraging efficiency and therefore higher chick provisioning (Brown, 1988; Rueda and McGraw, 2025). At the same time, higher bird density increases competition in cities, which can negatively affect bird productivity by reducing access to resources (Simons and Martin, 1990; Solonen, 2001). For example, in Great tits *Parus major* and Blue tits *Cyanistes caeruleus* high density and increased competition for resources have been associated with reduced clutch sizes (Solonen, 2001).

4.1.3 Population and abundance

The population and abundance of birds may also be affected by urbanisation. Abundance is defined as the number of individuals from one or several species in a specific area at a specific time (Preston, 1962; Parmesan et al., 2005).

Population size and density, their increases and decreases, affect the distribution and abundance of birds (Santini et al., 2023; Matthysen, 2005). Every population exists within a

fluctuating carrying capacity, which is determined by the habitat and available resources, including, for example, food supply and nesting sites (Newton, 1998). These resources are not evenly distributed throughout the habitat, which may affect differences in the abundance and distribution of birds (Newton, 1998). For example, European kestrels *Falco tinnunculus* did not breed if there were no available nesting sites in the area (Village, 1983). Factors which further impact populations are density-dependent (competition, predation) and density-independent (weather, climate change, floods, fires) (Newton, 1998). Density-dependent factors influence the number of individuals that will remain in a given habitat, fluctuating in accordance with rates of immigration, emigration, births and deaths (Newton, 1998). Additionally, site-dependent regulation mechanisms suggest that resource availability might not be the sole determinant of abundance; habitat saturation may prevent individuals from residing when optimal habitats reach their capacity (Rodenhouse et al., 1997; Marra and Holmes, 2001). For example, dominant individuals of American redstart *Setophaga ruticilla* aggregate in the high-quality parts of the habitat, forcing subordinates to the lower-quality spaces (Marra and Holmes, 2001). Consequently, the impact of density dependence on bird abundance is not a simple mechanism, but a nuanced feedback loop shaped by the interaction between birds' behaviours and the environment (Hixon & Johnson, 2009; Newton, 1998).

Distribution and abundance are positively correlated, meaning that animals with higher abundance are found in more habitats (Gaston, 1996; Brown, 1984). That said, this correlation is not always linear across all habitats. Some bird species can commonly occur in many habitats, yet their abundance is low (Gaston et al., 2000). If immigration and births increase, the population grows; if deaths and emigration increase, the population decreases (Newton, 2007). Species that are declining usually have fragmented distributions, while species that are increasing have more highly aggregated population structures, which are primarily influenced by habitat type and land use changes (Sirami et al., 2009). In some species, bird distribution is linked to the current population size, and it changes in response to fluctuations in the population, which can occur annually (Hinsley, 1996). If the population of a species decreases, the remaining birds are more likely to emigrate or die (Hinsley, 1996). The low density further decreases the breeding outcomes, which reduces chances for recolonisation. If the population is too large, food availability will eventually decrease, predator-prey relationships will change, or some individuals will migrate (Rodenhouse et al., 2003; Oro et al., 2006). In urban spaces, populations can also be impacted by humans. These include human disturbance, such as closing landfills or an increasing number of roads and buildings (Rock, 2005; Belant, 1997). Some of these can increase, and others decrease the population size.

4.1.4. Land cover and land cover change

Land cover and land cover change significantly impact bird abundance in all habitats, particularly in urbanised areas (Chace & Walsh, 2006; Patankar et al., 2021). Land cover refers to the Earth's surface, which encompasses various physical and biological components, including water bodies, forests, vegetation, buildings, roads, and agricultural fields (Foody, 2002; Lambin et al., 2001). Land cover change refers to the alteration of the land's surface over time, caused by environmental

and anthropogenic processes such as deforestation, urbanisation, or the expansion of agricultural fields (Lambin et al., 2001; Nagendra et al., 2004).

Various land cover categories have different levels of suitability as bird habitats, varying in their vegetation structure, microclimates, and accessibility to shelter, food, and nesting resources (Chace & Walsh, 2006; Patankar et al., 2021). The abundance of birds also varies across different categories of land cover (Zhai et al., 2024). Highly urbanised areas attract generalist birds, including gulls, *Larus spp.*, Rock doves *Columba livia* and Eurasian magpies *Pica pica* (Chamberlain et al., 2007; Chiron and Julliard, 2007; Gendall et al., 2015). They can adjust their diets and nesting behaviours to their surroundings by, for example, foraging on anthropogenic foods and nesting on buildings (Rock, 2005; Spelt, 2020). Specialist birds which are dependent on, for example, forested landscapes for foraging and nesting may not be able to move to other places with different land cover (Wolff et al., 2018; Chace and Walsh, 2006). These two different behaviours can contribute to varying spatial distributions and changes in abundance across different land covers and may put some species at a disadvantage, leading to biotic homogenisation across urban spaces (for example, Chace and Walsh, 2006; Wolff et al., 2018; Lokatis and Jeschke, 2022).

Therefore, land cover change can also lead to vast ecological shifts, including changes to bird distribution and abundance (Zhai et al., 2024; Chace and Walsh, 2006). Alterations in the plant cover may lead to changes in food availability, for example, through changes in insect abundance, which could eventually affect birds and their abundance (Buchanan et al., 2016; Huang et al., 2015). The Eurasian hoopoe *Upupa epops* forages on insects, including beetles belonging to Coleoptera, and may be affected by changes in vegetation, as shifts in plant coverage influence insect abundance and eventually food availability for Eurasian hoopoe (Huang et al., 2015). Additionally, habitat fragmentation, which includes the construction of roads, agricultural expansion, and deforestation, can further impact birds and their abundance (Watson et al., 2005; Reino et al., 2013; Mortelliti et al., 2010). Disrupted habitats alter the movement of birds, which consequently impacts breeding by reducing access to food and nesting sites available in the given area, exposing birds to increased predation and elevating their stress levels (Evens et al., 2018; Berg, 1997; Robinson, 2023). For example, Wedge-billed woodcreepers (*Glyphorhynchus spirurus*) were not able to reach their destination when forest gaps were of 100 m or more, demonstrating that habitat fragmentation impacts their movement (Ibarra-Macias et al., 2011). Therefore, it is essential to understand how land cover and its changes affect the abundance of birds, particularly during periods of increasing urbanisation.

4.1.5 Human-wildlife interactions

Human-wildlife interactions can be positive, negative or neutral. Most interactions between wildlife and humans occur in suburbanized areas (for example, Kretser et al., 2008; Soulsbury and White, 2015; Merkle et al., 2011). There has been an increase in human-wildlife conflict, which has led to increased research interest in this issue (for example, Messmer, 2000; Treves et al., 2009; Nyhus, 2016; Barua et al., 2013).

One area of conflict is the direct physical injury of humans or birds. Attacks by birds on humans and their pets are mostly performed to protect nests or young, in self-defence, or while obtaining food (Parker, 1999; Jones and Thomas, 1999; Belant, 1997). For example, Australian magpies *Cracticus tibicen* engage in swooping behaviours toward humans during the breeding season as a form of brood defence (Warne et al., 2010). On the other hand, birds can also die or get injured by humans (Klem, 2009; Ogden, 1996). These human-related pressures can include population size control by roadkill and predation from domestic cats, which significantly impact bird populations (Anderson, 2010; Rowden et al., 2008; Beckerman et al., 2007). Species such as the Common blackbird *Turdus merula*, experience some of the highest predicted mortality rates due to vehicle collisions (Grilo et al., 2020).

Another category of negative human-wildlife interactions includes property damage, nuisance behaviour, and public health issues. Bird-related property damage varies in degree of severity (Coluccy et al. 2001; Rodríguez, 2022). For example, Feral pigeons *Columba livia domestica* may dislodge the roofing material, and where large roosts are present, the accumulation of their faeces can corrode buildings, leading to structural damage and hygiene concerns (Spennemann et al., 2017; Magnino et al., 2009; Jadhav and Narkhede, 2025). The nuisance behaviours among birds can include loud noise and attacking people and food vendors, which are usually caused by the presence of food (Charles and Linklater, 2015; Belant, 1997). Bird presence, for example, of *Larus spp.* is also an issue around airports where they get trapped in aircraft engines and, in effect, caused US civil airlines \$20 million losses between 1990 and 2003 (Belant, 1997; Cleary et al., 1997). The spread of zoonotic or vector-borne diseases is another issue common in human-wildlife interactions (Bengis et al., 2004; Daszak et al., 2000; Vora, 2008). Some diseases can be spread between birds and humans through faeces (e.g., Newcastle Disease Virus – Blanco-González et al., 2024), saliva (e.g., *Salmonella* strains - Martín-Maldonado et al., 2020) or air (e.g., avian influenza- Spencer et al., 2020). These diseases can be transmitted to humans and cause health issues or even be fatal (Capua and Alexander, 2004).

Interaction with wildlife can also be positive and have a beneficial impact on human well-being, health, and academic development (Tzoulas et al., 2007; Sandifer et al., 2015; Magle et al., 2012). A particularly enjoyable activity across the Western world is supplying bird food in the feeders (Jones and Reynolds, 2008; Fuller et al., 2008). Feeding birds, such as House sparrows *Passer domesticus*, in the gardens was especially important during the COVID-19 pandemic when social interactions were limited (Doremus et al., 2023; Roll et al., 2021). Urban wildlife can also be beneficial, for example, in reducing insects in gardens (Orros and Fellowes, 2012) or by removing large rodents such as rats through predation by birds of prey such as Barn owl *Tyto alba* (Hindmarch and Elliott, 2015). Moreover, Hummingbirds *Trochilidae* contribute to pollination; Blackcap *Sylvia atricapilla* and Blackbird *Turdus merula* species can contribute to seed distribution (Anselmo et al., 2023; Cruz et al., 2013).

Species increasing in urban areas include Herring *Larus argentatus* and Lesser black-backed *Larus fuscus* gulls, which are the focus of this thesis. An increase in their population in urban areas may lead to more interactions with humans, some of which may be negative. Many private companies, as well as city councils, deal with the nuisance behaviours of gulls, and some of them

are described in the local press (Aberdeen City Council, 2024; North Yorkshire Council, 2024; Rock, 2012; Slow, 2023; Russel, 2024). Human-gull conflicts also include property damage, loud noise, and threats to public health, similar to those of other bird species (Belant, 1997; Rock, 2005).

Councils and private companies employ a range of lethal and non-lethal gull deterrent methods. To reduce property damage, spikes are often placed on top of buildings to prevent gulls from landing and causing damage through droppings (Trotter, 2019; Raven, 1997). Some building owners install netting around roofs to deter gull nesting, but it is usually not effective (Rock, 2005; Lowney, 2018). Councils are interested in reducing gulls' access to anthropogenic food sources. This can be done by covering the landfills, installing wires around them or using birds of prey to deter gulls (Belant, 1997; Rock, 2004). These methods may be effective for a short period, but they are also very costly, and over time, gulls learn to ignore them (Baxter & Robinson, 2007; Soldatini et al., 2008). To drastically reduce the number of gulls, lethal methods are employed, such as egg oiling, culling, or nest removal (Ross-Smith et al., 2014; Belant, 1997; Rock, 2005). Lethal control techniques may significantly influence population dynamics by accelerating population declines (Coulson and Coulson, 2009; Lopez et al., 2025). A population modelling study of Scottish gulls demonstrated that the level of licensed control might have a strong effect on the population trajectories (Lopez et al., 2025). Scenarios incorporating licensed control implemented in Scotland between 2020 and 2023 resulted in population declines and, in the case of the Great black-backed gull, led to projected local extinction within 25 years (Lopez et al., 2025). The model also demonstrated that sustained levels of licensed control could drive declines even in species with initially increasing populations, such as Lesser black-backed gulls (Lopez et al., 2025). These findings highlight the sensitivity of gull population trends to the intensity of lethal control. Lethal and non-lethal techniques can be effective in temporarily reducing the number of gulls, but they do not eliminate this human-gull conflict (Belant, 1997; Rock, 2012; Baxter & Robinson, 2007; Soldatini et al., 2008). Understanding the behaviour of urban gulls and factors impacting their abundance can help reduce this human-gull conflict.

4.2. Herring and Lesser black-backed gulls

Herring and Lesser black-backed gulls are examples of avian species increasing in urbanised areas. They successfully colonised anthropogenic landscapes due to their behavioural flexibility and generalist diet, which enabled them to explore new resources and utilise them (Spelt, 2020). Their increasing numbers in cities have led to an escalation in human-gull conflicts, which is especially evident in conflict “hotspots” characterised by a high abundance of gulls (Rock, 2005). These conflicts create a challenge for public health, infrastructure and urban management, which requires efficient solutions to be implemented by local councils and relevant stakeholders. This can be achieved by studying the factors that impact the abundance of urban gulls. This knowledge can enable the development of better-informed urban management strategies to mitigate human-wildlife conflict in cities. The following section will provide an overview of the current state of knowledge about both gull species.

4.2.1 Population numbers in Britain and Ireland

Herring gulls live in Northern and Western Europe and the UK (Malling-Olsen and Larsson, 2003). They include both resident and migrant populations; Herring gulls breeding in the UK are residents, whereas those breeding in northern Europe often migrate south (Mitchell et al., 2004; Malling-Olsen and Larsson, 2003). The species is classified as declining – red - on the Birds of Conservation Concern list (Stanbury et al., 2021). Lesser black-backed gulls coexist with Herring gulls, often in mixed colonies. Similar to Herring gulls, they breed in Northern and Western Europe (Malling-Olsen and Larsson, 2003). They are a migratory species which also breeds in Central and Northern Europe but migrates mainly to North Africa or Southern Europe during the winter (Malling-Olsen and Larsson, 2003). This species is classified as amber on the Birds of Conservation Concern list; however, in the European classification, it is categorised as least concern (Stanbury et al., 2021; BirdLife International, 2024). Both species are widely distributed across Britain and Ireland, occupying coastal regions, inland habitats, marshes, and increasingly, urban areas, yet both species are declining in the same regions (Malling-Olsen and Larsson, 2003).

Research indicates that resource availability is a crucial factor in selecting a breeding location, as it can enhance the success rate of breeding gulls (for example, Visser et al., 2006; Arcese and Smith, 1988; Møller et al., 2008). In natural colonies, Herring gulls nest on cliffs and rocky sites with no vegetation, while Lesser black-backed gulls usually nest in open spaces and cliffs with plant cover (Rock, 2005; Hosey and Goodridge, 1980). Urban gulls may nest on various structures across urban spaces. They utilise flat roofs of industrial buildings, sloping roofs of houses, and chimney stacks (Rock, 2005; Coulson & Coulson, 2009; Raven, 1997; Sellers & Shackleton, 2011). Yet, it is unclear whether roof-nesting has a positive impact on the breeding outcomes of all gull species. Some studies indicate that there are more chicks hatched in natural colonies than in colonies nesting on rooftops (Belant et al., 1998; Perlut et al., 2016). Other studies report higher productivity in urban populations than in non-urban areas, including those of a few different gull species (for example, Kroc, 2018; Zelenskaya, 2019). This contrast can be explained by different human disturbance levels, predation, and gull density between the sites (Perlut et al., 2016). Gulls also breed in cities due to the lower number of terrestrial predators, such as Red foxes *Vulpes vulpes*, and aerial predators, including birds of prey (Rock, 2005; Belant, 1997). Lower nest densities in urban spaces compared to rural areas are associated with reduced cannibalism rates, particularly affecting chicks and eggs (Monaghan, 1979; Perlut et al., 2016). Herring and Lesser black-backed gulls across the Britain choose to breed in urban spaces for many reasons, one of which is the higher temperatures in built-up areas (Arnfield, 2003; Rock, 2005). Higher air temperatures in cities may contribute to earlier breeding in urban populations of Herring and Lesser black-backed gulls compared with their rural counterparts, as observed in other birds, such as Florida scrub-jays *Aphelocoma coerulescens* (Rock, 2005; Capilla-Lasheras et al., 2022; Fleischer et al., 2003).

The increase in urban gull populations may also be caused by an improved availability of anthropogenic food sources, fewer predators, and longer visibility to find food resources due to streetlights (Spaans, 1971; Rock, 2005; Faria et al., 2022). Licensing for culling gulls has also

become stricter in recent years, partly due to the declining gull population (Defra, 2020; Burnell et al., 2021).

