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INTERACTIONS BETWEEN GULLS AND HUMANS IN URBAN AREAS: AN ECOLOGICAL AND CONFLICT MANAGEMENT PERSPECTIVE

Tese no âmbito do Doutoramento em Biociências, especialização em Ecologia, orientada pelo Professor Doutor Jaime Albino Ramos, pelo Doutor Vítor Hugo Rodrigues Paiva e pela Doutora Ana Marta dos Santos Mendes Gonçalves e apresentada ao Departamento de Ciências da Vida da Faculdade de Ciências e Tecnologia da Universidade de Coimbra.

Dezembro de 2021

Departamento Ciências da Vida
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Resumo

Várias espécies generalistas têm vindo a colonizar áreas urbanas como resultado da degradação dos seus habitats originais em combinação com o aumento de recursos alimentares previsíveis e das condições de reprodução em áreas urbanas. As gaivotas começaram a construir ninhos nos telhados de zonas urbanas por volta de 1890, e desde essa altura cada vez mais espécies de gaivotas têm vindo a reproduzir-se em edifícios localizados em vários países do mundo. O comportamento de reprodução e de procura de alimento associado com a colonização de ambientes urbanos tem causado diversos conflitos com a população humana, não só pelos distúrbios resultantes de interações entre humanos e gaivotas, mas também por estas serem reservatórios de agentes patogénicos. No entanto as áreas urbanas estão associadas a uma variedade de desafios no que toca a estudar estas aves, pelo que a ecologia de reprodução e alimentação das gaivotas urbanas ainda não é totalmente compreendida, e ainda não é claro se as áreas urbanas representam uma armadilha ecológica, com benefícios imediatos mas com possíveis consequências para a saúde dos indivíduos a longo termo. Portanto, no âmbito desta tese, vários parâmetros da vida das gaivotas urbanas foram caracterizados e avaliados para compreender quais são as vantagens e desvantagens que as gaivotas enfrentam quando colonizam novos ambientes urbanos; quais os fatores que despoletam e encorajam as gaivotas a usarem as cidades e como interagem com a sociedade humana. Em suma, esta tese inclui o estudo da dieta, estado de saúde, sucesso reprodutor, uso do habitat urbano e comportamento da Gaivota-de-patas-amarelas (*Larus michahellis*), na cidade do Porto.

Os principais resultados realçam: (1) a importância das atividades humanas ao criar condições desejáveis para o estabelecimento de novas colónias de gaivotas urbanas, contribuindo ao mesmo tempo para a deterioração das condições nas colónias tradicionais naturais, e a importância de realizar estudos de monitorização de longa duração que capturem a evolução das populações de gaivotas urbanas; (2) a importância que as presas marinhas ainda têm na dieta das gaivotas urbanas, particularmente na dieta das crias mais novas; (3) os compromissos que as gaivotas urbanas enfrentam entre as vantagens da reprodução em colónias urbanas de menor densidade populacional, onde a transmissão de doenças é menos provável de ocorrer, com as desvantagens de ter uma dieta antropogénica de menor qualidade; e por último, (4) a importância da temporada de inverno no uso de habitat urbano e na ocorrência de interações entre humanos e gaivotas nas praças da cidade, que tendem a aumentar durante esta época e que são sobretudo desencadeadas pela alimentação de aves pelo homem. A implementação de medidas que visem à redução de grandes fontes de alimento previsível, de áreas adequadas à nidificação urbana e à redução do sucesso reprodutor, em combinação com grandes campanhas de educação ambiental e de sensibilização, deverá melhorar a eficácia da gestão de conflitos entre humanos e gaivotas, ao abordar este problema de uma forma holística.

Abstract

Several generalist species have been increasingly colonizing urban areas as a response of the degradation of their original habitats combined with the increase of predictable food resources and desirable breeding conditions in urban areas. Gulls started to nest in rooftops around 1890s and after that several gull species have been increasingly breeding at rooftops in several countries around the globe. The breeding and foraging behaviour associated with this colonization has been causing a variety of conflicts with the human population, not only by increasing disturbance levels through direct human-gull interactions, but also by the concerning role of gulls as reservoirs of pathogens. However, urban areas present a variety of challenges when it comes to studying these birds, and the foraging and breeding ecology of urban gulls is not yet fully understood, it is also not clear if urban areas represent an ecological trap with immediate benefits but with longer-term health detrimental consequences. Thus, this thesis addresses several parameters of urban gulls' life to understand the trade-offs that they face when moving to this novel urban environment; what triggers and encourage gulls to keep using the cities, and how they interact with humans. In summary, this thesis includes the study of diet, general health, breeding success, urban habitat-use and behaviour of urban Yellow-legged gulls (*Larus michahellis*) in the city of Porto. The major findings highlight: (1) the importance of human activities to create desirable conditions for the establishment of new urban gull colonies, while at the same time contributing for the deterioration of conditions in traditional natural colonies; and the importance of conducting long-term monitoring

studies that capture the long-term establishment of urban gull populations; (2) the importance that marine prey still have in the diet of urban gulls, particularly for younger chicks; (3) the trade-offs that breeding urban gulls face between the advantages of breeding in urban colonies with lower nest density, where the transmission of diseases is less likely to occur, and the disadvantages linked to a lower quality ‘anthropogenic-derived’ diet; and lastly, (4) the importance of the winter season in the use of urban habitats by gulls and the occurrence of human-gull interactions, which tend to increase during this season in city-squares, and are mostly triggered by humans feeding birds. The implementation of measures that aim to reduce major sources of predictable anthropogenic subsidies, the availability of suitable urban nesting grounds and the urban gulls’ breeding output, combined with major environmental education and social awareness campaigns, should improve the efficiency of managing human-gull conflicts, by targeting this problem in a holistic manner.

Chapter 1

Introduction

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The increase in human population and consequent growing urbanization have been progressively leading to the reduction and fragmentation of natural habitats, and amplifying anthropogenic pressures on ecosystems (e.g. Gosling et al. 2017). Growing urban areas, however, also offer new ecological opportunities for wildlife to modify their behaviour and successfully colonize urban environments (Lowry et al. 2013). The habitat changes induced by urbanization, in combination with novel biotic interactions, result in several selection pressures that favour certain traits in urban populations (Alberti et al. 2017, Ouyang et al. 2018). For example, birds have adjusted to urban environments for many years, and in some cases changed migratory patterns, breeding phenologies and phenotypic traits such as song (Garcia et al. 2017, Sepp et al. 2017, Hensley et al. 2019). Certain traits may have facilitated a species' colonisation of urban environments including cognitive and problem-solving performance (Snell-Rood and Wick 2013, Audet et al. 2016, Castano et al. 2020), heightened tolerance and habituation (Lowry et al. 2013, Sol et al. 2013), and ability to shift their dietary niche (Pagani-Núñez et al. 2019, Murray et al. 2020), all of which could affect survival and reproductive success in the urban environment. These adjustments are particularly evident in generalist species with higher phenotypic and behavioural plasticity such as gulls, allowing them to overcome the challenges of a novel environment by, for example, adapting and exploiting novel food and nesting site opportunities (Belant 1997, Sayol et al. 2020, Carmona et al. 2021). Ultimately, the expanding urbanization and the colonization of urban areas by opportunistic species will increase instances of human-wildlife encounters, causing a variety of interactions and conflicts in the cities. This chapter provides an overview of the relationships between urban gulls and humans. To address patterns of urban gull population expansion by different gull species, and the challenges faced when studying the ecology of urban gulls, we overview the history of gull colonization of urban areas in the British Isles and North America. Then, we review the urban features influencing breeding success of urban gull populations and summarise the main human-gull interactions within cities. Lastly, we consider the importance of management actions to minimize conflicts related to urban gulls.