The majority of studies cite Operation Seafarer (Cramp et al., 1974), the Seabird Colony Register (Lloyd et al., 1991), Seabird 2000 (Mitchell et al., 2004), and the most recent Seabirds Count (2015-23; Burnell et al., 2023) as sources of estimated gull population size in Britain and Ireland. They counted AONs (apparently occupied nests). The inland colonies were counted only from 1998-02 (Mitchell et al. 2004).

Early records indicate that the Herring gull population increased by 13% between 1930 and 1970, due to reduced human persecution and possibly increased availability of anthropogenic food; however, since 1970, their population has been declining (Coulson, 2015; Coulson, 1991). Further surveys show a steady decline of Herring gull AONs of around 1% per year between 1969 and 2000 (Nager and O'Hanlon, 2016). There were 283,874 AONs in the 1969-1970 survey, which decreased to 142,942 AONs in 2000 (Cramp et al. 1974; Mitchell et al. 2004). This decline might have been caused by botulism, excessive culling, or changes in landfill practices (Coulson, 2015). The newest Seabirds Count (2015-23) showed that the number of Herring gulls in Britain and Ireland was 237,573 AONs across urban and natural nesting sites combined, and 61,077 AONs in natural sites only, which represented a decline of 44% since 2000 (Burnell et al., 2023). The decline of Herring gulls in their natural colonies has several possible reasons, including changes in natural food sources (Coulson, 2015; Nager & O'Hanlon, 2016).

In contrast, the number of AONs of Lesser black-backed gulls increased from 48,352 AONs in 1969-1970 to 111,835 AONs in 1998-02 (Cramp et al. 1974; Mitchell et al. 2004). In 2015-23 there were around 324,465 AONs (55,304 AONs in natural colonies, 269,161 AONs in urban colonies) across Britain and Ireland (Burnell et al., 2023).

Gulls nesting on rooftops can be spotted across European countries such as Italy, Poland, Bulgaria, France, or Austria (for example, Nankinov, 1992; Kajzer, 2012; Soldatini et al., 2008; Litwiniak et al., 2021). Gulls may relocate to urban areas due to nesting opportunities on buildings, increased food availability, and a reduced number of predators compared to rural areas (Nager and O'Hanlon, 2016). The breeding of urban gulls is believed to have started in Britain and Ireland between the 1940s and 1960s (Monaghan and Coulson, 1977; Cramp, 1971). The first known data on that matter showed that around 63 and eleven roof-nesting colonies of Herring gulls and Lesser black-backed gulls, respectively, were identified in Britain and Ireland in 1976 (Monaghan and Coulson, 1977; Mitchell et al., 2004). The number of urban gulls began increasing yearly in the second half of the 20th century; this may have been caused by anthropogenic food sources, which could facilitate breeding outcomes (Raven and Coulson, 1997). Birds were leaving overcrowded rural colonies and could have achieved a high breeding success rate in urban spaces (Chabryzk and Coulson, 1976; Monaghan and Coulson, 1977).

The number of roof-nesting Herring gulls in Britain and Ireland included 2,944 AONs in 63 colonies in 1976, and this number increased to 19,953 AONs in 218 colonies in the 1999-2002 census (Mitchell et al., 2004) and to 176,496 AONs in 2015-23 (Burnell et al., 2023). The number of Herring gulls is increasing as a roof-nesting bird, but its numbers are falling in the overall

population (Mitchell et al., 2004; Stanbury et al., 2021). The number of roof-nesting Lesser black-backed gulls was 325 AONs in eleven colonies across Britain and Ireland in 1976, and it increased to 10,790 AONs across 125 colonies in 1999-02 (Mitchell et al., 2004). In the 2015-23 survey, this number increased to 269,161 AONs for Lesser black-backed gulls (Burnell et al., 2023).

Calculating population trends of roof-nesting urban gulls was not conducted in the Seabirds Count (2015-23) survey due to issues with traditional methods used in urbanised landscapes (Burnell, 2021). Nest detectability in cities differs according to the building height and other variables, which were not identified in the Seabird 2000 Census, as the location of vantage points leads to an underestimation of AONs in that survey (Mitchell et al., 2004; Burnell, 2021; Coulson and Coulson, 2015). According to Rock (2005), the number of roof-nesting gulls was estimated to be around 100,000 in 2005.

The census data for the Merseyside region and Liverpool are fragmented. The first reports of urban roof-nesting gulls of both species colonising Liverpool in 1976 recorded more than 18 nests, which were not recorded anywhere else in Merseyside (Raven and Coulson, 1997). The next available data were collected in 1993-95, which recorded 18 breeding pairs (rooftop nesting) of Lesser black-backed gulls, which may have been underestimated (Raven and Coulson, 1997). There were 51 AONs recorded in two colonies of roof-nesting Lesser black-backed gulls in Merseyside in the Seabird 2000 survey (Mitchell et al., 2004). In the most recent survey (2015-23), only three AONs were recorded in natural sites across Merseyside, with no recorded nests on rooftops (Burnell et al., 2023).

One AON of the roof-nesting Herring gulls was recorded before 1976 (Monaghan and Coulson, 1977). This increased to 20 breeding pairs after 1976 (Raven and Coulson, 1997), and in 1999-2002, there were 59 AONs in two colonies in Merseyside (Mitchell et al., 2004). The most recent survey recorded no Herring gull AONs in Merseyside (Burnell et al., 2023). The Seabirds Count did not record any Herring gull nests in the Merseyside region because, at the time of the census, six surveyed sites did not have any AONs (D. Burnell, personal communication, March 13, 2025). I supplemented the national survey with the Seabird Monitoring Programme, which showed eleven AONs of Herring gulls and 16 AONs of Lesser black-backed gulls in 2019/20 across Merseyside (JNCC and BTO, 2024). Liverpool gulls are well known for their nuisance behaviour and often appear in media reports; however, their abundance and factors influencing it have not been thoroughly examined (for example, Thorp, 2024; BBC Radio Merseyside, 2023; BBC News, 2020). Residents of Merseyside and Liverpool often complain about people and pets being attacked, properties being damaged, and rubbish bins being opened (Thorp, 2024; BBC Radio Merseyside, 2023; BBC News, 2020). Although Merseyside gulls are often the subject of media attention and public concern, there is a gap in the literature regarding their abundance and the factors that impact it. Further examination of gull behaviour in Liverpool will contribute to mitigating human-gull conflict, often present in coastal cities in Britain and Ireland.

4.2.2 Foraging

Foraging is considered one of the most significant factors influencing the abundance of gulls. Both gull species eat food resources of terrestrial, marine, or anthropogenic origin (Gyimesi et al., 2016; Isaksson et al., 2016; Camphuysen, 2013). They are both foraging generalists and opportunistic scavengers; however, the Lesser black-backed gull relies more on marine food resources, while the Herring gull prefers food found on land and in the intertidal mudflats (Kim & Monaghan, 2006; Camphuysen, 2013; Bustnes et al., 2010; Shlepr et al., 2021). Herring gulls, while foraging on natural resources, feed on intertidal mudflats, lakes, and terrestrial spaces like fields and agricultural lands (Spelt, 2020; Rock et al., 2016). They also use refuse tips, water treatment plants, urbanised areas, and fishery discards (Pons, 1992; Camphuysen, 1995; Spelt, 2020). Gulls choose food based on availability, nutritional content needed and competition; these aspects differ in rural and urban areas (Washburn et al., 2013; Sherley et al., 2020; Isaksson et al., 2016; Bond, 2016). Gulls in both rural and urban spaces eat earthworms, eggs and chicks, small rodents, and insects (Nager and O'Hanlon, 2016; Monaghan and Coulson, 1977). However, urban gulls also rely on anthropogenic foods, such as fried chicken, bread, fries, fishery discards, or other general waste (Camphuysen, 1995; Raven, 1997; Coulson & Coulson, 2008; Washburn et al., 2013; Nager and O'Hanlon, 2016; Monaghan and Coulson, 1977).

If gulls cannot obtain preferred food, they rely on lower-quality food or sources which require more energy to obtain (Kitaysky et al., 2006). Sometimes, they may choose anthropogenic food sources because of their availability and predictability, which is not always the case with natural sources, such as marine foods (Lato et al., 2021). Settling for lower-quality food resources may impact chick condition, egg quality, or reduce the number of successfully fledged chicks (Hiom et al., 1991; Kitaysky et al., 2006; van Heezik, 1990). Yet, other studies do not report any negative consequences on breeding performance caused by low-quality food (for example, Hjernquist and Hjernquist, 2010; Serré et al., 2022). The decreased breeding performance observed in some studies may be attributed to the amount of food, energy, and parental ability to forage; food quality may not be the sole factor (Greig et al., 1983; Sotillo et al., 2019). Some studies have shown that marine foods provide higher nutritional value for breeding; however, gulls in Cumbria did not breed when access to landfills was limited, which may indicate their reliance on anthropogenic foods instead of natural ones (Pierotti and Annett, 1987, 1991; Bêlant et al., 1993; Bertellotti and Yorio, 1999).

Changes in the foraging behaviour show how the environment around gulls has altered (O'Hanlon, 2016). Gulls adjust to tidal (Irons, 1998), circadian (Spelt, 2020) or seasonal (Burger and Galli, 1987) food availability changes, but they can also follow patterns dictated by human behaviour, such as new food waste delivery to the landfill (Sibly and McCleery, 1983; Ouled-Cheikh et al., 2020). Gulls may choose foods in urban areas when they see humans eating the same food (Feist et al., 2023; Goumas et al., 2020). In some cases, urban gulls alter their foraging patterns during the breeding season; they spend more time in urban and suburban spaces during incubation and chick rearing, as they can gain more energy-dense food from anthropogenic sources than from marine ones (Spelt, 2020). They can also adjust their movement and foraging schedules to align with shift work patterns in mines or fisheries (Parra-Torres et al., 2020; Ouled-Cheikh et al., 2020).

On the contrary, there are also reports of humans acting as deterrents (Ikuta and Blumstein, 2003; Parra-Torres et al., 2020).

Historically, knowledge of gulls' movements relied on ringing data and diet samples; the recent deployment of GPS tracking devices has enabled a much finer-scale understanding of their movement ecology (Spelt, 2020; Isaksson et al., 2016; Langley et al., 2023). The comparison between coastal and urban Lesser black-backed gulls showed that gulls nesting in coastal areas actively avoided urban spaces (Langley et al., 2023). In contrast, urban nesting gulls preferred to forage in urban areas, showing strong colony-level segregation (Langley et al., 2023). However, the tracking study conducted on urban Lesser black-backed gulls in Bristol, UK, has shown a more nuanced perspective on urban gull populations and their movement (Spelt, 2020). This research demonstrated that urban nesting gulls rarely forage exclusively within the city boundaries (Spelt, 2020). Urban gulls rarely chose marine food sources even when they were within ten kilometres of their nest, and they preferred urban, suburban and rural green spaces (Spelt, 2020). Moreover, Spelt (2020) identified that urban gulls exploited urban and suburban areas more frequently between incubation and chick rearing than at other parts of the breeding season, suggesting increased nutritional needs. While Langley et al. (2023) highlight segregation between the urban and natural colonies, Spelt (2020) demonstrates that reproductive demands also impact the movement of gulls within urbanised spaces. This indicates that the foraging behaviour of Lesser black-backed gulls is driven by a combination of colony tendencies as well as time-dependent adjustments.

Scavenging occurs in both urban and rural areas, but in urbanised spaces scavenging may be a behavioural response to changing land cover that alters resource distribution (Belant, 1997). Scavenging may allow gulls to exploit the proximity to humans for foraging and obtaining predictable food sources (Camphuysen & Garthe, 2000; Belant, 1997). Variations in food availability can differently impact the behaviour and abundance of these two species, yet there may be interspecific competition between them, especially when they live in the same colony (Mudge and Ferns, 1982; Bukacinska et al., 1996; Garthe et al., 1999a; Kim and Monaghan, 2006a). An adult Herring gull needs around 336 kJ per day, which makes it around six trips to mussels and one and a half trips to the refuse tip (Lasiewski and Dawson, 1967; Pierotti and Annett, 1991). It was reported that Herring gulls increased their intake of anthropogenic food and plastic debris from 2% in the 1970s to 34% in the 2010s, which may contribute to poor hatching success and partially affect distribution and abundance (Bond, 2016).

It is unclear whether anthropogenic food affects adults as well; however, one short-term study has shown that this diet negatively alters gulls' fatty acid compositions and white blood cell count, which may lead to long-term health problems (Lopes, 2021; Annett and Pierotti, 1999). The advantage of anthropogenic food is its continuous availability in contrast to periodically available natural resources (Pierotti and Annett, 1991; Carmona et al., 2021; Burger and Galli, 1987). This may encourage them to continue foraging on anthropogenic resources, especially during the breeding season (Pierotti and Annett, 1991).

4.2.3 Environmental factors

Various environmental conditions, as well as the circadian and seasonal cycles, determine the abundance of gulls (Zorrozuza et al., 2020; Burger, 1983; Spaans, 1971; Burger, 1976). Time of day impacts the behaviour of gulls; they are more active throughout the daytime and are more likely to rest at night (Beauchamp, 2009; Hébert and McNeil, 1999; Lavin et al., 2003). They can also adjust to human activity patterns, increasing their chances of obtaining anthropogenic food (Spelt, 2020). Seasons also affect the abundance of gulls. This is mainly caused by increased nest attendance during the breeding season (Spelt, 2020; Isaksson et al., 2016).

Weather aspects which can impact gull movement include temperature (Burger, 1983), wind (McLaren et al., 2016), rain (Zorrozuza et al., 2020) and cloud cover (Isaksson et al., 2016). Bad weather affects the flying and foraging ability, and this eventually impacts their abundance and distribution (Zorrozuza et al., 2020; Isaksson et al., 2016). Gulls forage more on terrestrial food sources during cloudy weather and low air temperatures (Isaksson et al., 2016). Wind also impacts flying ability; the amount of energy spent during flight is often dependent on the wind strength (Safi, 2013; Sage et al., 2019). It has been found that gulls travel less frequently to marine locations during periods of strong winds (Zorrozuza et al., 2020). Many studies focus primarily on extreme weather conditions such as tsunamis or storms, neglecting the significance of non-extreme environmental conditions, including typical temperature and wind speed ranges within a given area (Newell et al., 2015; Yannic et al., 2014; Zuberogoitia et al., 2016). Tidal elevation also affects gull abundance, as they are able to forage on marine prey on uncovered tidal mudflats (Burger, 1983; Yoon et al., 2014; Lato et al., 2021). The water level changes on an hourly basis, which affects prey availability; however, it is unclear whether urban gulls prefer marine prey or anthropogenic food, depending on the accessibility of both (Sibly & McCleery, 1983; Burger, 1983). It is unclear which of these factors most significantly impacts gull abundance in urban areas, which is crucial for understanding and mitigating the human-gull conflict in cities.

Time of day and season

Gulls' abundance is related to the circadian and seasonal cycle (Spaans, 1971; Burger, 1976). This can depend on their foraging patterns, predator avoidance or resting needs (Spelt, 2020; Burger, 1983; Indykiewicz et al., 2021). Gulls forage throughout the day on anthropogenic and natural resources. They can adjust their daily foraging to human activity, such as waste delivery at landfills or school lunch breaks, where food availability is predictable at certain times of day (Spelt, 2020). They also utilise natural, time-dependent resources, such as food available on the tidal mudflats (Isaksson et al., 2016; Burger, 1983). Gulls can be active throughout the day and rest at night, but occasionally forage at night in urban spaces due to light pollution (Isaksson et al., 2016; Gutowsky et al., 2023). Secondly, predation avoidance also impacts the abundance of gulls. At night, when gulls are more vulnerable, they roost in large numbers to avoid nocturnal predators such as Red foxes, *Vulpes vulpes* (Beauchamp, 2009; Hébert and McNeil, 1999; Lavin et al., 2003). Communal roosting gives them an advantage of increased vigilance and reduces the chances of individual predation (Beauchamp, 2009). Resting urban gulls seek quiet areas with low human activity, such as rooftops, docks, or chimneys (Belant, 1997). During the daytime, when predation risk is lower

due to predators being less active, they leave their colonies to forage in small groups or individually (Lavin et al., 2003; Beauchamp, 2009). In summary, gull abundance can be affected by the time of day in various scenarios, and this daily rhythm is linked to the seasonal cycle.

Gulls change their movement patterns during the breeding season because of nest attendance and additional food requirements (Spelt, 2020; Isaksson et al., 2016). Isaksson et al. (2016) found that gull movement changes according to the stage of breeding. In the early stages of breeding, urban gulls select reliable sources of food, such as anthropogenic sources, which leads them to choose urban spaces. After hatching, offspring need easily digestible food, which can include fish, leading gulls to forage over water bodies. After fledging, juveniles learn from adults how to obtain food; therefore, they disperse to various locations to explore foraging techniques (Greig et al., 1983). It is still not fully clear whether all of these apply to both Herring and Lesser black-backed gulls, and it is essential to understand how daily and seasonal cycles affect gull abundance.

Light and cloud cover

Similar to tides, there has been research interest in the effect of light and cloud cover on gull abundance (Isaksson et al., 2016; Pugh and Pawson, 2016; Webb and Blumstein, 2005). Light impacts their daily activity, including foraging and resting, which may differ in urban and rural spaces, as urban settings are usually abundant in artificial lighting (Pugh and Pawson, 2016; Leopold et al., 2010). Research has shown that urban gulls can extend their foraging into nocturnal hours due to the increased artificial light in cities, which can impact their daily foraging patterns (Rock, 2005; Rock and Vaughan, 2013). Artificial light at night (ALAN), therefore, can alter their daily activity and often reduce sleep duration (Leopold et al., 2010; Pugh and Pawson, 2016).

Cloud cover that varies throughout the day may affect the abundance of gulls by reducing visibility and impacting their thermoregulation (Isaksson et al., 2016; Bartholomew and Dawson, 1979). Heavy cloud cover can negatively impact chick survival rates, as young birds are especially sensitive to cold and hot temperatures (Kim and Monaghan, 2005; Bartholomew and Dawson, 1979). Cloud cover can also reduce visibility, which can impact their ability to catch prey and, in turn, can alter their movement and foraging patterns (Whittingham, 2004). Gulls can also rely more on terrestrial food sources during periods of heavy cloud cover, probably due to easier access to prey such as invertebrates (Isaksson et al., 2016). Light and cloud cover are known to impact birds, yet it is not exactly known how they affect Herring and Lesser black-backed gulls in urban and rural areas and whether they impact their abundance in all cases.

Wind

It is known that wind, similarly to light, impacts birds' movement and distribution, yet it is not fully examined in gulls (Isaksson et al., 2016; Burger and Galli, 1987; Lewis et al., 2015). Gulls often rely on soaring and gliding while moving and foraging, which can be affected by wind conditions (Burger and Galli, 1987). Wind can affect flight energetics positively and negatively. High wind speeds can be beneficial for long-distance movement and reduce foraging time (Lewis et al., 2015; Spelt, 2020). Simultaneously, if the wind is too strong or becomes unpredictable, it can increase the energetic cost of movement and even become dangerous for gulls as it can push them towards

buildings or cars (Carr and Lima, 2010; Finney et al., 1999). The impact of wind speed and gust on gull abundance has not been thoroughly examined in either rural or urban gull populations, as the majority of studies focus on other avian species rather than Herring and Lesser black-backed gulls (Finney et al., 1999; Lewis et al., 2015; Pistorius et al., 2015).

Temperature

Air temperature has a significant impact on gull behaviour, especially on urban gull populations where the urban heat island (UHI) effect increases daily temperatures (Opp et al., 1987; Lopes, 2021; Spelt, 2020). High air temperatures in urban spaces can influence the foraging patterns of gulls, as cities tend to be warmer during the winter, making certain food sources more accessible than in rural areas (Maciusik et al., 2010; Seress & Liker, 2015; Barras et al., 2022). These include, for example, refuse tips and small water bodies, which do not freeze, unlike those in rural areas (Rock, 2005; Spelt, 2020). Higher temperatures in cities can bring forward breeding and extend the reproductive period before winter, therefore improving breeding performance by, for example, increasing the chances of having more than one clutch of eggs during the year in comparison to their rural counterparts (Kettel et al., 2018; Brown et al., 1999; Møller et al., 2015). On the other hand, too high temperatures can be fatal for chicks inside the nests (Skagen and Adams, 2012; Kim and Monaghan, 2005; Salzman, 1982). If nests are on rooftops, high temperatures can induce thermal stress and impact eggs, chicks, and adults if they are unable to access a shaded area (Kim and Monaghan, 2005; Salzman, 1982). It is apparent that temperature impacts the behaviour of gulls; this can become even more evident in the future because of climate change and rising temperatures.

Tide

Gull abundance can be affected by hourly changes in tidal elevation, which facilitate access to prey on the intertidal mudflats (Burger, 1983; Yoon et al., 2014; Lato et al., 2021). During low tides, marine prey such as fish and invertebrates become easily accessible for foraging (Sibly & McCleery, 1983; Burger, 1983). The intertidal mudflats become covered during high tide, at which point gulls forage on terrestrial food sources or can shift towards anthropogenic food sources if available, consequently impacting their abundance (Sibly and McCleery, 1983). Gulls also forage on intertidal mudflats during the breeding season, but they may choose to supplement their diet with anthropogenic foods (Yoon et al., 2014; Yorio et al., 2004). In contrast to these studies, Spelt (2020) showed that Lesser black-backed gulls in Bristol primarily foraged on anthropogenic food during the breeding season, rather than utilising marine resources despite having access to them. Despite the high interest in the subject of the impact of tidal elevation on the distribution and abundance of gulls, it has not been thoroughly examined how it impacts Herring and Lesser black-backed gulls in urban settings.

Climate change

Climate change is a long-term alteration of global weather patterns driven largely by human activities. The main issues include rising temperatures, changes in precipitation patterns, and rising sea levels, which in effect contribute to agricultural problems, increasing the risk of food insecurity

for people (Battisti and Naylor, 2009; Crick, 2004; Walther et al., 2002; Trenbreth, 2011; Mimura, 2013).

Rising temperatures alter predator-prey relationships through changes in prey abundance and food availability, ultimately affecting avian survival (Kubelka et al., 2018; Gaston and Elliott, 2013; Broitman et al., 2009). In marine ecosystems, increases in sea-surface temperatures may trigger bottom-up effects by altering the thermal stratification of the water column, restricting the upwelling of cold, nutrient-rich water to the surface (Behrenfeld et al., 2006; Doney, 2006). Such changes in the water temperature reduce nutrient availability, limiting both the abundance and the timing of phytoplankton blooms (Behrenfeld et al., 2006; Winder and Schindler, 2004). This reduction in primary productivity subsequently reduces zooplankton biomass, as many zooplankton species depend on phytoplankton as a primary food source (Lewandowska et al., 2014; Richardson and Schoeman, 2004; Brierley and Kingsford, 2009). Reduced zooplankton availability negatively affects the population of fish species, such as the Lesser sandeel *Ammodytes tobianus*, potentially affecting their abundance (Frederiksen et al., 2006). This in turn affects the breeding performance of planktivorous and piscivorous bird species, such as Parakeet auklet *Cyclorhynchus psittacula* or the Tufted puffin *Lunda cirrhata* (Kitaysky and Golubova, 2000).

Climate change also affects birds' migratory distances, arrival and departure dates, and cohort sizes (Miller-Rushing et al., 2008; Jenni and Kéry, 2003). It has been established that birds, including gulls, are expanding their ranges northward in North America and the United Kingdom due to global warming; this trend may also be observed in other regions (Hitch and Leberg, 2007; Gillings et al., 2015). Climate change also increases the frequency of extreme weather conditions such as storms, which, combined with rising sea levels, can damage natural coastal breeding habitats for gulls (Mac Nally et al., 2009; Newell et al., 2015; Trull et al., 2018). This may be one of the reasons which encourage them to breed in urban spaces, colonising rooftops and other man-made structures, which impacts their population numbers and abundance (Rock, 2005). There are contradictory results from studies, with some predicting the potential extinction of certain bird species and others reporting the opposite effect as a result of climate change (Huntley et al., 2008; Askeyev et al., 2019). However, short-term studies cannot always detect all gull population and abundance changes, which is a problem yet to be solved regarding climate change (Fletcher et al., 2013).

4.3 Study aims and research question

The abundance and distribution of gulls have been documented for decades; however, research has largely focused on natural coastal colonies, leaving gaps in the understanding of urban Herring and Lesser black-backed gull populations (Coulter, 1975; Coulson and Butterfield, 1985; Raven and Coulson, 1997; Schwemmer and Garthe, 2005; Yorio et al., 2016; Jankowiak et al., 2024). Understanding gull abundance and factors impacting it, cannot only help in species conservation but also act as a first step towards mitigating human-gull conflict (Canterbury et al., 2000). This is especially true for the increasing number of urban gulls living in an ever-changing environment across the UK (Furness and Camphuysen, 1997; Navarro et al., 2016; Galimany et al., 2023). The

interaction between environmental and anthropogenic factors influencing the abundance of urban gulls in Liverpool, UK, has not been studied. Therefore, this research aims to address the knowledge gap by understanding which factors impact gull abundance at the fine scale and across the seasons. The results of this study may aid in mitigating human-gull conflict and improve conservation efforts for these two declining species of gulls in other British coastal cities. The research question is **“Which environmental and anthropogenic factors have the strongest impact on the abundance of urban gulls in Liverpool?”**

5. Methods

5.1 Study location and species

Point count locations were established in Liverpool, in the North West of England in the United Kingdom (53° 24' 0" N, 2° 59' 0" W). Liverpool is located on the east of the River Mersey, which flows into the Irish Sea. The city primarily consists of urban and suburban land cover, with several patches of grasslands and woodlands located on the city's outskirts (CORINE Land Cover, 2018). The human population of Liverpool consists of around 496,770 inhabitants across 133.4 km² of city area (ONS, 2024).

For this study, I selected two gull species that regularly form breeding colonies (Garthe et al., 1999a). The herring gull *Larus argentatus* is a resident, and the Lesser black-backed gull *Larus fuscus* is a migratory species (Landsborough, 1924). Lesser black-backed gulls migrate to the South of England, the Iberian Peninsula, France and Africa during autumn and winter; they return to the North in March (Shamoun-Baranes et al., 2017; Burton et al., 2012). These two species were chosen because they inhabit similar environments, their foraging and breeding behaviours partially overlap, and both are of conservation concern in the UK (for example, Calladine, 1997; Camphuysen et al., 2010; Garthe et al., 1999a; Kim and Monaghan, 2006a, 2006b; Stanbury et al., 2021). Studying both of these species simultaneously within one area, such as Liverpool, offers an advantage in understanding their interactions and the possible attraction to other conspecifics, which impacts their abundance. The conservation status of the Herring gull is red, and the Lesser black-backed gull is amber on the List of Birds of Conservation Concern in Great Britain, even though they thrive in coastal cities like Liverpool (Eaton et al. 2015).

5.2 Point counts

Nine long-term point count locations were established across Liverpool, and data were collected throughout 2022. Point counts were spaced at least 200 m apart; this was also set as a minimal distance between point count locations in other studies (Marsden, 1999; Norvell et al., 2003). Gulls can fly around 50 km/h to travel quickly between destinations, so this distance did not eliminate the

probability of pseudoreplication but lowered it to acceptable levels (Shamoun-Baranes and Van Loon, 2006).

Point counts were chosen based on the land cover, which was grouped into three categories: urban areas, suburban areas, and green urban spaces (Fig. 1). Each category was assigned according to the major land cover category surrounding the count point (CORINE Land Cover, 2018; Schueler, 2009). For urban areas (~60-100% of built-up area), these included mostly urbanised areas with buildings, roads, and industrial and commercial units, often in the city centre. The suburban category (~20-59% of built-up area) included less densely urbanised areas than the first category, with more residential buildings, fewer industrial units and more open space. The green urban spaces (~0-19% of built-up area) were located within urban environments but included vegetated surfaces, such as parks or botanical gardens, which feature shrubs and trees. There were three locations in each group. Urban count points were based at the Strand (53° 24' 8.028" N, 2° 59' 25.224" W) (Fig. 1. B1), Liverpool Square (53°24'23.6"N 2°58'59.6"W) (Fig. 1. B2), and Lime Street (53°24'31.9"N 2°58'52.8"W) (Fig. 1. B3). Suburban count points were based at Mill Street Park (53° 22' 59.844" N, 2° 58' 7.14" W) (Fig. 1. B4), mosque (53°23'39.3"N 2°57'36.3" W) (Fig. 1. B5) and Smithdown (53° 23' 54.996" N, 2° 54' 52.812" W) (Fig. 1. B6). Green urban spaces included: Princes Park (53° 23' 6.576" N, 2° 57' 15.084" W) (Fig. 1. B7), Sefton Park (53° 23' 10.284" N, 2° 56' 43.62" W) (Fig. 1. B8) and Wavertree (53° 23' 26.412" N, 2° 55' 21.756" W) (Fig. 1. B9). Counts were conducted for a year, from January to December 2022. Counts began at each site at 8 am and continued until sunset, which varied across the seasons. Data were collected at each of these points every hour between these times. Not all observations scheduled for the location were always conducted on the same day. Count points were split into two groups: Strand, Lime Street and Liverpool Square formed one group, and Mill Street Park, Mosque, Princes Park, Sefton Park, Smithdown and Wavertree formed the second group. The sampling schedule followed an alternating order; points were visited in the sequences listed above, followed by the reverse order on the subsequent count. Effectively, counts were executed at each site every month throughout the year. Each place was visited at least nine times per month and, on average, 115.5 ± 1.86 (mean $\pm$ SE) times in the year. This design prevented bias due to the time of day and changing tidal elevation on the River Mersey, which impacts the detectability of birds (Woltmann, 2005). The total number of counts included 1,040 data points. In a few cases, data could not be collected in order or at all due to factors beyond my control, such as terrain obstructions (closed events without entry) or illness. These instances were minimal, and each count point location was sampled at least 100 times throughout the year.

Counts were executed with a limited distance of a 50 m radius from the centre of each count point, where the covered area of the point was 7853.98 m² (Hutto et al. 1986). This method was implemented to estimate the number of birds in a fixed area and the factors that impact it. The advantage of point counts is that it may be utilised across the seasons and applied to various bird species (Hutto et al., 1986).

The sampling process was the same across all points. The single count took no more than five minutes, as the majority of gulls were easily detectable within the first few minutes. Only birds present in the location at the time of the count were recorded. Stationary or walking individuals

were included, and any birds flying or hovering above the count point were ignored. When any of the variables were missing or no species could be recognised because of adverse weather conditions, these counts were excluded from the analysis. Gulls were assigned to several groups during the count. The first group included adult Herring gulls, which comprise individuals four years old and older. They are characterised by a white head and lower part of the body; their wings are light grey with black tips and white mirrors (Malling Olsen and Larsson, 2003). They have white, grey or yellow eyes, and their beak and legs are yellow (Malling Olsen and Larsson, 2003). The second group included juvenile Herring gulls, which were gulls from a few months old to three years old. They were not divided into one-, two-, or three-year-old age groups, as the sample size would be small and uneven in comparison to the adult numbers. Herring gull juveniles were recognised by their grey and brown plumage; their head and underbody become whiter with each winter (Malling Olsen and Larsson, 2003). Their beak and eyes are black, and their feet are pink (Malling Olsen and Larsson, 2003). The third group contained adult Lesser black-backed gulls, which are characterised by a white head and white ventral plumage. They have black upper parts of the wing with white mirrors at the tips (Malling Olsen and Larsson, 2003). Adult Lesser black-backed gulls have pale yellow eyes and yellow legs and beaks (Malling Olsen and Larsson, 2003). The fourth group consisted of juvenile Lesser black-backed gulls, ranging from a few months old to three years old. The reason for including all juvenile ages into one group is the same as in the case of Herring gulls. Juvenile Lesser black-backed gulls have grey and black plumage; however, their upper wings are slightly darker than those of juvenile Herring gulls (Malling Olsen and Larsson, 2003). With each winter, their head becomes whiter, and their upper wings become darker (Malling Olsen and Larsson, 2003). Their eyes and beaks are black, and their legs are pale pink (Malling Olsen and Larsson, 2003).