1.1. History of urban gull populations, with particular incidence in the British Isles and North America

Studying urban gull populations comes with a variety of challenges, particularly when counting and predicting population size, because these areas rarely provide good vantage points with an unobstructed view to all surrounding nests. This results in a likely underestimation of the true size of urban gull populations worldwide (Coulson and Coulson 2015). Counting effort of urban-nesting gulls seemed to have been conducted more consistently in the British Isles than elsewhere, perhaps because it was one of the first places where gulls started nesting on roofs outside of the Black Sea region, where roof-nesting European Herring Gulls (*Larus argentatus*; Herring Gull hereafter), were first recorded in the early 1890s (Goethe 1960, Nankinov 1992). ‘Urban nesting’ can be defined as nesting on buildings or other man-made structures, such as bridges, in areas frequented by humans (Cramp 1971), including factory roofs and other industrial buildings outside urban centres. This definition was used in all the censuses in the British Isles. The first known records of roof-nesting Herring Gulls in the British Isles dates from 1910 at two sites in Cornwall, southwest England (Cramp 1971). Herring Gulls nesting on buildings remained very rare before the second World War, with just six known sites in 1939 concentrated in the southwest of England, and all with less than 10 breeding pairs per site (Witherby et al. 1938-1941, Cramp 1971). It is unclear what drove Herring Gulls to construct their first nest on roofs and several reasons had been considered. For example, Took (1955) speculated that long-range artillery fire during the war drove Herring Gulls off their usual nesting sites on chalk cliffs around the city of Dover, and onto roof-tops, particularly into the city centre. It is possible that the architecture of traditional British houses, with several separate chimney stacks and small ledges and niches on the roof, provided attractive nesting sites that resembled more the Herring Gulls' natural nesting sites on cliffs than that of Lesser Black-backed Gulls (*Larus fuscus*), that nest more on flat grounds (Goethe 1960). From the beginning of the 20th century until the early 1970s the Herring Gull population in the British Isles increased at a rate of 12-13% per annum, possibly due to reduced persecution and increased availability of anthropogenic food resources from human activities (Cramp et al. 1974). During that time, the roof-nesting habit of Herring Gulls also increased, spreading from southwest England to many coastal towns along the southern parts of the British Isles, and then expanded inland and to the north (Cramp 1971, Monaghan and Coulson 1977). In Scotland, the first roof-nesting pair of Herring Gulls was recorded in Inverness in 1965 (Parslow 1967).

In 1969-70, the first census of roof-nesting gulls in the British Isles was organized as part of a national census of seabirds (Cramp et al. 1974), and by then roof-nesting Herring Gulls had spread to at least 61 sites and numbered 1,252 nests (Fig. 1.1a), with five sites occupied by over 100 breeding pairs, and the largest colony of roof-nesting gulls being at Dover, with 225 nests (Cramp 1971, updated by Monaghan and Coulson 1977). Although the breeding productivity of roof-nesting Herring Gulls was high, possibly due to the local availability of food from anthropogenic sources and reduced nest predation (Monaghan 1979, Rock 2005), it is unlikely that the reproductive output from local roof-top breeders alone could have sustained the observed large increase in numbers (Chabrzyk and Coulson 1976). Hence, roof-nesting colonies were likely recruiting from natural sites in the surroundings, where large Herring Gull colonies were possibly reaching saturation levels in the 1970s (Monaghan and Coulson 1977). Therefore, the increasing number of roof-nesting Herring Gulls was likely a consequence of the species' rapid population growth in the 20th century, when young breeders were forced to find alternative nesting grounds (Monaghan and Coulson 1977). In addition, culling and disturbance by human activities at natural sites could also have dispersed Herring Gulls away from those sites and into built-up areas (Raven and Coulson 1997). At that time, the only other gull species recorded breeding on roofs in the British Isles was the Lesser Black-backed Gull, first recorded nesting on an inland factory-roof in Glamorgan, in 1945 (Salmon 1958). By 1969-1970 the species expanded to a total roof-nesting population of at least 61 pairs in seven locations mainly confined to south Wales (Cramp 1971). The smaller numbers and slower increase of the roof-nesting Lesser Black-backed Gulls was likely due to their slower rate of increase of the total British population, compared to Herring Gulls at that time. Further censuses of roof-nesting gulls in Britain, using the same methods as the 1969 census, were conducted in 1976 (Monaghan and Coulson 1977), in 1994 (Raven and Coulson 1997), in 1998-2002 (Mitchell et al. 2004); the next one is expected to be concluded in 2021.

Since the 1970s the population of Herring Gulls nesting at natural sites in the British Isles fell by 43% in 1985 (Lloyd et al. 1991) and a further 13% in 2000 (Mitchell et al. 2004), however the numbers of roof-nesting gulls kept increasing (Fig. 1.1a), but at a slower rate than the declines at natural sites, so that the overall population of Herring Gulls in the British Isles decreased. Roof-nesting Herring Gulls had spread to at least 92 locations with a minimum of 2,968 breeding pairs in 1976, corresponding to an increase of 17% per annum (Monaghan and Coulson 1977), growing faster than populations nesting at natural sites had been growing before the 1970s (13% per annum; Chabrzyk and Coulson