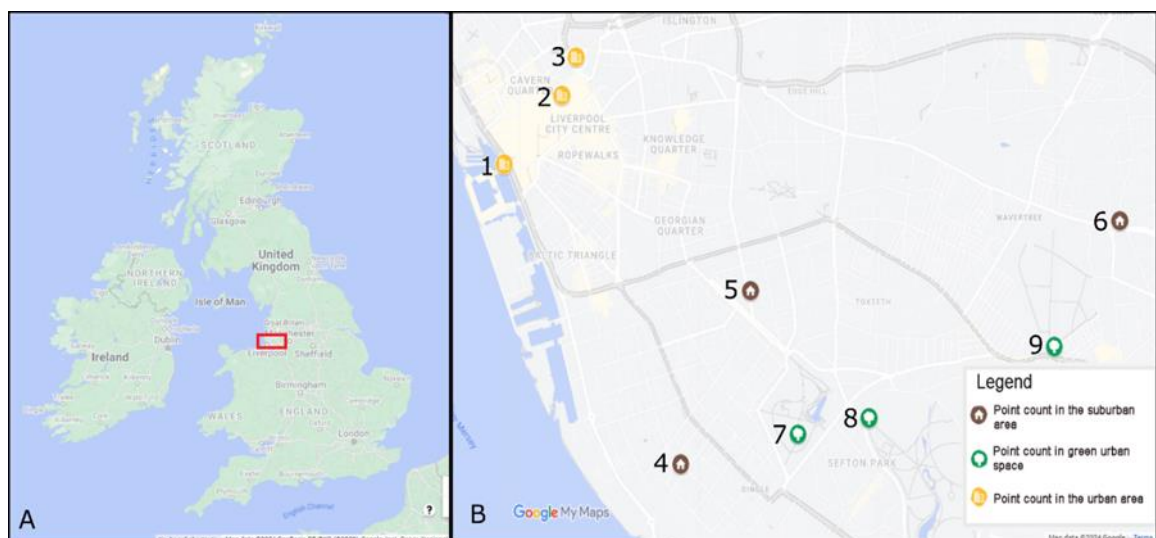


Figure 1. A. Map of the United Kingdom with study area highlighted in red. B. Map showing nine count point locations across Liverpool. Locations are as follows: 1. Strand, 2. Liverpool Square, 3. Lime Street, 4. Mill Street Park, 5. Mosque, 6. Smithdown, 7. Princes Park, 8. Sefton Park, 9. Wavertree. Classification of point count locations is based on the CORINE Land Cover (2018).

Each count started with recording the time and date. Secondly, the light measurement was recorded by a Lux Light Meter Pro (Doggo Apps, 2024). The app utilised the sensors in the mobile

phone screen to measure light intensity in lux units. The phone used to measure light intensity was a Samsung Galaxy S10e. The device was held one metre above the ground, with the screen facing up, and was not obscured during the measurement. Afterwards, the number and species of gulls, as well as the number of people, were recorded. The next variable recorded was tide, which was recorded in Gladstone Dock in Liverpool (Tide Times and Tide Chart for Liverpool [Gladstone Dock], 2024). Weather variables were obtained after finishing the count from online databases, which are described below.

5.3 Environmental variables

The tidal elevation was recorded on the basis of predicted tides in Gladstone Dock in Liverpool (Tide Times and Tide Chart for Liverpool [Gladstone Dock], 2024). It was recorded in metres above the Chart Datum. The continuous values were then categorised as either 'high' or 'low' tide. Low tide was defined as all tidal elevation values recorded two hours on each side of the lowest tide in Gladstone Dock, sourced from Tide Times and Tide Chart for Liverpool Gladstone Dock (2024). All remaining values outside of that time period were classified as high tide. This was implemented to explore the impact of uncovered tidal mudflats during low tide, where gulls forage on invertebrates (Sibly and McCleery, 1983).

I also included breeding and non-breeding seasons as variables; the breeding season was assigned to data collected from April to August, and the non-breeding season was from September to March.

The weather conditions were the next variable included in my dataset. Measurements of temperature, wind speed and cloud cover were obtained via the Environmental-Data Automated Track Annotation on the Movebank website (Dodge et al., 2013; Wikielski et al., 2024). These were sourced from various datasets available via movebank.org; these data were obtained after the execution of the count. Temperature was sourced from the 'ECMWF ERA5 SL Temperature' dataset (Hersbach et al., 2023). It is measured two metres above the ground, calculated by interpolating between the lowest model level and the Earth's surface. The measurement is accurate to the hour of the count; it was originally provided in Kelvins, which I converted to degrees Celsius. The wind speed was sourced from the ECMWF ERA5 SL 10 Metre Wind Gust dataset (Hersbach et al., 2023). The wind speed was estimated in m/s by the weather model for a given time based on the maximum wind speed at ten meters above the ground and taking into consideration surface stress, surface friction, wind shear and stability. The final measurement was cloud cover sourced from 'ECMWF ERA5 SL Total Cloud Cover' (Hersbach et al., 2023). It measured the proportion of the 'grid box' area covered by the clouds, which included the count point location. It assessed the cloud cover on many levels of the atmosphere and its overlap at different heights. The unit was a proportion; 0 represents 0% cloud cover, and 1 represents 100% cloud cover in the given location.

The temperature, wind speed, and cloud cover described above were sourced from ECMWF datasets, which utilise advanced weather forecasting models and historical observations from weather stations, satellites, or weather balloons (ECMWF, 2023). ECMWF reanalysis products

combine these observations with numerical weather prediction models to generate spatially and temporally consistent estimates of past atmospheric conditions. As the ECMWF data was sourced from the Movebank website (Wikielski et al., 2024), it utilised bilinear interpolation in cases where data for the exact location or time was not available. The website calculates unknown values by estimating the measurement from known data points within the same range (Wikielski et al., 2024). Bilinear interpolation utilises the estimation of four known data points surrounding the unknown value, weighting them based on distance; data points closer to the requested value carry a higher weight than those further away.

5.4 Statistical analysis

Data were analysed with R version 4.4.1 (R Core Team, 2023; Posit Team, 2024). The response variable was the count of gulls, and its distribution was not normal. The Levene test for variance showed that the data were overdispersed. Based on this information, Generalised Linear Mixed-Effects Models (GLMMs) were chosen for data analysis, using the *glmmTMB* package (McGillucuddy et al., 2025). To account for overdispersion and excessive zeros in the response variables (gull counts), I used a zero-inflated model with a negative binomial distribution and log link function (Zuur et al., 2009a). These models included two components: the first count component was modelling the non-zero count data using a negative binomial distribution (henceforth referred to as “the conditional model”), and the second component was modelling the excess zero counts (henceforth referred to as “the zero component”).

Prior to model fitting, correlation matrices were generated using the *stats* package to evaluate relationships between explanatory variables and to examine potential correlations between gull species and age classes (R Core Team, 2023). Correlations among explanatory variables did not reveal any significant correlations which would prevent their inclusion in the same model. However, significant correlations were identified between gull count groups. Collinearity among explanatory variables was further assessed using variance inflation factors (VIFs) calculated with *the car* package in R (Fox and Weisberg, 2019). All VIFs were low (<2), indicating no collinearity issues among these variables. Preliminary attempts to include all gull species and ages in a single model failed due to convergence issues, likely due to the complex differences in responses among the different groups and strong correlation relationships between gull count groups. Consequently, four models were constructed and applied to data: Herring gulls - adults, Herring gulls - juveniles, Lesser black-backed gulls – adults, and Lesser black-backed gulls - juveniles.

The nine-point count locations were sampled as a repeated measure, so they were set as a random factor across all models. The fixed factors included the independent variables: number of people (continuous variable), tidal elevation (categorical with two levels: low, high), temperature (continuous), wind speed (continuous), time of the day (categorical with three levels: morning [8 am – 12 pm], afternoon [12 pm – 6 pm], evening [6 pm – 9 pm]), cloud cover (continuous proportion from 0 to 1), season (categorical with two levels: breeding, non-breeding), land cover (categorical with three levels: urban, suburban and green urban spaces). Interaction between *Season*Temperature* was added to the juvenile Herring gull model. No interaction terms were used

in the rest of the models, as they were not significant and caused issues with model convergence and validation.

The models were chosen on the basis of the backward stepwise model selection described by Zuur et al. (2009a). Starting with all explanatory variables in the model (except for the juvenile Lesser black-backed gulls model, where including the 'Light' and 'Season' variables caused convergence issues, so they were removed at the beginning), I removed non-significant variables one by one, using the highest p-value as a marker. After each removal, I compared the Akaike Information Criterion (AIC) values between the models and selected the one with the lowest value. To check and interpret interactions between variables and within levels of categorical factors, I performed post hoc Estimated Marginal Means tests using the *emmeans* R package (Lenth, 2025). Categorical variables in the models with more than three levels were also tested with the *emmeans* package, and the p-value was adjusted by the Tukey method (Lenth, 2025). Model assumptions were validated by inspecting diagnostic plots for dispersion, outliers, and patterns in residuals. The results obtained from GLMMs of continuous variables were reported with estimated coefficients (β) and p-values. Results for categorical variables were reported with values obtained from the Type II Wald chi-square test. The conditional and marginal R^2 of models were calculated using the *performance* R package (Lüdtke et al., 2021). The conditional R^2 measured the variance of the model explained by fixed and random factors, while the marginal R^2 measured the variance explained by the fixed effects. Plots displaying predicted values were based on the corresponding GLMMs; the calculations were performed by the *ggeffects* R package (Lüdtke, 2018). The significance level was set at $\alpha = 0.05$ across all models.

6. Results

6.1 Adult Herring gulls

This analysis included the number of adult Herring gulls as the response variable. The best-fit GLMM included the following variables in the conditional component: location (random factor), light, cloud cover and time of day. The zero component of the chosen model included the following variables: number of people, land cover, temperature, tide, cloud cover, and time of day. The best-fit model had the lowest AIC value, differing by more than two ΔAIC units from the next best model (Table 1). Conditional and marginal R^2 were calculated for the best-fit model (Table 2). Point count locations were set as a random factor in all models used in this study.

In the conditional component, an increase in cloud cover significantly decreased the number of adult Herring gulls (Table 2., Fig. 2). The next significant variable which impacted gull numbers was time of day ($\chi^2 = 10.15$, $df = 2$, Fig. 3). The post hoc Estimated Marginal Means (EMM) test showed that the number of gulls was significantly higher in the afternoon than in the evening (*estimate* = 0.624, *SE* = 0.200, *z* = 3.118, *p* = 0.005). The EMM test did not report any significant differences

between afternoon and morning (*estimate* = 0.157, *SE* = 0.107, *z* = 1.472, *p* = 0.304) or evening and morning counts (*estimate* = - 0.467, *SE* = 0.199, *z* = -2.338, *p* = 0.051).

In the zero-inflation component of the model, a few variables were statistically significant. Their statistical significance indicated which factors affected gull presence or absence, rather than the number of gulls if they were already present. Higher temperatures (Table A2) and increased cloud cover (Table A2) lowered the probability of zero counts. Adult Herring gulls' presence was also negatively affected by low tide (Table A2). Time of day had a significant effect on the likelihood of gull presence ($\chi^2 = 26.99$, *df* = 2, Table A2). The EMM test showed that the probability of zero counts was lower in the morning compared to the afternoon (*estimate* = 1.966, *SE* = 0.380, *z*-ratio = 5.171, *p* < 0.001). The differences between afternoon and evening (*estimate* = 0.851, *SE* = 0.506, *z*-ratio = 1.681, *p* = 0.213) or evening and morning (*estimate* = 1.116, *SE* = 0.559, *z*-ratio = 1.997, *p* = 0.113) were not significant. The last significant difference in the zero component was recorded for the land cover variable ($\chi^2 = 57.15$, *df* = 2, Table A2). The EMM pairwise comparisons showed that the probability of zero counts was higher in green urban areas compared to suburban (*estimate* = 1.81, *SE* = 0.340, *z*-ratio = 5.333, *p* < 0.001) and urban areas (*estimate* = 5.61, *SE* = 0.932, *z*-ratio = 6.024, *p* < 0.001). The test also revealed that suburban areas had a higher probability of zero inflation than urban areas (*estimate* = 3.80, *SE* = 0.948, *z*-ratio = 4.011, Table A2).

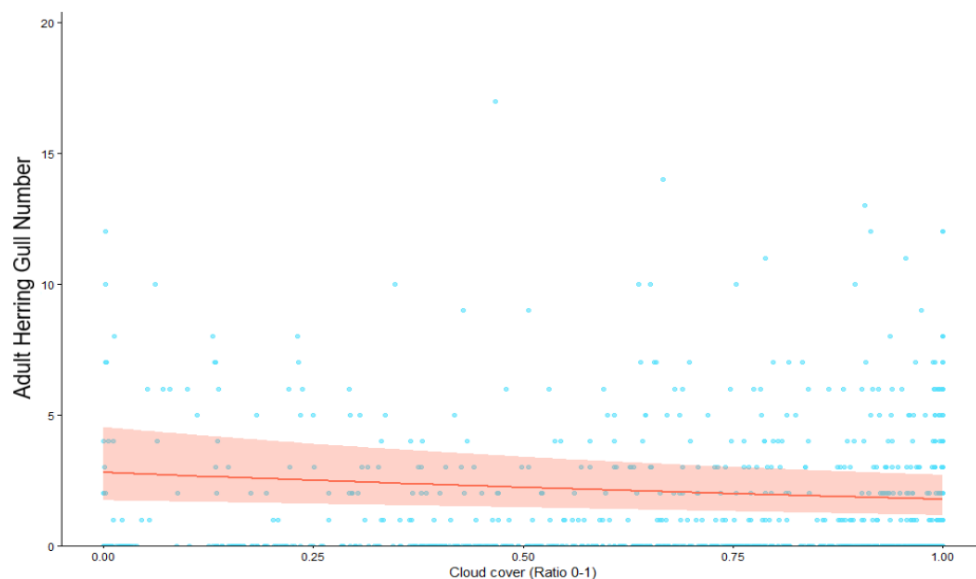


Figure 2. The Effect of Cloud Cover on Observed Adult Herring Gull Numbers. Observed counts of adult Herring gulls are shown as blue points plotted against the cloud cover (ratio 0-1). Plot includes a red trend line fitted on the basis of zero-inflated negative binomial GLMM. The orange shaded area around the trend line indicates a 95% confidence interval band.

Table 1. Model selection for Adult Herring gulls of the three GLMMs on the basis of lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold. All preliminary models are included in appendix.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Adult Herring Gulls	1 (Full model)	(1 Place) + Light + people + temperature + tide + wind + clouds + Season + Time_of_day + Land	Light + people + Land + temperature + tide + wind + clouds + Season + Time_of_day	1014	2777	0	-1363	1175
	2	(1 Place) + Light + clouds + Time_of_day	people + Land + temperature + tide + clouds + Season + Time_of_day	1023	2766	11	-1366	1172
	3 (Best-fit model)	(1 Place) + Light + clouds + Time_of_day	people + Land + temperature + tide + clouds + Time_of_day	1024	2764	13	-1366	1171

Table 2. The results of the best Zero-Inflated GLMM for adult Herring gulls, juvenile Herring gulls, adult Lesser black-backed gulls and juvenile Lesser black-backed gulls. It represents the effects of predictors on the gull numbers. The results include estimates (β) and standard errors (SE). The table also includes conditional and marginal R^2 . Significant effects are in bold.

Predictor	β	SE	P-value
Model	Herringgulls adults (Conditional component)		
(Intercept)	1.085	0.255	<0.001
Light	0.000	0.000	0.186
Clouds	-0.457	0.170	0.007
Time of day evening	-0.624	0.200	0.002
Time of day morning	-0.157	0.107	0.141
Conditional R^2 0.384			
Marginal R^2 0.058			
Model	Herringgulls juveniles (Conditional component)		
(Intercept)	-1.012	0.645	0.117
Season: Non-breeding	1.458	0.593	0.014
Temperature	0.074	0.033	0.022
Wind	-0.040	0.023	0.091
Season: Non-breeding* temperature	-0.067	0.042	0.110
Conditional R^2 0.553			
Marginal R^2 0.069			
Model	Lesser black-backed gull adults (Conditional component)		
(Intercept)	-1.488	0.616	0.016
Season: Non-breeding	-0.925	0.224	<0.001
Light	0.000	0.000	0.071
Temperature	0.051	0.022	0.019
Conditional R^2 0.713			
Marginal R^2 0.086			
Model	Lesser black-backed gull juveniles (Conditional component)		
(Intercept)	-6.500	2.931	0.027
Tide: Low	1.069	0.825	0.195
Time of day: evening	-0.260	1.080	0.809
Time of day: morning	-3.756	0.923	<0.001
Land: Suburban	2.721	2.183	0.213
Land: Urban	5.527	2.453	0.024
People	-0.119	0.031	<0.001
Temperature	-0.158	0.112	0.157
Wind	0.665	0.176	<0.001
Conditional R^2 0.903			
Marginal R^2 0.713			

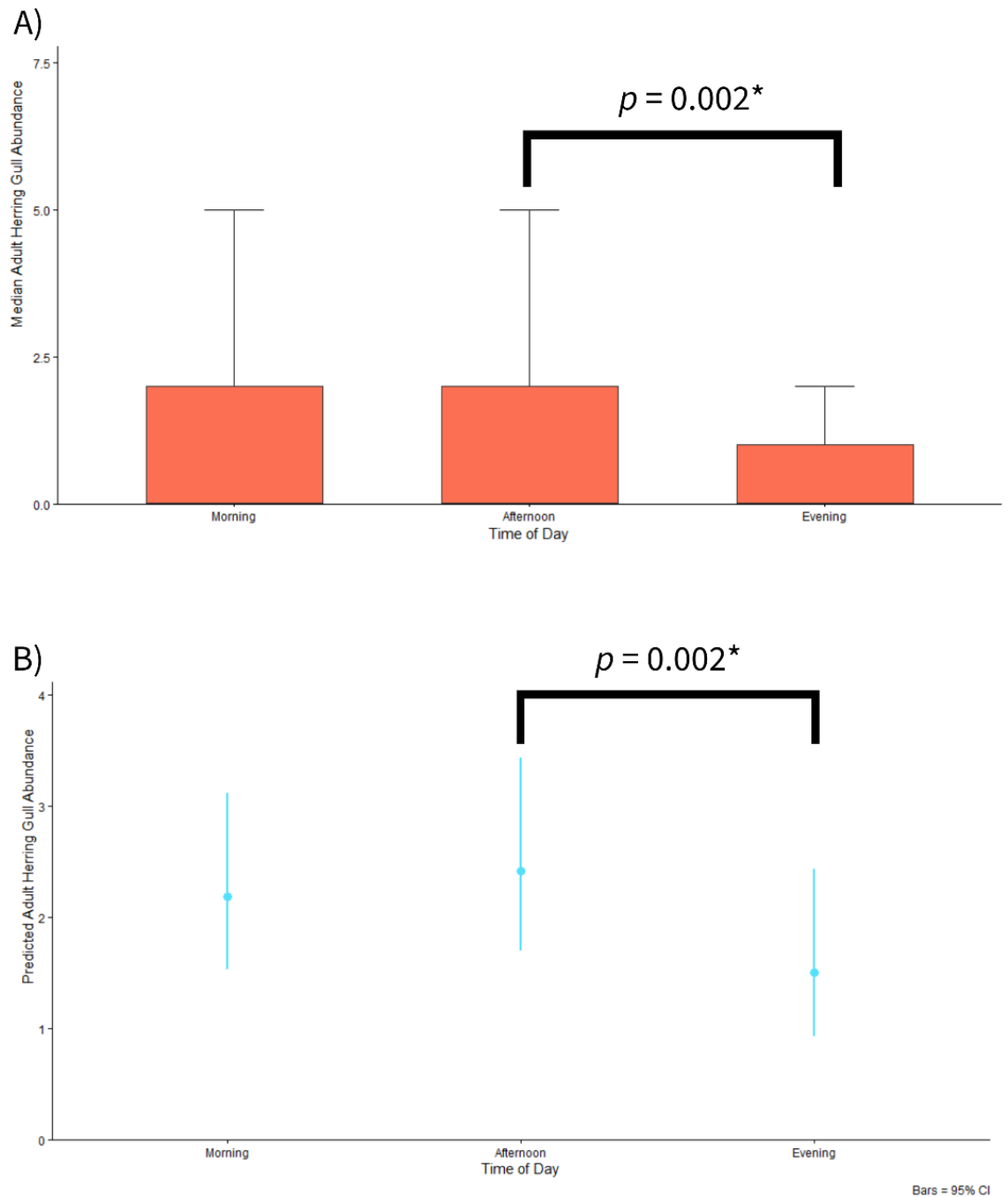


Figure 3. **Plot A.** The Effect of Time of Day on Observed Adult Herring Gull Counts. Boxplots depict the interquartile range (25 %, 50 %, 75 %) with whiskers extending to the lowest and highest ($\pm 1.5 \times$ IQR). The significant difference between afternoon and evening is shown by a p-value on the plot, it is based on the EMM post hoc test. **Plot B.** The Effect of Time of Day on Predicted Adult Herring Gull Numbers obtained from a zero-inflated negative-binomial generalised linear mixed model (GLMM). Vertical error bars show 95% confidence intervals. The significant difference between afternoon and evening is shown by a p-value on the plot, which is based on the EMM post hoc test.

6.2 Juvenile Herring gulls

The second model included the number of juvenile Herring gulls as the response variable. The best-fit model included the following explanatory variables in the conditional component: location (random factor), wind speed and the interaction between season and temperature. The zero inflation component included: tide, time of day, land cover, light and temperature. The best-fit model had the lowest AIC value, differing by zero Δ AIC units from the next best model (Table 3). The model was kept because of better dispersion diagnostics in the final model, despite no difference in the AIC values. Conditional and marginal R² were calculated for the best-fit model (Table 2).

The conditional component showed that, with an increase in temperature, the number of juvenile Herring gulls also increased (Table 2, Fig. 4). The gull count also increased during the non-breeding season compared to the breeding season (Table 2).

The zero-inflation component of this model revealed, similarly to adult Herring gulls, that higher temperatures (Table A4) decreased the number of zero counts. The number of zero inflation also decreased depending on the time of day ($\chi^2 = 20.004$, $df = 2$, Table A4). The EMM test showed that the likelihood of zero counts was lower in the morning in comparison to both the afternoon (*estimate* = 3.19, SE = 0.808, z-ratio = 3.945, $p < 0.001$) and the evening (*estimate* = 4.35, SE = 0.995, z-ratio = 4.376, $p < 0.001$). There was no significant difference between the counts done in the afternoon and evening (*estimate* = -1.16, SE = 0.642, z-ratio = -1.816, $p = 0.165$). Low tide (Table A4) and higher light intensity (Table A4) increased the zero inflation for juvenile Herring gulls. Lastly, the zero component of this model showed that land cover had a significant impact on the zero counts ($\chi^2 = 37.71$, $df = 2$, Table A4). The pairwise comparison of the EMM test showed that there was a higher probability of zero inflation in the green urban spaces in comparison to urban (*estimate* = 4.83, SE = 0.786, z-ratio = 6.140, $p < 0.001$) and suburban spaces (*estimate* = 2.91, SE = 0.685, z-ratio = 4.252, $p < 0.001$). The post hoc test also revealed a higher likelihood of zero counts in suburban compared to urban spaces (*estimate* = 1.91, SE = 0.57, z-ratio = 3.355, $p = 0.002$). These results suggest that the structural zeros were highest in green urban spaces and lowest in urban areas.

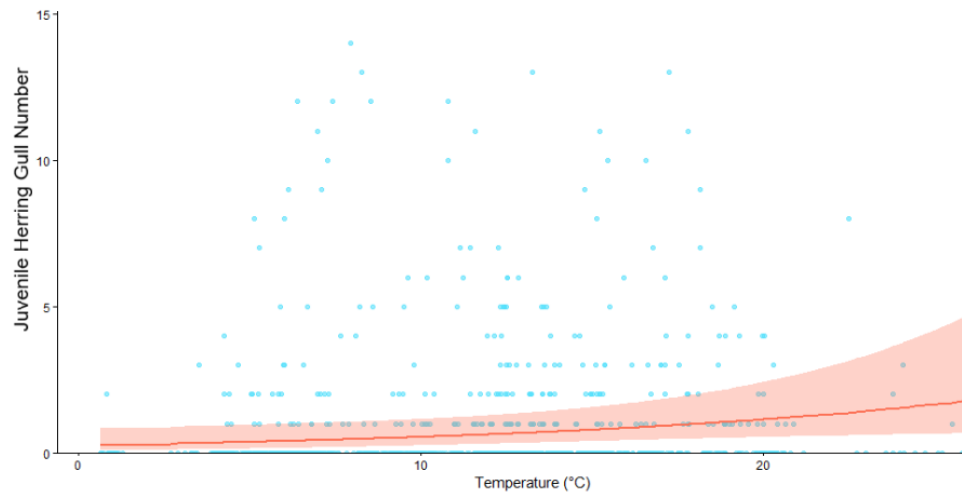


Figure 4. The Effect of Temperature on the Observed Counts of Juvenile Herring Gulls. Observed gull numbers are shown as blue points plotted against the air temperature (°C). Plot includes a red trend line fitted on the basis of zero-inflated negative binomial GLMM. The orange shaded area around the trend line indicates a 95% confidence interval band.

Table 3. Model selection for juvenile Herring gulls of the three GLMMs on the basis of lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold. All preliminary models are included in appendix.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Juvenile Herring Gulls	1 (Full model)	(1 Place) + Season +tide + Time_of_day+ Land + Light +people +temperature+wind + clouds	Season +tide + Time_of_day+ Land + Light +people +temperature+wind + clouds	1014	1910	0	-929	668
	2	(1 Place) + Season*temperature+wind	tide + Time_of_day+ Land + Light +temperature+clouds	1024	1894	16	-931	682
	3 (Best-fit model)	(1 Place) + Season*temperature+wind	tide + Time_of_day+ Land + Light +temperature	1025	1894	16	-932	689

6.3 Adult Lesser black-backed gulls

This model included the number of adult Lesser black-backed gulls as the response variable. The best GLMM included the following explanatory variables in the conditional component: location (random factor), season, light and temperature. The zero component of the chosen model included: season, tide, time of day, land cover, light, number of people, temperature, wind speed and cloud cover. The best-fit model had the lowest AIC value, differing by one Δ AIC unit from the next-best model (Table 4). Conditional and marginal R^2 were calculated for the best-fit model (Table 2). The conditional component of the model indicated that higher temperature increased the count of gulls (Table 2, Fig. 5). The other significant variable was season. The number of gulls was significantly lower during the non-breeding season than during the breeding season (Table 2).

The zero-inflated component of the model indicated that land cover impacted the number of zero counts ($\chi^2 = 24.71$, $df = 2$, Table A6). The EMM test revealed that the probability of zero inflation was more likely in green urban spaces compared to urban (*estimate* = 10.22, *SE* = 2.80, *z-ratio* = 3.656, $p < 0.001$) and suburban spaces (*estimate* = 5.46, *SE* = 1.10, *z-ratio* = 4.952, $p < 0.001$). The difference in the probability of zero counts between urban and suburban spaces was not significant (*estimate* = 4.77, *SE* = 2.21, *z-ratio* = 2.157, $p = 0.078$). Further analysis revealed that higher light intensity (Table A6) and stronger wind speed (Table A6) increased the probability of zero observations. A similar pattern was found for a greater number of people (Table A6) and greater cloud cover (Table A6), both of which increased the zero inflation in adult Lesser black-backed gulls. In contrast to the previous results, higher air temperature decreased the number of zero counts (Table A6). Lastly, the zero inflation increased during the non-breeding season (Table A6).

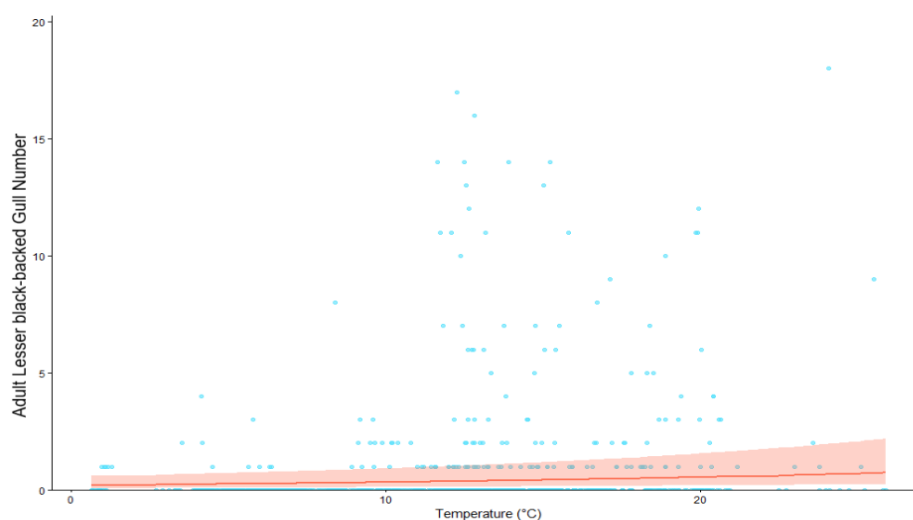


Figure 5. The Effect of Temperature on Observed Counts of Adult Lesser Black-backed Gulls. Gull numbers are shown as blue points plotted against the air temperature (°C). Plot includes a red trend line fitted on the basis of zero-inflated negative binomial GLMM. The orange shaded area around the trend line indicates a 95% confidence interval band.

Table 4. Model selection for adult Lesser black-backed gulls of the three GLMMs on the basis of lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold. All preliminary models are included in appendix.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Adult Lesser black-backed Gulls	1 (Full model)	(1 Place) + Season + tide + Time_of_day + Land + Light + people + temperature + wind + clouds	Season + tide + Time_of_day + Land + Light + people + temperature + wind + clouds	1014	1189	0	-568	464
	2	(1 Place) + Season + Light + temperature + wind	Season + tide + Time_of_day + Land + Light + people + temperature + wind + clouds	1021	1178	11	-570	468
	3 (Best-fit model)	(1 Place) + Season + Light + temperature	Season + tide + Time_of_day + Land + Light + people + temperature + wind + clouds	1022	1177	12	-571	472

6.3 Juvenile Lesser black-backed gulls

The last model included the number of juvenile Lesser black-backed gulls as a response variable. The best-fit model included the following variables in the conditional component: location (random factor), tide, time of day, land cover, number of people, temperature and wind speed. The zero component included the following variables: tide, time of day, land cover, number of people, temperature, wind speed and cloud cover. The best-fit model had the lowest AIC value, differing by one Δ AIC unit from the next best model (Table 5). Conditional and marginal R² were calculated for the best-fit model (Table 2).

The conditional component of this model showed that time of day impacted the number of gulls ($\chi^2 = 16.604$, $df = 2$, Table 2). The EMM pairwise comparison indicated that gull numbers were significantly higher in the morning in comparison to the afternoon (*estimate* = 3.76, $SE = 0.923$, z -ratio = 4.071, $p < 0.001$) and evening (*estimate* = 3.50, $SE = 1.350$, z -ratio = 2.593, $p = 0.258$). There was no significant difference between afternoon and evening counts (*estimate* = 0.26, $SE = 1.080$, z -ratio = 0.241, $p = 0.968$). The next result showed that the number of gulls increased during higher wind speeds (Table 2). In contrast to the previous result, the number of gulls decreased with greater human density during counts (Table 2, Fig. 6). The conditional model showed that there were more gulls recorded in urban spaces in comparison to the intercept – green spaces (Table 2). However, this result was not supported by the Type II Wald chi-square test and showed no significant result ($\chi^2 = 5.096$, $df = 2$, Table 2). A similar result was shown in the post hoc EMM test (*estimate* = -5.53, $SE = 2.45$, z -ratio = -2.253, $p = 0.062$). This inconsistency may have been caused by the small sample size of juvenile Lesser black-backed gulls recorded across different land types, which could limit the statistical power of the above tests.

The zero-inflated component of this model showed that a greater number of people (Table A7) and higher air temperatures (Table A7) both decreased the probability of zero counts. Stronger wind speed significantly increased the number of zero-inflated counts among juvenile Lesser black-backed gull counts (Table A7). Lastly, the time of day also affected the number of zero counts in this model ($\chi^2 = 6.139$, $df = 2$, Table A7). The post hoc EMM test indicated that the probability of zero inflation was lower in the morning in comparison to the afternoon (*estimate* = 8.13, $SE = 3.28$, z -ratio = 2.476, $p = 0.035$). The differences between afternoon and evening (*estimate* = -1.70, $SE = 1.80$, z -ratio = -0.944, $p = 0.612$) as well as evening and morning (*estimate* = 9.83, $SE = 4.25$, z -ratio = 2.310, $p = 0.054$) were approaching significance.