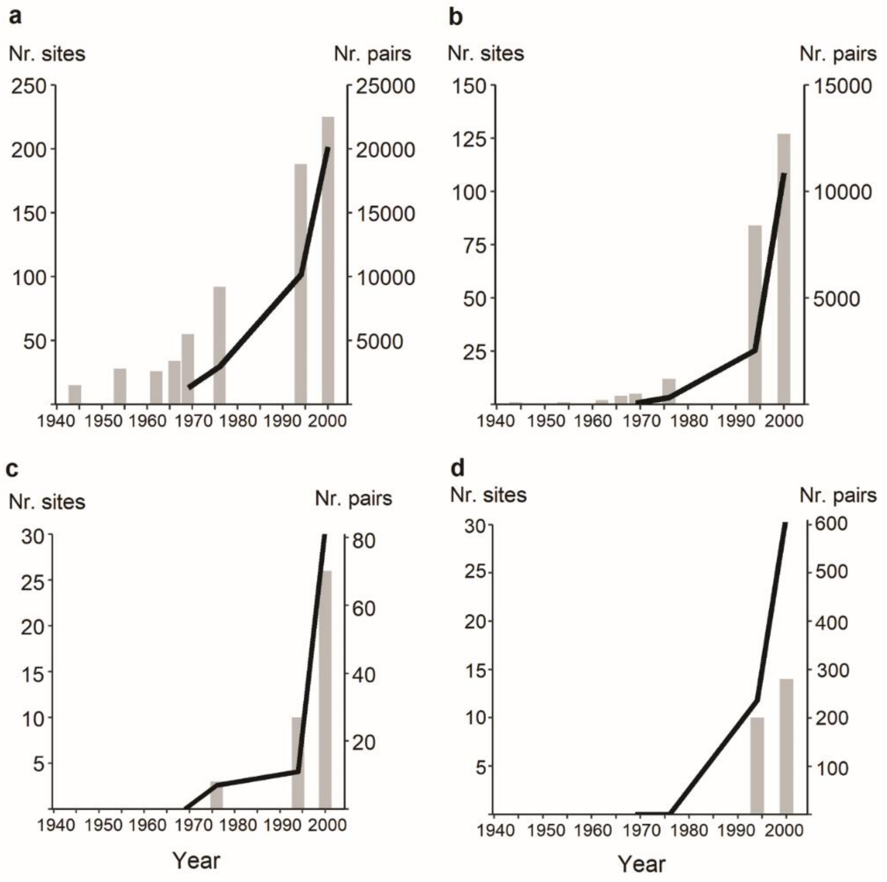


Figure 1.1. *Increase in the number of sites (histogram and left axis) and number of pairs (black line and right axis) of the four Larus species that have been recorded to nest on roofs in built-up areas in the British Isles, from their earliest records until the census of 1998-2002: (a) European Herring Gulls (*Larus argentatus*), (b) Lesser Black-backed Gulls (*Larus fuscus*), (c) Great Black-backed Gulls (*Larus marinus*) and (d) Mew Gulls (*Larus canus*). Note that the scale differs between vertical axis due to the large differences in numbers of roof-nests between the species. Data from Cramp (1971), Monaghan and Coulson (1977), Raven and Coulson (1997) and Mitchell et al. (2004).*

1976). By 1994, at least 188 sites with 10,184 breeding pairs across most of Britain were occupied by roof-nesting Herring Gulls (Raven and Coulson 1997), and by the most recent census in 1998-2002 this further grew to at least 225 sites with 20,170 breeding pairs (Fig. 1.1a; Mitchell et al. 2004). Another study estimated more than 100,000 Laridae pairs nesting on roofs in 2004 (Rock 2005), but this was an extrapolation from a stronghold of roof-nesting gulls to the rest of the British Isles. Not only did roof-nesting

Herring Gulls colonize new sites, including sites further away from the coast, but also the average number of nests at those sites increased. The mean size of roof-nesting colonies increased from 49 pairs in 1976 to 75 in 1994 (Raven and Coulson 1997), and to 90 pairs in 2000 (Mitchell et al. 2004). Although most urban colonies were modest in size, a few colonies became very large, such as the city of Aberdeen, Scotland, that had 3350 Herring Gull roof-nests in 2001 (Mitchell et al. 2004). Roof-nesting gulls increased from 0.6% to 8.2% and 13.7% of the total British Herring Gull population in 1976, 1994 and 2000, respectively. The rate of increase of roof-nesting Herring Gulls slowed down after the 1970s with 10% per annum between 1976 and 1994 (Raven and Coulson 1997), and 3% per annum between 1994 and 2000 (Mitchell et al. 2004). Increased breeding density in built-up areas might be one of the factors explaining the slowing of the expansion of roof-nesting Herring Gulls towards the end of the 20th century (Raven and Coulson 1997). The continued increase in roof-nesting Herring Gulls from the 1970s onwards, despite a large decline in numbers at natural breeding sites, could possibly be attributed to the deterioration of foraging condition and increased predation and persecution at natural sites, leading to birds looking for refuge in built-up areas (Nager and O'Hanlon 2016), where the availability of food and nesting sites safe from predation are favourable (Monaghan and Coulson 1977, Raven and Coulson 1997, Rock 2005).

Numbers of roof-nesting Lesser Black-backed Gulls and the number of colonized sites in built-up areas also increased after 1990 (Fig. 1.1b) while the overall population also kept increasing, with a higher rate of increase than in Herring Gulls (Raven and Coulson 1997). In most coastal regions of the British Isles, roof-nesting Lesser Black-backed Gulls joined existing Herring Gull colonies and were outnumbered by them. However, some inland areas, for example the Forth-Clyde region of Scotland, was first colonized by Lesser Black-backed Gulls and then Herring Gulls followed later, with roof-nesting Lesser Black-backed Gulls being more numerous there than Herring Gulls (Raven and Coulson 1997). Between 1970s and 2000s, Herring Gull and Lesser Black-back Gull populations showed a different relationship between numbers nesting at natural sites and on roof-tops (Nager and O'Hanlon 2016). While for Herring Gulls the number of roof-nests increased as the number of nests in natural sites decreased, showing an apparent negative correlation between numbers at natural sites and built-up areas; Lesser Black-backed Gull populations were still expanding in natural sites, and the numbers of roof-nests also increasing, showing an apparent positive correlation between the number of breeding pairs at natural and urban sites. This suggests that as with observations for Herring Gulls before 1970s, young Lesser Black-backed Gulls might have been forced to disperse from saturated natural sites into built-up areas. In both cases the changes in numbers at natural sites were larger than in built-up areas.

Other gull species were slower to turn to roof-nesting in Britain and Ireland, probably due to their lower numbers and slower population increases at the time. The first roof-nesting pairs of Great Black-backed Gulls (*Larus marinus*) were recorded in 1970 for a single pair in Cornwall, and by the turn of the century this has expanded to at least 83 pairs at 26 sites (Fig. 1.1c) (Mitchell et al. 2004), mostly in small colonies of 1-2 pairs with other gulls on surrounding roofs (Raven and Coulson 1997). In 1971 a breeding pair of Mew Gulls (*Larus canus*) was recorded on a roof in Inverness (Cramp 1971), and by 2000 there were at least 621 roof-nesting pairs at 14 locations in Scotland (Fig. 1.1d; Mitchell et al. 2004). In addition to the *Larus* spp. gulls, it is worth mentioning that Black-legged Kittiwakes (*Rissa tridactyla*) were also recorded nesting on man-made structures (mainly piers and window ledges of warehouses) from the early 1930s in south-east Scotland and spread along the British North Sea coast to seven colonies, with a total of at least 410 pairs in 1969-70 (Cramp 1971). This number increased to between 664 to 755 breeding pairs in 2007-2009 in one area of northeast England (Turner 2010), but more recent counts in other areas are not known.

Over time, large gulls have also colonized cities across all of Europe, North America, Australia and Japan (Cramp 1971, Rock 2005), mostly during the late 20th century such as the first records from 1971 for Italy by Yellow-legged Gulls (*Larus michahellis*; Cignini and Zapparoli 1996), and those from the 1980s for Japan by Slaty-backed Gulls (*Larus schistisagus*; Artyukhin 2002 in Zelenskaya 2019). However, information on the history of urban-nesting gulls in regions outside Europe is scarce, with some records from North America and isolated accounts of their behaviour in other parts of the world (e.g., Turbott 1969, Chávez-Villavicencio 2014, Yorio et al. 2016). North American records of roof-nesting gulls are far less detailed than those from the UK; although some jurisdictions appear to survey urban gull populations periodically (e.g., Roby et al. 2007), most urban counts result from location- or species-specific research rather than initiatives at the national scale as in the British Isles (cf. Hooper 1998, Blight et al. 2019).