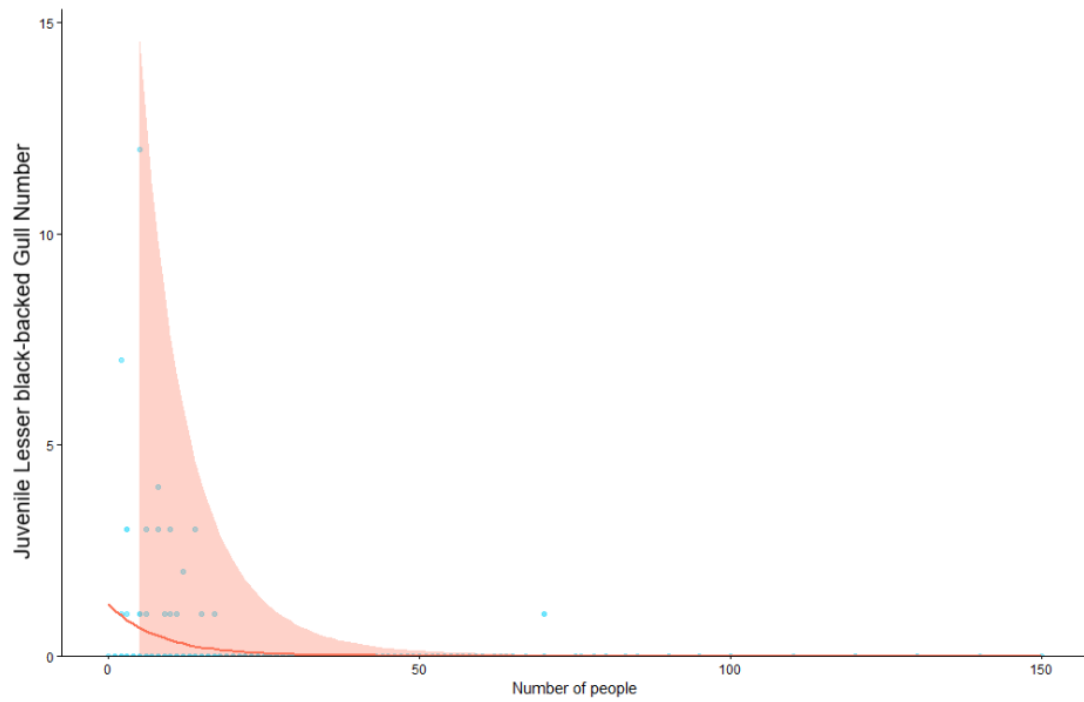


Figure 6. Observed counts of juvenile Lesser black-backed gulls are shown as blue points plotted against the number of people. The plot includes a red trend line fitted on the basis of a zero-inflated negative binomial GLMM. The orange shaded area around the trend line indicates a 95% confidence interval band.

Table 5. Model selection for juvenile Lesser black-backed gulls of the three GLMMs on the basis of lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold. All preliminary models are included in appendix.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Juvenile Lesser black-backed Gulls	1 (Full model)	(1 Place) + Season + tide + Time_of_day+ Land +people +temperature+ wind + clouds	tide + Time_of_day+ Land +people +temperature+ wind + clouds	1017	254	0	-104	110
	2	(1 Place) + Season + tide + Time_of_day+ Land +people +temperature+ wind	tide + Time_of_day+ Land +people +temperature+ wind + clouds	1018	252	2	-104	110
	3 (Best-fit model)	(1 Place) + tide + Time_of_day+ Land +people +temperature+ wind	tide + Time_of_day+ Land +people +temperature+ wind + clouds	1019	251	3	-105	107

7. Discussion

The primary aim of this study was to examine the anthropogenic and environmental factors that impact the abundance of gulls across nine count point locations in Liverpool. The findings provided new insight into the seasonal patterns of gulls, with higher numbers of Herring gulls and lower numbers of adult Lesser black-backed gulls during the non-breeding season. The data further indicated that a greater number of people negatively impacted the number of juvenile Lesser black-backed gulls. The higher air temperature had a positive effect on both juvenile Herring gulls and adult Lesser black-backed gulls. Collectively, the results illustrate the variability of the impact of anthropogenic and environmental factors on each gull species and age group in Liverpool, highlighting the complexity of the issue.

7.1 Weather conditions

Weather conditions had a varying effect on gull abundance. The results indicated that stronger **wind speeds** increased the number of juvenile Lesser black-backed gulls. This might have been caused by gulls seeking shelter or foraging away from the riverside, where flying and foraging could be more difficult during strong winds (Burger, 1983). With the exception of one, all point counts were situated far from the River Mersey, which could explain this trend, as gulls may have used these terrestrial areas for resting, foraging and loafing. The influence of wind speed on juvenile gull movement behaviour in urban landscapes remains poorly studied. However, literature shows that juveniles of other seabird species, such as Great frigatebirds *Fregata minor*, lack the flight techniques required to compensate for wind drift, skills that are acquired by their adult counterparts through experience and physical maturation (Wynn et al., 2020). The inability to minimise the energy expenditure during high wind speeds may explain why juvenile Lesser black-backed gulls were more abundant on land during periods of high winds (Suzuki et al., 2026; Shamoun-Baranes and van Loon, 2006).

In contrast, wind speed did not show a significant effect on juvenile Herring gulls, despite being included in the final model. As Herring gulls are opportunistic foragers that heavily exploit anthropogenic resources, their juveniles may use urban spaces more efficiently than juvenile Lesser black-backed gulls, as the latter may prefer to forage on marine resources (Rock, 2005; Langley et al., 2022; Lato et al., 2021). Juvenile Lesser black-backed gulls may naturally prefer to forage in open marine spaces where wind is felt more intensely (Langley et al., 2022; Shepard et al., 2016). This contrasts with Herring gulls, which predominantly forage in urban areas characterised by tall buildings that obstruct wind flow (Rock, 2005; Langley et al., 2022; Shepard et al., 2016). This sheltering effect may explain the lack of a significant wind impact on juvenile Herring gulls.

Wind speed was excluded as a variable for both the adult Herring and Lesser black-backed gulls models, as its removal optimised model fit by lowering AIC. The lack of a significant effect of wind speed on the adult gulls might be caused by their greater flight experience and physical maturation, which allows them to navigate adverse weather conditions more effectively than juveniles

(Isaksson et al., 2016; Ruaux et al., 2020). This is supported by a study conducted on adult Lesser black-backed gulls, which reported no effect of wind on the choice of the foraging area, despite foraging being one of the main drivers for gulls' movement (Isaksson et al., 2016). Ultimately, the varying responses to wind conditions may be attributed to the complex combination of species, age, and environment (Isaksson et al., 2016; Burger, 1983; Shepard et al., 2016).

Cloud cover did not show a consistent impact on gull abundance across all species and age classes. It significantly decreased only the number of adult Herring gulls, and did not have any effect on the remaining groups of gulls. Consequently, the cloud cover variable was excluded from the other models during the backward stepwise selection to improve model fit. Burger (1983) suggested that gulls may be more successful at foraging in water during cloudy conditions due to the absence of sun glare on the water surface, which improves the visibility of prey. This mechanism could explain the result of my study, as adult Herring gulls could abandon terrestrial sites during cloudy weather to forage on the River Mersey.

This relationship, however, was absent in juvenile Herring gulls. This null result may be explained by biological differences between adults and juveniles, particularly regarding foraging efficiency and social hierarchies (Estévez and Aparicio, 2019; Marchetti and Price, 1989). Juvenile gulls are often subordinate to adults when selecting a foraging patch (Gimeno et al., 2023; Wunderle, 1991). Adults may exclude juveniles from foraging sites during optimal environmental conditions, forcing them to utilise the best patches only after adults vacate them (Wunderle, 1991). This may be reinforced by the predictability of anthropogenic food resources, which may attract juveniles due to the ease of obtaining them (Lato et al., 2021; Skórka and Wójcik, 2006). Unlike the marine prey in the aquatic environment, anthropogenic food sources in the terrestrial sites remain similarly available regardless of cloud cover (Burger, 1983).

Species-specific results in my study showed no significant effect of cloud cover on adult and juvenile Lesser black-backed gulls. Herring gulls forage more frequently in the intertidal mudflats and shallow waters than in open marine environments, whereas Lesser black-backed gulls predominantly forage in marine sites as well as around trawlers (Garthe et al., 1999a; Kim and Monaghan, 2006a). Therefore, Herring gulls may rely more on overcast conditions to mitigate water surface glare and detect prey in the shallow waters (Burger, 1983). In contrast, Lesser black-backed gulls often rely on the fish discards from fishing vessels, and are less constrained by visibility conditions (Burger, 1983; Garthe et al., 1999a).

The air temperature was excluded from the adult Herring gull model because its effect on gull abundance was non-significant, and its removal improved the model fit. The absence of a temperature effect on adult Herring gull abundance may stem from their resident status. In temperate regions such as the UK, Herring gulls typically remain within the country throughout the year, although they may disperse away from breeding colonies during the non-breeding season (Burger, 1983; Coulson and Butterfield, 1985). In urban locations like Liverpool, adult Herring gulls possess both the access and foraging skills necessary to obtain natural and anthropogenic food

sources year-round (Fuirst et al., 2018; Washburn et al., 2018; Lato et al., 2021). Although air temperature may influence the availability of certain food sources such as earthworms, as they are opportunistic foragers, they can easily switch between prey (Spelt, 2020; Görres et al., 2016; Washburn et al., 2018). This diverse range of food resources paired with high flexibility may reduce their dependence on short-term changes in air temperature; therefore, temperature may not have an impact on that particular group. While other studies have shown that adult Herring gulls can be sensitive to particularly cold and windy weather, during which they seek shelter from adverse conditions near ponds (Burger, 1988; Burger, 1982), this pattern was not observed in the present study, likely due to a lack of count points near open water bodies, except for the count point in the Strand.

Higher air temperature was positively associated with increased juvenile Herring gull abundance. This pattern was evident in the conditional part of the model, as well as in the zero-inflation components, indicating that higher temperatures decrease the probability of recording zero gulls during counts. This is consistent with studies that found gulls are attracted to urban areas due to higher temperatures, partially caused by the 'urban heat island' effect (Opp et al., 1987; Lopes, 2021; Spelt, 2020). Gulls can relocate to urban spaces because of easier food access enabled by higher temperatures (Maciusik et al., 2010; Seress & Liker, 2015; Spelt, 2020; Kettel et al., 2018). On the other hand, some studies found an increase in gulls in terrestrial areas during low air temperatures caused by higher soil invertebrate activity (Isaksson et al., 2016). However, this contrasting trend may not apply to my results, as six out of nine count points were established in places with various degrees of urbanisation, where soil invertebrate foraging opportunities were limited.

The contrasting responses between adult and juvenile Herring gulls to air temperature may reflect age-related differences in foraging skills, strategy and efficiency (Washburn et al., 2018; Burger, 1982; Greig et al., 1983). Juveniles possess less foraging experience than adults, and may rely more heavily on easily accessible anthropogenic foods, which are more abundant during warm weather when human outdoor activity may increase food waste production (Greig et al., 1983; Spelt, 2020). Adults are more experienced at locating and exploiting diverse food resources across Liverpool; therefore, their overall abundance may not be impacted by daily temperature changes (Washburn et al., 2018; Fuirst et al., 2018; Spelt, 2020).

Higher air temperature was associated with higher abundance of adult Lesser black-backed gulls. Similarly to juvenile Herring gulls, adult Lesser black-backed gulls may be attracted to urban areas because of the 'urban heat island' effect (Opp et al., 1987; Lopes, 2021). Gulls may choose urban spaces because of easier access to food and an earlier onset of the breeding season, both enabled by higher temperatures (Maciusik et al., 2010; Seress & Liker, 2015; Spelt, 2020; Kettel et al., 2018). In adult Lesser black-backed gulls, this relationship may also reflect seasonal migration rather than the direct effect of air temperature (Ross-Smith et al., 2015; Ross-Smith, 2014). Higher temperatures coincide with the breeding season, when adult migrants return to the UK, increasing their numbers in Liverpool (Malling Olsen and Larsson, 2003; Burton et al., 2013).

Juvenile Lesser black-backed gulls' abundance was not affected by air temperature. Lesser black-backed gulls are not year-round residents in Liverpool, as the majority migrate south for the winter

(Ross-Smith et al., 2015; Malling-Olsen and Larsson, 2003). Juveniles spend the early part of the breeding season in the nest before fledging and subsequently migrating, making their abundance more strongly dependent on phenology rather than short-term temperature changes (Camphuysen et al., 2023; Spelt, 2020; Camphuysen, 2011). Juveniles are not sexually mature and do not typically return to their natal breeding colonies during the breeding season, as they start breeding from the fourth year onwards (Ross-Smith et al., 2015; Ross-Smith, 2014). This may have contributed to the low number of juvenile Lesser black-backed gulls recorded across the count points in Liverpool and the high proportion of zero counts, which was modelled using a zero-inflated model but may nevertheless have reduced the statistical power to detect a relationship between variables (Martin et al., 2005; Zuur et al., 2009b).

The contrasting effects of air temperature on adult and juvenile Lesser black-backed gulls may reflect differences in their seasonal occurrence in Liverpool. More adult than juvenile Lesser black-backed gulls were recorded during the surveys. Juveniles migrate south after fledging and usually do not return to their natal breeding colonies to breed until they are approximately four years old (Ross-Smith et al., 2015; Ross-Smith, 2014). Therefore, even if there was a relationship between juvenile Lesser black-backed gull abundance and air temperature, the relatively low number of juveniles may have obscured that effect (Martin et al., 2005; Zuur et al., 2009b).

The differing responses of Herring and Lesser black-backed gulls to air temperature may be due to their migratory strategies. As a resident species in Liverpool, Herring gull abundance remains relatively stable throughout the year, potentially reducing the influence of seasonal changes in air temperature on their abundance (Malling-Olsen and Larsson, 2003; Burton et al., 2013). In contrast, the increase in adult Lesser black-backed gull abundance with higher temperatures may be related to their return to the UK during the breeding season, when air temperatures are naturally higher than during the non-breeding season (Ross-Smith et al., 2015; Camphuysen et al., 2023). Consequently, the positive relationship between air temperature and adult Lesser black-backed gull abundance observed in this study may reflect seasonal migration patterns, which are not observed in Herring gull populations.

7.2 Tidal elevation

Tidal elevation unexpectedly did not affect gull abundance across species and ages in the conditional components of the models. However, the zero component of juvenile and adult Herring gull models showed that during low tide, there was a higher probability of zero counts. This suggests that the tide influences the presence of the species, but not their number, when other birds are already present. Previous studies have reported that Herring and Lesser black-backed gulls forage on intertidal mudflats during low tides, which may reduce their numbers across terrestrial foraging locations (Burger, 1987; Sibly & McCleery, 1983; Burger, 1983). The lack of a significant effect of tidal elevation on gull numbers may be caused by their resting and loafing behaviour near the riverside, even after low tide, or by utilising their diving ability to obtain underwater prey. Comparable behaviour was found in Lesser black-backed gulls near Texel Island in the Netherlands, where gulls did not return to the colony after low tide but rested at sea

(Shamoun-Baranes et al., 2011). Likewise, a study conducted on urban gull population in Bristol did not show any effect of tides on gull distribution, as they foraged only on anthropogenic food sources, regardless of tidal elevation (Spelt, 2020).

Adult Herring and Lesser black-backed gulls might have established foraging routines not related to tides, and they may be mostly reliant on urban refuse or, in the case of Lesser black-backed gulls, on marine food sources (Spelt, 2020; Lato et al., 2021; Kim and Monaghan, 2006a). This pattern has been shown in the studies conducted on both of these species in urban settings (Spelt, 2020; Lato et al., 2021). Juveniles may also focus on easily available food sources, such as human refuse or waste from commercial fishing vessels, which do not depend on the tidal elevation of the River Mersey (Ramos et al., 2009; Holt et al., 2012; Bertellotti and Yorio, 2000). Their lack of experience in obtaining prey in natural habitats, such as crabs or shrimp, may discourage them from relying exclusively on tidal mudflats for foraging (Lato et al., 2021; Skórka and Wójcik, 2006). Overall, these findings may suggest that both species rely on predictable anthropogenic, terrestrial or marine food sources, which may explain the lack of an effect of tidal elevation on their abundance.