The first North American record of urban-nesting gulls appears to have been of Western Gulls (*Larus occidentalis*) breeding in San Francisco, California, circa 1920 (Fisk 1978). This same species first colonized Seattle, in Washington state further north on the US Pacific coast, in 1946, nesting on buildings near the port (Eddy 1982). Further north still, the first roof-top nesting record for the Pacific coast of Canada was in 1962, in Vancouver, for a single Glaucous-winged Gull (*Larus glaucescens*) nest near the port (Oldaker 1963). The apparently rapid initial expansion of this species in the city of Vancouver was reasonably well-documented until the 1980s, with four nests described in one city neighbourhood in 1972-73 (Sanford 1974), and a total of 88 nests found at two other localities later in this same decade (Campbell 1975, Poynter 1976). By 1986, Vermeer et al. (1988) estimated that 500 pairs nested in the northeast quadrant of the city on buildings near the waterfront, including the downtown core. About 30 years later, in 2017, this population was estimated at 1231 pairs (95% CI: 1182, 1279; E. Kroc, LBK and W. Cao, unpublished data). The same authors estimated that the total breeding population in Vancouver was 1690 pairs (95% CI: 1626, 1755), with an additional 200 nests at least occupying the city's adjacent coastline to the south in the bordering city of Richmond. Their estimation for the downtown core breeding population (449 pairs, 95% CI: 441, 457) were essentially unchanged from 1988; with the current Vancouver population occurring at a low density over much of the city, and no longer clusters near the harbour (E. Kroc, LBK and W. Cao, unpublished data). In the absence of control measures it is likely that this population will continue to grow (Kroc et al. 2018). For this same species in the nearby maritime city of Victoria, Hooper (1988) reported that in 1986, 114 pairs nested on various structures (mostly on roof-tops) near the waterfront. In 2017–2018, Blight et al. (2019) used drones to estimate a population of 346 pairs in their survey area, with an additional 102 pairs at a warehouse colony excluded from the drone survey, for a total of about 448 pairs through the downtown core and adjacent neighbourhoods. As with Vancouver, the growing population of nesting gulls in Victoria maintained a low density and spread farther into the urban area over time, rather than aggregating at increasing densities near the waterfront. This same pattern seems to be repeating itself in the nearby city of Nanaimo, British Columbia as well (Kroc et al. 2018). Like the European Herring Gull in the British Isles after the 1970s, these two urban population increases have occurred at a time when the overall regional population was in decline, implying a shift in preferred habitats by nesting Glaucous-winged Gulls in this region of Pacific Canada (Blight et al. 2015, Blight et al. 2019).

Elsewhere on the west coast of North America, urban nesting habitats have facilitated a range expansion of Heermann's Gulls (*Larus heermanni*). In 1979 the species began nesting on the central California coast, when a single pair nested on Alcatraz Island in San Francisco Bay for three consecutive years. In the 1980s and 1990s 1–2 pairs nested at natural offshore sites in this same region, then in 1999 three pairs successfully nested at an artificial island on a lake in the city of Seaside in the Monterey Bay area. As this island eroded, the population subsequently relocated to the region's roof-tops, and has since increased to about 100 pairs (Howell et al. 1983, Roberson et al. 2001, Golden Gate Audubon Society 2021). This location is seen as facilitating a potential northwards range shift in the face of climate change (Herrera 2019). Western Gulls have also continued to colonize urban centres along the California coast. As far back as 1935, Western Gulls have nested on roof-tops throughout San Diego County in extreme southern California (Unitt 2004), while gulls in San Francisco have been recorded nesting along the downtown shoreline and nearby Alcatraz Island (Pierotti and Annett 2001). Western Gulls have also colonized urban centres around Monterey Bay and will sometimes nest on roof-tops of structures that are immediately adjacent to nesting Heermann's Gulls (Kroc and Blight 2019). In the extreme north of the continent, small populations of both Herring and Mew Gulls (10-20 pairs each) have been documented nesting on roof-tops in and around the downtown core of Anchorage, Alaska (Kroc and Blight 2019). Interestingly, Mew Gulls have also been documented nesting atop lampposts in the small, subarctic city of Whitehorse in Canada's Yukon Territory (J. Helmer personal communication; Kroc and Blight 2019), more than 250 km from the nearest (Pacific) ocean. Somewhat surprisingly, the first record of urban-nesting birds for the East Coast of North America (for American Herring Gulls, *Larus smithsonianus*, in Boston, USA) does not appear in the literature until 1961, although 150 nests were thought to have become established some years earlier; these subsequently expanded by the 1970s (Paynter 1963, Fisk 1978). In the Great Lakes region, first roof-top nests were documented in Ontario, Canada, in the early 1970s, for Ring-billed Gulls (*Larus delawarensis*) and American Herring Gulls (Blokpoel et al. 1990), and in 1978 on the US side of the Great Lakes for these same two species (Dwyer et al. 1996). In the Canadian Great Lakes, American Herring Gulls grew in number from 440 to 1,300 pairs from 1976 to 1990 (about one-third were urban colonies), while Ring-billed Gulls increased from 56,000 to 283,000 pairs (13 of 27 colonies were urban) during this same period, with concerns about health and economic effects of the urban portion of these gull populations increasing apace (Blokpoel and Tessier 1991). By the mid-1990s, 4% of the US Great Lakes' growing American Herring Gull population was nesting on roof-tops, as were 2% of Ring-billed Gulls in the region, for a total of 7,922 pairs of both species (Dwyer et al. 1996). Although these two gull species have been declining in the Great Lakes region since about 1990 (Morris et al. 2003, 2011, Hebert et al. 2008), the urban-nesting habit, gained in their population expansion stage, has been retained and they continue to breed in urban habitats (Morris et al. 2011; LKB and E. Kroc, unpublished data). On the Atlantic coast, American Herring Gulls and Great Black-Backed Gulls have been documented nesting atop waterfront roof-tops around New York City harbour for the past 35 years (Elbin et al. 2019, Kolodzinski et al. 2019). Urban breeding populations reached peak numbers of 2516 and 792 pairs, respectively, in 1990, but have since declined (Elbin et al. 2019). These species have also been observed nesting in the downtown cores of the Canadian coastal cities of Saint John, Halifax, and St. John's, with an aggregated estimate of more than 200 pairs (Kroc and Blight 2019).

It seems based on disparate studies to date that gulls colonized urban habitats for nesting either while their regional population was expanding, possibly surplus individuals seeking new nesting opportunities, or while their regional populations declined (individuals finding a refuge when conditions at natural sites deteriorated). Once gulls have expanded into an urban habitat, they remain, regardless of the status of their original source populations. The reasons for this are unclear, though may be related to the greater breeding success experienced by some urban colonies (below); the geographic structuring of gull metapopulations comprised of both urban and natural colonies is clearly a direction for future research.

1.2. Factors affecting the success of urban gull populations

Many studies have reported a higher breeding success for urban gull colonies than gulls breeding at natural sites (Monaghan 1979, Kroc 2018a, Zelenskaya 2019), which may be linked to the lower nest density and consequently lower intraspecific aggression from other nesting adults in the neighbourhood. This suggests that roof-top habitats may represent suitable breeding grounds of equal or higher quality than that offered by natural coastal or insular habitats at that time (Monaghan 1979). However, other studies found no differences in breeding parameters between gulls nesting at natural and urban sites. Hooper (1988) found a high egg and chick mortality in urban-nesting Glaucous-winged Gulls in Victoria, British Columbia, which was mostly caused by the predation of Northwestern Crows (*Corvus caurinus*) and other adult gulls, leading to hatching (72%) and fledgling success (51%) that were similar to those observed at a natural site on nearby Mandarte Island (70-83% and 36-58%, respectively; Vermeer 1963). More recently, Perlut et al. (2016) studied the breeding parameters of a roof-top breeding population of American Herring Gulls in Portland, Maine, USA, and found a lower clutch size (mean of 2.3 eggs per clutch) and hatching success (46-48%), but higher chick survival up to 30 days of age (62-73%), than for a population nesting at a natural site on Appledore Island

(2.6 eggs per clutch, 56-71% hatching success and 49-53% chick survival). Nest failure in Portland was mostly caused by predation (38%), weather conditions (27%) and management interventions of nest removal during incubation (23%). There was also no evidence of a difference in breeding success between natural and urban colonies in Yellow-legged Gulls in the Venice region, Italy, possibly because these were recently established colonies assumed to be mostly composed of younger birds with a poorer breeding performance (Soldatini et al. 2008). Vermeer et al. (1988) found great variation in the breeding success of roof-nesting Glaucous-winged Gulls in downtown Vancouver, Canada, with colonial breeders having lower (35%) fledgling success than solitary and more experienced breeding pairs (73%), although human disturbance may have caused some chick mortality among colonial breeders.

Numerous other factors might influence differential breeding success between natural and urban sites, such as the quality of the diet of adult breeders. Some studies have reported a higher breeding output in gulls foraging on natural marine resources (Hunt 1972, Annett and Pierotti 1999, O'Hanlon et al. 2017), which commonly include prey with high energetic and nutritional value, particularly rich in essential fatty acids and micronutrients (Gladyshev et al. 2009, EFSA NDA Panel 2014). The view that a marine diet is beneficial to growing chicks is further supported by the observation that breeding gulls often switch their diet during the chick-rearing period to more marine prey (Annett and Pierotti 1989, Isaksson et al. 2016, Pais de Faria et al. 2021a, but see Sotillo et al. 2019 for an alternative view). However, some studies found that gulls feeding on anthropogenic food did better compared to gulls feeding on natural resources (Pons and Migot 1995), such as the high hatching success in Lesser Black-backed Gulls (Gyimesi et al. 2016) and the higher fledgling rates in European Herring Gulls, when compared to gulls feeding on natural marine prey (van Donk et al. 2017), both in the Netherlands. It is likely, however, that urban-nesting gulls use the same food resources as the birds nesting in the surrounding natural sites (e.g. Huig et al. 2016, Rock et al. 2016, Spelt et al. 2019). The higher breeding success observed in gulls with an anthropogenic diet, from both natural and urban colonies, might be a result of the higher predictability of these food recourses (Oro et al. 2013, Martinez-Abrain and Jimenez 2016). Some studies have recently shown the ability of gulls to adapt their foraging behaviour to follow predictable human habits. Spelt et al. (2021) showed that gulls breeding in Bristol, UK, matched their foraging patterns to the times when anthropogenic food becomes available at school breaks and opening hours of a waste centre. Other than matching their foraging patterns to predictable human activities, in a highly touristic area in the centre of Porto, Portugal, Yellow-legged Gulls were reported defending favourable vantage spots on the top of traffic lights near food outlets, from where they could swoop down and steal the food carried by humans coming out of the shops and waiting to cross the street (Pais de Faria et al. 2021b). Overall, the increase in the availability of anthropogenic food sources in cities and landfills, coupled with fishery discards in nearby marine areas and ports, likely contributed to the growth of urban gull populations.

Urban habitats may also provide a range of other potentially favourable conditions for gulls. Urban areas typically provide a milder microclimate than surrounding areas (Chown and Duffy 2015), with warmer temperatures (heat island effect), and shelter from extreme weather conditions by roof-top structures (e.g. chimneys or walls; Fig. 1.2), both potentially promoting the success of urban gull populations. General conditions in urban areas may also be favourable to gulls all year-round, with some gulls no longer migrating and keep occupying their nesting grounds during the entire year (Rock 2005, Kroc 2018b, Pais de Faria et al. 2021b). Lower disturbance levels on uninhabited buildings within the cities seem to provide suitable breeding opportunities for a range of avian species

(Reynolds et al. 2019), but the effect of microclimate and availability of uninhabited buildings on roof-nesting pairs has not yet been studied in gulls.

Figure 1.2. *Rooftop nests of Yellow-legged gulls in the city of Porto, Portugal.*

Proximity to water bodies is another feature of urban areas that can make them attractive to gulls. Colonisation of built-up areas by gulls initially started in coastal or estuarine areas and progressively expanded to more distant inland areas (e.g. see the expansion of the British roof-nesting gull populations). For example, Zelensky (2019) studied the growth of the urban population of Slaty-backed Gulls in Magadan, Russia, and reported an increasing distance of nest sites to the coast as the population expanded. The same pattern of expansion away from the immediate shoreline was observed in

Seattle, USA, from 1961 to 1982, and in Victoria, British Columbia, between the 1980s and 2000s (Eddy 1982, Blight et al. 2019). Freshwater bodies are commonly used by gulls as roosting locations (Clark et al. 2016) and their availability in or near built-up areas may also attract gulls to urban areas (Vermeer et al. 1988, Washburn et al. 2016). Although exploiting predictable anthropogenic resources would allow gulls to potentially reduce the energetic costs of foraging, urban environments are also commonly associated with an increased risk of disturbance (Møller 2008) or exposure to contaminants (Chen et al. 2012, Isaksson 2018, Zapata et al. 2018, Sorais et al. 2020) and pathogens (Alm et al. 2018, Smith et al. 2020), potentially jeopardizing their health condition and producing long-term negative effects for gulls and humans.

1.3. Human-gull interactions within the cities

Gulls have always been part of coastal landscapes, where positive relationships and culturally positive connections were common between humans and gulls. Recently, however, human-gull relationships have been changing, with gulls increasingly becoming a constant part of urban landscapes worldwide (Belant 1997), causing several conflicts with the human population, such as damage to urban structures, nuisance, and spilling waste when foraging in trash containers (Fig. 1.3). Negative human-gull interactions seem to intensify during the gulls' breeding season, when they are constrained by breeding duties and show higher aggressive territorial behaviour near their roof-top nests, and take higher risks to obtain food (e.g. stealing food from humans; Belant 1997, Huig et al. 2016). Huig et al. (2016) reported human-gull interactions for the Lesser Black-backed and Herring Gulls breeding at natural sites, but visiting the city of The Hague, Netherlands, during the breeding season, causing several nuisance events such as raiding rubbish bags or searching for food scraps in residential areas, especially during the chick-rearing period. However, the number of urban gulls in some cities may be larger outside the breeding season, as observed in areas of Southern Europe when migratory gulls join the local resident populations (Pais de Faria et al. 2021b).