7.3 Time of day and season

The adult Herring gull model did not include the season as one of the explanatory variables, as it was removed during the backward stepwise elimination process. The variable did not have a significant effect on Herring gull abundance, and its removal optimised model fit by lowering AIC. While the literature indicates that adult Herring gulls show nest attentiveness during the breeding season (Spelt, 2020; Isaksson et al., 2016), this behaviour is constrained temporally, lasting around three months, when at least one adult is at the nest (Spelt, 2020). In contrast, the present study defined the breeding season as a broader five-month window (April to August), encompassing not only nesting but also chick-rearing and fledging stages. The difference between the two types of categorisation could have obscured any detectable seasonal variance in the abundance of this resident species. Future studies could improve the precision of seasonal analyses by observing a sample of local nests to determine the exact timing of nesting activities and align the seasonal categorisation with breeding stages of the focal species.

The results showed that the abundance of juvenile Herring gulls was positively associated with the non-breeding season. The number of juvenile gulls may increase during the non-breeding season because of phenology. Juveniles would have only recently hatched and remained as chicks in their nests during much of the breeding season, and they only left the nests in autumn (Spelt, 2020; Greig et al., 1983). During the non-breeding season, they begin to explore urban habitats for the first time and follow their parents to anthropogenic and natural food sources, thereby increasing their detectability in terrestrial sites (Greig et al., 1983).

The difference in the results observed between adult and juvenile Herring gulls may reflect their breeding status. During the breeding season, at least one adult from each Herring gull breeding pair regularly leaves the nest to forage while provisioning chicks, making them more likely to be recorded during counts (Spelt, 2020; Malling-Olsen and Larsson, 2003). In contrast, juvenile Herring gulls spend much of this period at or near the nests before fledging, reducing their likelihood of being recorded during counts (Spelt, 2020; Greig et al., 1983).

Adult Lesser black-backed gull numbers decreased during the non-breeding season, as they are migrants and usually leave the North of England during the winter months (Malling-Olsen and Larsson, 2003). Their number may again increase during the breeding season as they return to the UK (Malling-Olsen and Larsson, 2003; Ross-Smith et al., 2014).

Season was removed from the final model for juvenile Lesser black-backed gull abundance during the backward stepwise selection process. Removing season improved the model fit by lowering AIC of the model, as season did not significantly affect the abundance of juvenile Lesser black-backed gulls. The results may reflect consistently low abundance of juvenile Lesser black-backed gulls throughout the year. During the breeding season, juveniles spend much of their time at or near the nest, then after fledging migrate south and some of them do not return to the UK until they reach sexual maturity (Malling-Olsen and Larsson, 2003; Ross-Smith et al., 2014; Ross-Smith et al., 2015). Therefore, the lack of a significant seasonal effect on the abundance of juvenile Lesser black-backed gulls might have been caused by their low numbers.

The difference in the results observed between juvenile and adult Lesser black-backed gulls may arise from age-specific migration behaviour. Adults migrate south in the non-breeding season and return to the UK during the breeding season, increasing their abundance in Liverpool (Malling-Olsen and Larsson, 2003; Ross-Smith et al., 2014). In contrast, juveniles remain scarce throughout the year, as they spend the majority of the breeding season at the nest after hatching (Malling-Olsen and Larsson, 2003; Ross-Smith et al., 2014; Ross-Smith et al., 2015). After fledging, they migrate and may not return to the UK until reaching full sexual maturity (Ross-Smith et al., 2014; Ross-Smith et al., 2015). This contrast may reflect different age-related migration patterns within the same species.

The contrasting seasonal effect on Herring and Lesser black-backed gull abundance may be related to the differences in their migration strategies. Herring gulls are largely resident in the UK, meaning that seasonal changes in abundance are mainly related to local breeding behaviour, such as juveniles remaining at or near the nests (Malling-Olsen and Larsson, 2003; Spelt, 2020). In contrast, Lesser black-backed gulls are migratory, with adult abundance decreasing during the winter months as individuals leave the UK, which is not observed in adult Herring gulls (Malling-Olsen and Larsson, 2003; Ross-Smith et al., 2014; Ross-Smith et al., 2015).

The adult Herring gull abundance was higher in the afternoons in comparison to evenings. Gull activity in the afternoons may reflect the temporal availability of anthropogenic food sources. Gulls

can adjust to human activities, such as waste deliveries to refuse tips or lunch breaks at schools, by exploiting foraging opportunities in urban spaces (Spelt, 2020). The lower number of gulls in the evenings is consistent with other studies, which show that gulls usually rest in the evenings and at night, a pattern partly affected by reduced visibility, which may therefore hinder their foraging efforts (Isaksson et al., 2016; Sibly and McCleery, 1983; Beauchamp, 2009). By contrast, some studies report nocturnal activity in urban gulls due to light pollution (Isaksson et al., 2016; Gutowsky et al., 2023). Accordingly, nocturnal activity may also occur among gull populations in Liverpool. In this study, six out of the nine count points were established in the urbanised areas with various levels of artificial lighting at night, which could facilitate nocturnal foraging in these spaces. The methodology of my study was restricted to counts executed during the daytime hours; therefore, it was not possible to conclusively determine whether urban gulls in Liverpool were more active at night than during the day.

The time of day factor was not included in the final model for juvenile Herring gull abundance, as it did not have a significant effect on their abundance. It was removed during the backward stepwise selection process because omitting it improved the model fit by lowering the AIC value. Previous studies focusing on the abundance of gulls frequently omit juveniles, making a comprehensive comparative analysis difficult (Raven and Coulson, 1997; Belant et al., 1995; Kajzer et al., 2012). However, other studies researching gull movements have discovered that urban gulls adjust to predictable human schedules, for example, aligning their foraging activities with school lunch breaks when anthropogenic food is more accessible (Spelt, 2020; de Faria et al., 2021). This may not have been the case in my study, as juvenile Herring gulls may not have learned to associate human activities with foraging opportunities. Consequently, they may not adjust their foraging patterns to the time of day, which could explain why their abundance was not affected by the time of day. Alternatively, the lack of a time-of-day effect may indicate that juvenile Herring gulls were not actively seeking or avoiding interactions with humans. This latter explanation aligns with the findings of my study, which also failed to find a correlation between juvenile Herring gull abundance and human density.

In my study, the time of day might not have had a significant effect on the abundance of juvenile Herring gulls because they were possibly not adept at recognising these human activity patterns (Gimeno et al., 2023; Ravasi et al., 2023). This differs from experienced adult Herring gulls, which were significantly more abundant in the afternoons than in the evenings (Gimeno et al., 2023; Ravasi et al., 2023). Differences in foraging experience and the ability to recognise profitable foraging opportunities may explain the contrasting results between juvenile and adult Herring gulls.

The final model for adult Lesser black-backed gull abundance did not include time of day as a factor. Time of day did not significantly affect the abundance of adult Lesser black-backed gulls in my study, and its removal improved the model fit by lowering the AIC of that model. A study conducted on adult Lesser black-backed gulls in Bristol, UK, showed that this species is active throughout the day (Spelt, 2020). Their movements were particularly linked to human activity patterns such as school lunch breaks or waste tip deliveries, where they could partially predict when food would become available. However, adult Lesser black-backed gulls did not show a single, uniform abundance pattern across habitat types; instead, they foraged and moved between

different sites on the basis of immediate food availability (Spelt, 2020). Consequently, the abundance of adult Lesser black-backed gulls in Liverpool may not have been influenced by time of day or predictable human activities occurring at particular times, as their movements are likely driven by the availability of a wider range of food resources, including terrestrial as well as marine sources (Kim and Monaghan, 2006a; Malling-Olsen and Larsson, 2003).

The number of juvenile Lesser black-backed gulls was lower in the mornings compared to afternoons and evenings. Similar to adult Herring gulls, this may reflect greater anthropogenic food availability in the afternoons than in the mornings. Juveniles may be more active in the evenings than in the mornings, possibly due to the higher utilisation of artificial lights and reduced competition for food resources after sunset (Gutowsky et al., 2023; Lavin et al., 2003; Beauchamp, 2009). As they are not yet skilled at foraging, this may be their opportunity to obtain food at places with otherwise high intraspecific competition (Monaghan et al., 1986). The lack of increased gull numbers in the mornings is contrary to the findings from other studies, which show that gulls forage early in the morning in green urban spaces, feeding on soil invertebrates such as earthworms, *Lumbricus terrestris* (Spelt, 2020). However, in my study, this could have been caused by the low number of sampling locations based in urban parks, as only three out of nine count points were based in green urban spaces, while the remainder were in areas with varying degrees of urbanisation with limited access to soil invertebrates.

The differing effects of time of day on adult and juvenile Lesser black-backed gull abundance may reflect age-related differences in their foraging behaviour. Adult Lesser black-backed gulls were not affected by time of day; this might be explained by structured abundance patterns that occurred locally within specific sites, but became obscured when examining generalised abundance patterns across all habitats, similarly to Spelt's (2020) results. In contrast, juvenile Lesser black-backed gulls might have been affected by time of day due to their heavier reliance on the predictable feeding opportunities (Spelt, 2020). This temporal pattern may be linked to their lack of foraging experience, which causes lower efficiency in obtaining food, and requires them to forage for longer durations than adults (Morel et al., 2024; Marchetti and Price, 1989). Consequently, juveniles may forage for longer in the same localised habitats (Morel et al., 2024), relying on the predictable peaks of food availability during certain times of the day, which may explain these temporal patterns observed in my study.

The contrasting results of adult Herring and Lesser black-backed gulls regarding the time of day may reflect differences in their foraging ecology (Spelt, 2020; Kim and Monaghan, 2006a). Herring gulls are highly opportunistic foragers and may adjust to the activity of humans, while Lesser black-backed gulls may explore various other food resources (Spelt, 2020; Kim and Monaghan, 2006a).

The time of day affected the abundance of juvenile Lesser black-backed gulls, but not juvenile Herring gulls, possibly because of their distinct foraging behaviour (Kim and Monaghan, 2006a; Garthe et al., 1999a, 1999b). Juvenile Lesser black-backed gulls may rely more on the food resources which are available at certain times of day, such as anthropogenic foods (Kim and Monaghan, 2006a; Spelt, 2020). This behavioural trait suggests that juvenile Lesser black-backed gulls may travel to the riverside in the mornings to forage for fish from fishing vessels or exploit waste disposal sites during daily morning refuse deliveries, both of which operate on a predictable

morning schedule (Gyimesi et al., 2016; Spelt, 2020; Ramírez et al., 2015). In contrast, juvenile Herring gulls are highly generalised opportunists and may not rely heavily on a single predictable food source, as they are still learning to optimise their foraging efficiency (Greig et al., 1983; Gimeno et al., 2023; Sibly and McCleery, 1983).

7.4 Land cover and the number of people

Surprisingly, land cover had only an impact on the abundance of juvenile Lesser Black-backed gulls. Results have shown that with an increase in urbanisation, the number of juvenile Lesser black-backed gulls increased. Juveniles may rely more on anthropogenic foods, which are easily available in urbanised areas, consistent with their increased numbers during afternoons and evenings. As they still lack experience in catching marine prey, human refuse may be easier to obtain (Marzluff, 2001). Cristol et al. (2017) found that juvenile Herring gulls were less efficient at foraging but were choosing the same foraging patches as adults in natural habitats. This behaviour may differ in urbanised areas, where tall buildings and an altered landscape can hinder juveniles' ability to follow adults as easily as they do in their natural habitats. Adult gulls can effectively forage on anthropogenic food sources as well as on natural ones, which can reduce the impact of urbanisation on their abundance, driven by foraging opportunities (Kim & Monaghan, 2006; Isaksson et al., 2016). However, this result differs from what is already described in the literature. Several studies have shown that when gulls have a choice of foraging between urbanised and non-urbanised spaces, they often prefer urban areas (Spelt, 2020; Huig et al., 2016; Lato et al., 2021). Insufficient anthropogenic food sources around the chosen count points may also explain the lack of detectable impact of urbanisation on adult gulls. Adult gulls may favour only places with reliable and abundant foraging opportunities, also taking into consideration nutritional value and competition; if this is not the case, they switch habitats (Washburn et al., 2013; Sherley et al., 2020; Isaksson et al., 2016; Bond, 2016). Juvenile gulls, by contrast, may not be experienced in recognising the best foraging opportunities, relying heavily on general land cover cues.

The effect of urbanisation was not observed in the abundance of adult or juvenile Herring gulls; this may be explained by species-specific differences in foraging ecology and their degree of reliance on urban habitats. Herring and Lesser black-backed gulls are highly opportunistic generalists and exploit urban and non-urban spaces; however, specific foraging patterns may change depending on the environmental conditions (Spelt, 2020; Kim and Monaghan, 2006a). Earlier studies documented that Lesser black-backed gulls primarily foraged at sea, whereas Herring gulls mainly utilised intertidal zones, although both species also exploited urban areas opportunistically (Belant et al., 1998; Kim and Monaghan, 2006a). More recent GPS-based studies have shown greater variability in abundance and distribution patterns related to foraging (Spelt, 2020; Lato et al., 2021). For example, Lesser black-backed gulls in a Bristol study rarely foraged in marine habitats, and instead concentrated their foraging efforts in urban, suburban and agricultural areas (Spelt, 2020). Similarly, another GPS tracking study showed that Herring gulls also spent a large proportion of their foraging time in urban areas (Lato et al., 2021). These findings suggest that foraging patterns and abundance are dependent on geographical location, land cover and also the methods used to quantify foraging behaviour and movement. Therefore, the lack of an effect of urbanisation on

Herring gulls observed in my study may reflect the ability to exploit a wider range of habitats and food resources. In contrast, juvenile Lesser black-backed gulls may rely more on the predictable anthropogenic foods while developing their foraging techniques and strategies, which may reflect why their higher abundance in more urbanised areas (Morel et al., 2024; Marchetti and Price, 1989). Despite growing research interest in the subject, relatively little is still known about the foraging ecology of Lesser black-backed gulls in coastal cities such as Liverpool. These explanations are not conclusive; however, they may provide a foundation for further research.

The human presence had a significant effect only on the number of juvenile Lesser black-backed gulls. The conditional component of the model indicated that with an increasing number of people, the number of juvenile Lesser black-backed gulls decreased. The zero component in the same model indicated that the increasing number of people reduced the likelihood of zero counts for juveniles of this species. This suggests that the human presence initially attracts juvenile Lesser black-backed gulls, but larger human gatherings seem to act as a deterrent. This is consistent with results from other studies. For example, large crowds of people and a lack of foraging opportunities accompanying their presence may act as a deterrent for gulls (Spelt, 2020; Burger and Galli, 1987). Overall, juvenile Lesser black-backed gulls may respond more to foraging opportunities than to the number of people, and their fearfulness may deter them from large gatherings of people.

The abundance of adult Lesser black-backed gulls was not affected by human density, whereas the abundance of juveniles of the same species decreased with increasing human density. This may be because adults are more experienced foragers and less sensitive to human disturbance (Borgmann, 2011; Price, 2008). Adult Lesser black-backed gulls may be more accustomed to the presence of humans and better able to distinguish between threatening and non-threatening situations, whereas juveniles may be cautious of large numbers of humans, therefore actively avoiding areas with higher human activity (Burger, 1986; Liu et al., 2025).

Human density did not significantly affect the abundance of juvenile or adult Herring gulls. This may be explained by the fact that human density may not accurately represent food availability at a given site. Several studies suggest that food availability, rather than human presence itself, is the main attractant of gulls to urban habitats, although most studies did not record the exact number of people present (Faria et al., 2021; Spelt, 2020; Liu et al., 2025). Specific human behaviours, such as intentional feeding events, school lunch breaks, or refuse deliveries to the waste tips, may attract large numbers of gulls regardless of the number of people present, as these events increase the availability of food resources (Faria et al., 2021; Spelt, 2020; Liu et al., 2025). The methodology of the present study did not include observations of specific human behaviours, such as feeding events, and did not quantify the availability of food resources at each count point. These factors could have influenced gull abundance independently of human density; therefore, future studies should include these variables to better differentiate between the effects of human density and food availability.