Figure 1.3. *Gulls exploring the city: adult and immature gulls Larus sp. spilling waste when foraging in trash containers in the street (top left) and in a small city park (top right), in the city of Porto, Portugal. Gulls resting in an urban pond (bottom) within the city of Matosinhos, Portugal, at the end of the day.*

The common use of landfills and large waterbodies by foraging and roosting gulls raises several human public-health concerns, as gulls might end up serving as pathogen vectors (Alm et al. 2018), contributing to the dissemination of pathogens from landfills into these roosting locations, commonly shared with humans (e.g. beaches, ponds, lakes, rivers and reservoirs; Fig. 1.3; Clark et al. 2016). In fact, several studies have reported the presence of antimicrobial-resistant (AMR) bacteria and Avian Influenza viruses in gull species from different countries (Antilles et al. 2015, Arnal et al. 2015). For example, in France, researchers found identical populations of *Escherichia coli* on Yellow-legged Gull and humans, suggesting that gulls may be contaminated in landfills and then act as an environmental reservoir of AMR pathogens (Bonnedahl et al. 2009). In Berlenga Island, Portugal, gulls are considered a major source of faecal pollution in coastal waters near a beach that is highly visited by tourists (Alves et al. 2014, Araujo et al. 2014), and to carry AMR *E. coli* (Radhouani et al. 2009).

1.4. Goals and structure of the thesis

The goals of this thesis were to characterize and evaluate several parameters of urban gulls' life, to understand the trade-offs that urban birds face when moving to this novel urban environment, to understand what triggers and encourage gulls to keep using the cities and how they interact with our society.

This introductory chapter provided an overview of urban gulls' colonization history in the British Isles and North America, urban features influencing the breeding success of urban gull populations and some general comments regarding the main human-gull interactions occurring in the cities. The following chapters will address more particularly life features of Yellow-legged gulls (*Larus michahellis*) breeding in the city of Porto compared to gulls breeding in natural traditional colonies, specifically: the Chapter 2 will be focused on gulls' health and breeding success, by evaluating physiological parameters (erythrocyte sedimentation rate, heterophils/lymphocytes ratio, haemoglobin concentration and measurements of oxidative stress), reflecting gulls' general health condition and their nutritional, immune and stress status; combined with breeding parameters describing nest density, clutch and egg sizes, hatching success, early chick growth and adult body condition, to evaluate the adequacy and quality of rooftops as novel breeding grounds.

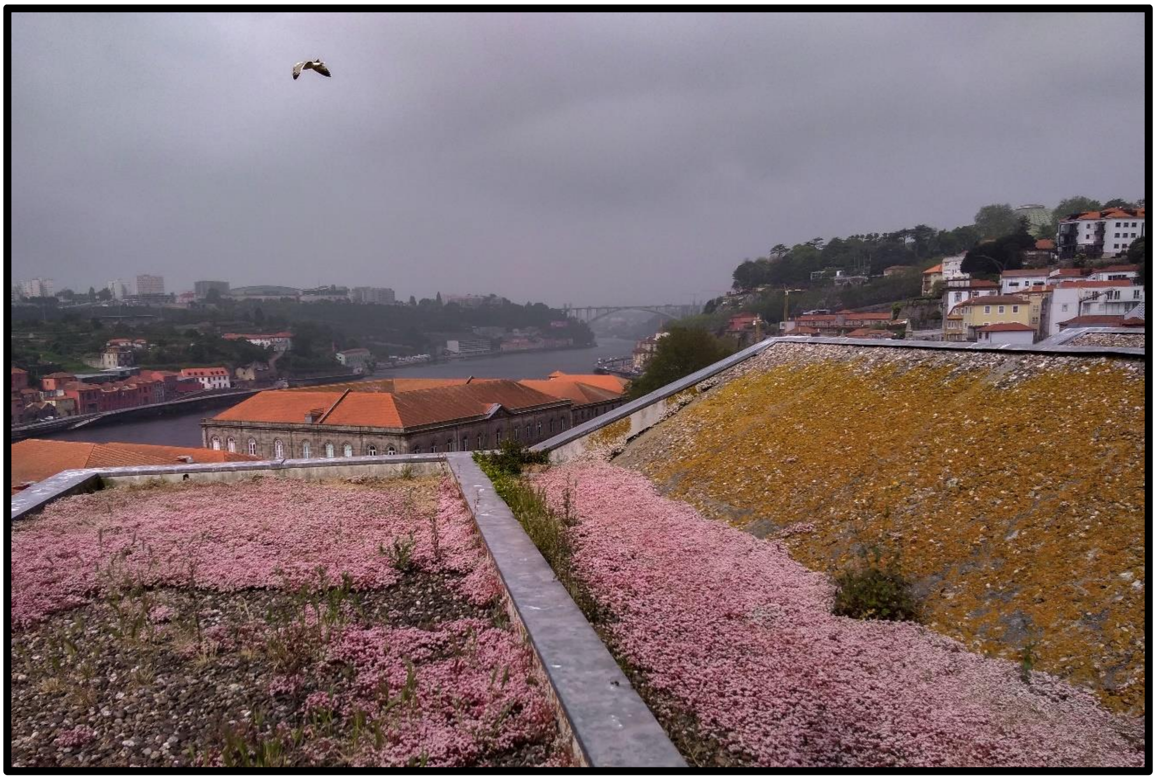
In the chapter 3, the reader can find a complete evaluation of the diversity and quality of gulls' diet during different seasons of the year and the occurrence of marine prey in the items delivered to growing chick gulls. The methods used included the analysis of pellets, which reflected the hard parts of items ingested in gulls' previous meal; the comparison of isotopic niches from natural and urban gull colonies and their consistency over time; the quantification of items delivered to chicks from different ages, documented during scheduled observations in highly urbanized breeding areas, and the analysis of fatty acids (FA) composition in fledglings from natural and urban colonies.

Chapter 4 will address spatial and temporal dynamics of urban habitat use and human interactions with urban gulls in the city of Porto, through the quantification of seasonal variation in the behaviour and use of different urban habitat types by Yellow-legged adult gulls and *Larus* spp. immature gulls. This was achieved by combining year-round monthly surveys, to document the number of gulls using the sampled area and characterize the foraging/resting/breeding behaviours per habitat type; with the 10-hour daily surveys to capture gulls' daily routines and interactions with humans during the winter and breeding seasons.

Finally, the chapter 5 presents an integrative discussion of the findings and their ecological meaning of the results achieved in all chapters, also providing additional comments on their implications for our society and for human-gull dynamics. This chapter also includes a section related with the management of growing urban gull populations and the associated challenges and limitations, with suggestions to avoid common pitfalls.

Chapter 2

Plenty of rooftops with few neighbours occupied by young breeding Yellow-legged gulls: does this occur at the expense of their health condition?



This chapter is under review as:
Pais de Faria J, Paiva VH, Veríssimo SN, Lopes CS, Soares R, Oliveira J, dos Santos I, Norte AC, Ramos JA. Plenty of rooftops with few neighbours occupied by young breeding Yellow-legged gulls: does this occur at the expense of their health condition? Ibis

Abstract

Gull populations have been increasingly breeding in several cities around the world, but is still unclear whether urban habitats have equal or higher quality than the traditional coastal or insular habitats; or if they represent an ecological trap with immediate reproductive benefits, but with longer-term health detrimental consequences. Here we present a comprehensive study including breeding parameters (nest density, egg dimensions, clutch size, hatching success and adult body condition), and physiological parameters (erythrocyte sedimentation rate, heterophils/lymphocytes ratio, haemoglobin concentration and measurements of oxidative stress), as indicators of the general health condition of adult and chick Yellow-legged gulls breeding in natural and urban colonies. Breeding parameters in the most urbanized colony in Porto, Portugal, were generally consistent with the features of a growing population being established by younger unexperienced breeders - i.e. low but increasing nest density, production of smaller eggs, lower clutch size and large variation in the hatching success between years (56-88%) compared to the 67-66% observed in the Deserta natural colony. Urban gulls from Porto did not differ in their adult body condition, however they showed significantly lower occurrence of inflammatory processes, in both adult and chick gulls, lower haemoglobin concentration, in adult gulls, and a slower early chick growth, than gulls breeding in the natural colony of Deserta Island. This suggests that urban gulls might be facing important trade-offs between the advantages of breeding in lower density urban colonies, with less intraspecific interactions and a lower disease transmission probability; and the disadvantages of having an anthropogenic diet usually lower in nutritional value.

2.1. Introduction

The increasing urbanization in the last centuries has been changing the dynamics between our societies and wildlife (Oro et al. 2013). As a response to the increase of predictable anthropogenic subsidies and a reduction of natural resources, several species have been adjusting their breeding behaviour to explore novel urban environments (Garcia et al. 2017, Møller 2009), especially those with higher plasticity such as several gull species that now nest in rooftops of coastal cities around the world. One of the older records of rooftop nesting dates from 1890s near the Black Sea, by Herring Gulls (*Larus argentatus;* Goethe 1960, Nankinov 1992), however the majority of reports of such behaviour began during the 20th century: 1910 in the British Isles by Herring Gulls (Cramp 1971), 1971 in Italy by Yellow-legged gulls, *Larus michahellis* (hereafter YLG; Cignini and Zapparoli 1996 *in* Soldatini et al. 2008) and 1980s in Japan by Slaty-backed gulls (*Larus schistisagus;* Artyukhin 2002 *in* Zelenskaya 2019).

Some studies suggest that rooftop habitats may represent suitable breeding grounds of equal or higher quality than the traditional coastal or insular habitats (Monaghan 1979). Advantages associated with rooftop breeding include the higher predictability of anthropogenic subsidies near the breeding grounds; warmer temperatures (Rock 2005); protection from extreme weather conditions by rooftop structures (e.g. chimneys or walls); no egg and chick predation by mammals; lower disturbance levels, especially in older or abandoned buildings, and lower nest density, with usually 1-2 nests per rooftop (Kroc 2018), often resulting in a lower intraspecific competition and predation, and a general increase in breeding success (Monaghan 1979, Kroc 2018, Zelenskaya 2019). Sometimes, younger gulls seem to disperse to urban areas once traditional colonies reached saturation levels (Pais de Faria et al. in press), affecting the overall urban population breeding success, which tends to be lower in unexperienced younger breeders (Pyle et al. 1991, Sydeman et al. 1991). Gulls breeding in urban areas also tend to feed themselves and their chicks more often with lower quality human food subsidies (Pais de Faria et al. 2021a), being more exposed to higher levels of contaminants and pathogens (e.g. while feeding in landfills; Alm et al. 2018, Zapata et al. 2018, Smith et al. 2020, Sorais et al. 2020). Additionally, physiological deleterious effects have been associated with the use of urban environments by several bird species (Partecke et al. 2006, Dominoni et al. 2013, Watson et al. 2017, Kleist et al. 2018, Salmón et al. 2018). Considerable phenotypic discrepancies have been reported between urban individuals and their rural conspecifics (Isaksson 2018), such as the decrease in the plumage coloration intensity in urban Great Tits (*Parus major*), resulting from a lower consumption of carotenoids, consequently affecting their physiology and breeding success (Isaksson 2018); or the significantly shorter telomeres observed in Great Tits growing in urban environments (Salmón et al. 2016), which will likely jeopardize their long-term survival.

Despite the recent increase in the number of studies addressing urban gulls' breeding success, it is still unclear whether urban areas represent suitable quality habitats, or if they represent an ecological trap with immediate reproductive benefits, but with longer-term consequences for the health condition of breeders. General health condition can be assessed by measuring a panel of physiological parameters whose mechanisms of variation are well understood and characterise different biological functions of an individual organism (Norte et al. in press). Those include the erythrocyte sedimentation rate (ESR), white blood cell counts (WBC), particularly the ratio of heterophils/lymphocytes (H/L), concentration of haemoglobin (Hb), and oxidative stress, among others. The ESR is a measurement of the velocity that red blood cells precipitate in a blood sample, which is usually enhanced by the presence of higher levels of proteins and immunoglobulins associated with inflammatory processes, thus higher ESR levels usually represent an impaired health condition caused by chronic or acute inflammatory events (Saadeh 1998, Heylen and Matthysen 2008). White blood cell counts (WBC) can be used as a general indicator of the immune system activity, with birds commonly showing a higher WBC as a result of inflammations caused by localized or systemic infections or other non-infectious causes (Thrall et al. 2012). Inflammatory and stressful events that trigger the release of stress related hormones (like corticosterone) in the blood stream are also commonly associated with an increase in the number of circulating heterophils (H), with higher ratios of heterophils to lymphocytes indicating lower health and more stressful conditions (Norte et al. 2009, Norte et al. 2021, Davis et al. 2008). The concentration of Hb in the blood can be used as a proxy of physiological status, and lower values of Hb are commonly correlated with lower body condition, lower diet quality, breeding events (e.g. egg laying) and the presence of haematophagous ectoparasites (Norte et al. 2013, Minias 2015). Oxidative stress has been recently studied in association with urban environments, where the concentration of potentially oxidant pollutants tends to be higher (Salmón et al. 2018). This stress arises when an organism shows an unbalance between the amount of damaging reactive oxygen species (ROS) and the total capacity to annul their negative effects (via several processes involving their antioxidant defences), resulting in several unquenched reactive oxidants that will cause further cell molecules' damaging reactions. In some cases, the exposure to oxidants might lead to an upregulation of the antioxidant system, without necessarily resulting in oxidative stress (reviewed by Monaghan et al. 2009). Therefore, both sides of this equation (ROS and antioxidant capacity) need to be measured, when assessing oxidative stress.