The absence of an effect of human density on adult Herring and Lesser black-backed gull abundance may reflect similarities in their opportunistic foraging strategies despite differences in

their preferred food sources (Spelt, 2020; Kim and Monaghan, 2006a). Although Herring gulls more often rely on anthropogenic food resources and Lesser black-backed gulls have been considered more reliant on marine resources (Belant et al., 1998; Kim & Monaghan, 2006a), neither resource is necessarily associated with areas of high human density. Consequently, food availability rather than human density may be a better predictor of adult gull abundance.

In contrast, juvenile gulls showed different responses to human density. The number of people did not affect the abundance of juvenile Herring gulls, whereas juvenile Lesser black-backed gull abundance decreased with higher human density. These contrasting results may reflect species-specific responses to human disturbance (Price, 2008; Borgmann, 2011; Burger, 1986). Juvenile Herring gulls may be more tolerant of human presence or more capable of exploiting a wider range of food resources, reducing their dependence on local human density as an indicator of foraging opportunities (Kim and Monaghan, 2006a; Price, 2008). In contrast, juvenile Lesser black-backed gulls may be more sensitive to human disturbance, while still benefiting from anthropogenic food resources but avoiding areas with larger crowds (Noreen et al., 2025; Price, 2008; Burger, 1986).

7.5 Management implications in mitigating human-gull conflict

The results of this study may improve the human-gull conflict mitigation techniques, which are already in use across the UK. Waste collection and management is one of the biggest drivers of gull nuisance in urbanised areas. The results have shown that gull numbers increase in the afternoons and evenings; therefore, waste should be collected before the afternoon. To avoid gulls foraging on refuse, rubbish should also be promptly removed from bins and streets during warm and windy atmospheric conditions. This is also important, especially in the highly urbanised areas, as urban land cover may increase their number. Litter levels should be monitored in city centres, shopping areas, schools, and parks, where there is usually a high number of uncleared refuse, which can attract gulls and increase nuisance events.

In the past, various techniques have been employed to deter gulls from buildings and various protected areas such as airports. Some of the methods include professional falconry, noise deterrents or flashing lights (Belant, 1997; Rock, 2005). As they are not a long-term solution, their efficiency should be increased as much as possible. Mentioned deterrents should be utilised during times of the highest abundance of gulls, which would make them most efficient. Based on this study, gull repellents would be most useful during afternoons and evenings and when it is least cloudy and the air temperature is high, which is also when gulls are most abundant and possibly causing most human-gull conflicts.

Public education is a critical component of strategies to decrease human-gull conflict (Ross-Smith, 2019). Certain human behaviours, such as littering, attract gulls, leading to human-gull conflict (Rock, 2005). The community should be educated on why it might be dangerous to leave out unsecured rubbish, as it may lead to aggressive gull behaviours and put public health in danger (Daszak et al., 2000; Martín-Maldonado et al., 2020; Rock, 2005). At the same time, the Herring and Lesser black-backed gulls are declining species in the UK (Stanbury et al., 2021), and a negative perception of their nuisance behaviour may lead to retaliation toward gulls, which would

further contribute to their decline. Public education should include information about the conservation status of gulls, their ecological importance, as well as guidance on the dangers of littering. These initiatives will enable communities to better understand their impact on gull species, promote coexistence, and reduce human-gull conflicts, which are particularly prevalent in cities.

7.6 Limitations

The limited number of count points and repetitions might have been a potential constraint in this study. Although nine count points could capture the differences between different land covers, the increased number of locations could better reflect urban gradients and more detailed spatial variation. This design choice was made due to the logistical and time constraints associated with travelling to multiple sites within a short period. It could be improved by having a better transportation system in place, which would allow access to more checkpoints across the entire Merseyside region.

Another potential constraint could be variability in the behaviour of gulls and humans. Recording various gull behaviours during counts could have provided additional context for interpreting the results of this study. Gulls may exhibit different behaviours across various times of day, seasons, and weather conditions, which could, in effect, explain certain results of this study and help better understand gull abundance (Faria, 2022; Spelt, 2020). During the study, it would have been useful to record any intra- or interspecific interactions, as well as anthropogenic food availability (such as anthropogenic feeding and open rubbish bins). Human behaviour can also impact gull abundance, as gulls exhibit different behaviours during public feeding or when actively deterred by humans (Burger and Galli, 1987). The direct behavioural observations could have improved the outcomes of this study by recording human-gull interactions and incorporating them into the analysis and interpretation of the results.

8. Conclusions

The understanding of the abundance of urban gulls has gained increasing attention in recent years due to its importance for public health, urban management and mitigation of human-gull conflict (Stanbury et al., 2021; Eaton et al., 2015; Rock, 2005). Additionally, some gull species, such as Herring and Lesser black-backed gulls, are declining, which should be accounted for when conducting studies related to their conflict with humans (Stanbury et al., 2021; Eaton et al., 2015; Burnell et al., 2023). Increasing urbanisation and a rising number of urban gulls lead to various conflicts between people and gulls, including aggressive behaviour, droppings, and property damage (Rock, 2005; Belant, 1997). These issues require swift intervention by city councils and stakeholders to mitigate the risk and protect public health, while also protecting the declining population of gulls (Bosch et al., 2000; Coulson & Coulson, 2009).

Despite the growing research conducted on the subject, it remains unclear which factors have the greatest impact on the abundance of gulls. Previous studies have mainly focused on one aspect of the issue without considering the combined effects of anthropogenic and environmental variables, such as weather, tides, land cover, and human population (Spelt, 2020; Isaksson et al., 2016; Faria, 2022). Moreover, to date, no other study has been conducted in Liverpool, UK, that compares gull abundance throughout the entire year, including breeding and non-breeding seasons, and is based on monthly observations.

This study has identified how various natural factors impact the abundance of adult and juvenile Herring and Lesser black-backed gulls living in the same urban area. It was found that stronger wind gusts were associated with an increased abundance of juvenile Lesser black-backed gulls, which may indicate that juveniles potentially shift towards terrestrial areas, away from the riverside, during periods of strong winds. This study also showed that higher temperatures had a significant positive impact on the abundance of juvenile Herring gulls as well as adult Lesser black-backed gulls. This was already found in other studies, and may be linked to the 'urban heat island' effect and easier access to anthropogenic food resources (Opp et al., 1987; Lopes, 2021; Spelt, 2020). It was found that greater cloud cover negatively impacts the abundance of adult Herring gulls, which may be related to low visibility and therefore hinders the foraging abilities of gulls.

The next result showed that the number of adult Herring gulls was higher in the afternoon in comparison to the evening. This may be caused by the higher detectability of this species in the afternoons as they usually rest in the evening in quiet places, making them less detectable. Conversely, juvenile Lesser black-backed gulls increased during afternoons and evenings in comparison to mornings. This is possibly caused by higher anthropogenic food availability in the afternoons and reduced inter- and intraspecific competition in the evenings. The juvenile Herring gull abundance was higher during the non-breeding season in comparison to the breeding season. It might reflect becoming more independent and leaving nests in the autumn and winter, while during the breeding season, their movement was limited to the nest. The opposite was found in the adult Lesser black-backed gulls, as their numbers declined during the non-breeding season. They migrate after the breeding season, leaving the North West, which decreases their number. The findings of this study have also shown that the greater the number of humans, the lower the juvenile Lesser black-backed gull abundance, possibly caused by gulls being more attracted to the foraging opportunities rather than to humans themselves. Finally, the study found that the number of juvenile Lesser black-backed gulls increased in the urbanised areas in comparison to green urban areas. This may be due to easier access to highly calorific, anthropogenic foods available across the city centre. This study provides an insight into how fine-scale anthropogenic and natural factors impact gull abundance, reducing a gap in the knowledge of urban avian ecology, especially for these two declining species and their particular age groups.

The findings of this study contribute to a better understanding of how environmental and anthropogenic factors impact the abundance of urban gulls. Urban gull abundance is highly complex, varying across gull species and age classes. It was demonstrated that weather, season, time of day, and number of people impact gulls differently, depending on their species and age, which should be taken into account when developing management strategies. Appropriate

management applications are essential in light of declining natural habitats and changing land cover, which affect all species, including declining Herring and Lesser black-backed gulls. These species increasingly rely on urban areas for breeding and foraging needs, which in effect increases human-gull conflict. Implementation of the findings of this study by stakeholders through targeted waste management, education, and improved urban design can reduce the human-wildlife conflict and foster long-term coexistence for both.

9. References

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10. Appendix

Table A1. Model selection for adult Herring gulls out of GLMMs on the basis of the lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Herringgull adults	1	(1 Place) + Light + people + temp + tide + wind + clouds +Season+Time_of_day+Land	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1014	2777	0	-1363	1175
	2	(1 Place) + Light + temp + tide + wind + clouds +Season+Time_of_day +Land	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1015	2775	2	-1363	1175
	3	(1 Place) + Light + temp + tide + clouds +Season+Time_of_day+Land	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1016	2773	4	-1363	1173
	4	(1 Place) + Light + temp + tide + clouds +Season+Time_of_day	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1018	2771	6	-1364	1180
	5	(1 Place) + Light + temp + clouds +Season+Time_of_day	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1019	2770	7	-1364	1181
	6	(1 Place) + Light + temp + clouds +Time_of_day	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1020	2769	8	-1365	1182
	7	(1 Place) + Light + clouds +Time_of_day	Light + people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1021	2770	7	-1366	1170
	8	(1 Place) + Light + clouds +Time_of_day	people + Land+ temp + tide + wind + clouds + Season + Time_of_day	1022	2768	9	-1366	1172
	9	(1 Place) + Light + clouds +Time_of_day	people + Land+ temp + tide + clouds + Season + Time_of_day	1023	2766	11	-1366	1172
	(Best-fit model)10	(1 Place) + Light + clouds +Time_of_day	people + Land+ temp + tide + clouds + Time_of_day	1024	2764	13	-1366	1171

Table A2. The results of the best Zero-Inflated GLMM for adult Herring gulls, representing the effects of predictors on the gull zero inflation in the zero component. The results include estimates and standard error (SE). Significant results are in bold.

Zero Component - Herring Gull Adults			
Term	Estimate	Std.Error	P.value
(Intercept)	4.052	0.571	<0.001
people	0.012	0.013	0.350
temp	-0.116	0.033	<0.001
tideLow	0.642	0.295	0.029
clouds	-1.315	0.493	0.008
Time_of_dayevening	-0.851	0.506	0.093
Time_of_daymorning	-1.966	0.380	<0.001
LandSuburban	-1.811	0.340	<0.001
LandUrban	-5.614	0.932	<0.001

Table A3. Model selection for juvenile Herring gulls of GLMMs on the basis of the lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Herringgull juveniles	(Full model) 1	(1 Place) + Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1014	1910	0	-929	668
	2	(1 Place) + Season +tide + Time_of_day+ Land + Light +people +temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1015	1908	2	-929	668
	3	(1 Place) + Season +tide + Land + Light +people +temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1017	1907	3	-931	675
	4	(1 Place) + Season +tide + Land + Light +temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1018	1905	5	-931	675
	5	(1 Place) + Season + Land + Light +temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1019	1903	7	-931	675
	6	(1 Place) + Season + Light +temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1021	1901	9	-932	680
	7	(1 Place) + Season +temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1022	1899	11	-932	682
	8	(1 Place) + Season* temp+ wind	Season +tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1021	1899	11	-930	683
	9	(1 Place) + Season* temp+ wind	tide + Time_of_day+ Land + Light +people +temp+ wind + clouds	1022	1897	13	-930	681
	10	(1 Place) + Season* temp+ wind	tide + Time_of_day+ Land + Light +people +temp+ clouds	1023	1895	15	-931	680
	11	(1 Place) + Season* temp+ wind	tide + Time_of_day+ Land + Light +temp+ clouds	1024	1894	16	-931	682
	(Best-fit model) 12	(1 Place) + Season* temp+ wind	tide + Time_of_day+ Land + Light +temp	1025	1894	16	-932	689

Table A4. The results of the best Zero-Inflated GLMM for juvenile Herring gulls, representing the effects of predictors on the gull zero inflation in the zero component. The results include estimates and standard error (SE). Significant results are in bold.

Zero Component - Juvenile Herring Gulls			
Term	Estimate	Std. Error	p-value
(Intercept)	5.423	0.930	<0.001
tideLow	1.178	0.479	0.014
Time_of_dayevening	1.165	0.642	0.069
Time_of_daymorning	-3.189	0.808	<0.001
LandSuburban	-2.914	0.685	<0.001
LandUrban	-4.825	0.786	<0.001
Light	0.000	0.000	0.021
temp	-0.271	0.063	<0.001

Table A5. Model selection for adult Lesser black-backed gulls out of GLMMs on the basis of the lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Lesser black-backed gulls adults	(Full model) 1	(1 Place)+Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1014	1189	0	-568	464
	2	(1 Place)+Season+tide+Time_of_day+Land+Light+temp+wind+clouds	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1015	1187	2	-568	463
	3	(1 Place)+Season+tide+Time_of_day+Light+temp+wind+clouds	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1017	1183	6	-569	463
	4	(1 Place)+Season+tide+Light+temp+wind+clouds	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1019	1180	9	-569	467
	5	(1 Place)+Season+tide+Light+temp+wind	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1020	1179	10	-569	464
	6	(1 Place)+Season+Light+temp+wind	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1021	1178	11	-570	468
	(Best-fit model) 7	(1 Place)+Season+Light+temp	Season+tide+Time_of_day+Land+Light+people+temp+wind+clouds	1022	1177	12	-571	472

Table A6. The results of the best Zero-Inflated GLMM for adult Lesser black-backed gulls, representing the effects of predictors on the gull zero inflation in the zero component. The results include estimates and standard error (SE). Significant results are in bold.

Zero Component - Adult Lesser black-backed Gulls			
Term	Estimate	Std. Error	p-value
(Intercept)	-0.069	1.668	0.967
SeasonNon-breeding	3.159	0.888	<0.001
LandSuburban	-5.459	1.102	<0.001
LandUrban	-10.220	2.796	<0.001
Light	0.000	0.000	0.025
people	0.069	0.028	0.013
temp	-0.494	0.131	<0.001
wind	0.509	0.167	<0.01
clouds	3.179	1.472	0.031

Table A7. The results of the best Zero-Inflated GLMM for juvenile Lesser black-backed gulls, representing the effects of predictors on the gull zero inflation in the zero component. The results include estimates and standard error (SE). Significant results are in bold.

Zero Component - Juvenile Lesser black-backed Gulls			
Term	Estimate	Std. Error	p-value
(Intercept)	4.887	4.776	0.306
tideLow	3.149	1.713	0.066
Time_of_dayevening	1.699	1.799	0.345
Time_of_daymorning	-8.128	3.283	0.013
LandSuburban	1.977	2.525	0.434
LandUrban	6.907	4.039	0.087
people	-0.167	0.075	0.026
temp	-0.733	0.220	<0.001
wind	1.142	0.536	0.033
clouds	-4.798	3.094	0.121

Table A8. Model selection for juvenile Lesser black-backed gulls out of GLMMs on the basis of the lowest AIC. All models compared Zero-Inflated Negative Binomial models. The terms in the table include: logLik = log-likelihood ratio statistic, df = degrees of freedom. AIC = Akaike information criterion, dAIC = difference between AIC units, comparing full model to the current model. Best-fit model is in bold.

Model response variable	Model version	Conditional Component	Zero component	df	AIC	dAICc	Loglik	Deviance
Lesser black-backed gulls juveniles	(Full model) 1	(1 Place)+Season +tide + Time_of_day+ Land +people +temp+ wind + clouds	tide + Time_of_day+ Land +people +temp+ wind + clouds	1017	254	0	-104	110
	2	(1 Place)+Season +tide + Time_of_day+ Land +people +temp+ wind	tide + Time_of_day+ Land +people +temp+ wind + clouds	1018	252	2	-104	110
	(Best-fit model) 3	(1 Place) +tide + Time_of_day+ Land +people +temp+ wind	tide + Time_of_day+ Land +people +temp+ wind + clouds	1019	251	3	-105	107