A comprehensive study comprising multiple metrics encompassing reproductive parameters and the general health condition of adult and chick gulls, from natural and urban colonies, is necessary to better understand the costs and benefits of breeding in urban environments. In this study we compared breeding and physiological parameters of nesting Yellow-legged gulls in urban and traditional natural colonies during two breeding seasons. We hypothesize that breeding parameters, which are highly influenced by the nutritional quality, should be negatively impacted by the urban environment, resulting in lower clutch and egg sizes, lower body condition of adults and chicks, and slower early chick growth in urban gull populations. Physiological parameters reflecting nutritional, immune and stress status are also expected to indicate an aggravated overall health condition of urban adult and chick gulls, resulting in comparingly higher ESR and H/L ratios, lower Hb and an unbalance in the presence of ROS and the antioxidant capacity in gulls breeding in the urban environment.

2.2. Methods

2.2.1. Study areas

Samples were collected in a total of two natural breeding colonies (Deserta and Berlenga islands) and two urban breeding colonies (Peniche and Porto cities). Deserta is a sand-barrier island in the south of Portugal, with approximately 1400 YLG breeding pairs, and Berlenga Island is at 12 km distance from the Peniche coast and has the biggest YLG colony in Portugal with about 8500 breeding pairs (ICNF, unpubl. data 2017). Both urban colonies, with unknown gull populations, are close to fishery landing areas: Porto, a large urban centre, with ca. 215 000 inhabitants (INE 2018), is located at the mouth of Douro river and near a major fishery landing harbour, and Peniche, a small piscatory city with ca. 26 500 inhabitants (INE 2018). Natural elements were commonly used as building nest material and visual coverage of nests in the natural colonies. Rooftop nests were built with vegetation and artificial materials (Lopes et al. 2020), and were commonly constructed near rooftop structures (e.g. chimneys, walls, water drainage system) that would sustain the nests and provide weather protection.

2.2.2. Sample collection: breeding parameters

Clutch size, egg size, distance to the nearest nest and parent body condition were recorded in all colonies during the incubation period for 115-119 nests and 39 adults in 2018, and 101-135 nests and 51 adults in 2019 (Table S2.1). We measured egg length (L) and egg width (W) using digital callipers and obtained the egg volume using the formula: $L \times W^2 \times 0.476$ (Harris 1964). The distance to the nearest nest was considered as the linear distance between each nest (Hooper 1988) and was directly measured in the field, for the natural colonies, and using imagery software (Google Earth Pro), for the urban colonies. The nearest nest in the urban colonies was located from higher observational points providing unobstructed view of all surroundings, to minimize the error of omitting nests. The breeding adults' body mass and wing length were measured during the incubation period of both years, by capturing adults with a walking trap over their nests. Body condition was considered as individuals' body mass corrected for their body size (i.e. wing length; Steigerwald et al. 2015), and hatching success was considered as the proportion of chicks that hatched from a given clutch size, which was only possible to obtain in the colonies of Deserta and Porto, during both years.

During the breeding season of 2019, chicks from the Deserta and Porto colonies were marked after hatching, with colourful livestock marking crayons, and their weight was measured daily, up to 5 days old. Due to chick mortality and accessibility limitations to the urban nests, continuous weight measures were only obtained for 10 chicks in the Deserta colony and 7 chicks in the Porto colony, and their early chick growth was then calculated by using the quadratic formula: $Md = M0 + ad + bd^2$ (Md = chick weight on day d, M0 = estimated chick weight on day 0, d = age in days, a = linear growth, b = quadratic growth parameter; Ramos 2002, Paiva et al. 2006).

2.2.3. Sample collection: health parameters

Blood samples were collected during the breeding season of 2019 from incubating adults of all colonies (N = 27 – 48; Table S2.1) and from chicks with 5 - 10 days old (N = 12-23; Table S2.1), in the natural colony of Deserta and the urban colony of Porto. After being captured, blood samples were immediately collected from adults' tarsal vein using 1ml syringes, and from chicks' brachial vein using heparinized capillaries (up 0.3 ml of total blood volume). One heparinized capillary filled with blood from both adults and chicks was stored vertically at - 4ºC during 4h, to measure the erythrocyte sedimentation rate (ESR), and then transferred to microtubes and stored frozen. The remaining blood samples were separated into plasma and blood cells, using a centrifuge (15 min at 2,910 g), and plasma was stored frozen at -20ºC and later transferred to -80ºC. During the sample collection, blood smears were also prepared and fixed for 2 min in 100% methanol. In the laboratory, blood smears were stained using Giemsa method and observed at the microscope at 1000x magnification to count white cells (Bennett 1970, Bobby Fokidis et al. 2008, Norte et al. 2008) which were characterized based on their morphology (Julian et al. 1962, Mallory et al. 2015). WBC was estimated by counting the number of white blood cells per 10000 red blood cells (Norte et al. 2008) and H/L was obtained after classifying 100 white blood cells per slide in heterophils, eosinophils, basophils, lymphocytes and monocytes (Mallory et al. 2015). Hb was measured in the whole blood samples with a commercial kit (Hemoglobin Assay Kit, Sigma-Aldrich) according to manufacturer's instructions.

Reactive Oxygen Metabolites (d-ROMs, Diacron, Grosseto, Italy) test was used to measure the presence of hydroperoxides, a common group of non-radical oxidants (Costantini 2008, Monaghan et al. 2009), in the plasma samples. The antioxidant capacity measured using the OXY-adsorbent test (Diacron) measures the plasma capacity to prevent oxidation caused by adding a potent oxidant, hypochlorous acid (HCLO), during the assay. d-ROMs and OXY-adsorbent assays were conducted following the manufacturer instructions and adapted for a 96 well microplate reader. Instructions provided with the kits were adapted for a microplate reader with the following modifications: d-ROMs: plasma sample 10 µL in adult birds, 20 µL in chicks. Incubation: 65 min at 37 ºC; OXY: plasma sample 2 µL. ROMs are presented as Carratelli Units (1 CARR U = 0.08 mg H_2O_2/dL), and OXY as µmol HClO/mL. Inter-assay variation was 7.24% (ROMs) and 9.96% (OXY), and intra-assay variation was 5.41% (ROMs) and 2.62% (OXY).

2.2.4. Statistical Analysis

The effect of *Colony* on the Distance to Nearest Nest, Egg Volume and Parent Body Condition was assessed with Generalized Linear Models (GLM), with a negative binomial distribution, using the *glmmTMB* package (Brooks et al. 2017) in R version 3.6.0 (R Core Team 2019). The interaction between *Colony* and *Year* was included as a fixed factor only when improving the performance of a model, i.e. lowering the model's Akaike Information Criteria (AIC) value. Differences in the Clutch Size between colonies and years were tested using Ordinal Regression Models (ORM) applying the *polr* function within the MASS package (Venables and Ripley 2002). Differences in the linear chick growth rate between Deserta and Porto colonies, during 2019, were tested using a GLM, with a negative binomial distribution from the *glmmTMB* package. The effect of *Colony* on all health parameters was also tested using a GLM, with a Poisson distribution for the Hb, and a negative binomial distribution for the remaining health parameters. All the linear models were validated using *performance* (Lüdecke et al. 2021) and *DHARMa* packages (Hartig 2019) to check overdispersion, residual patterns and observed *versus* fitted values evaluation. The categories 'Deserta' and '2018' were always set as reference levels of the variables *Colony* and *Year*. We were not able to collect enough blood sample to measure Hb in the Deserta, therefore for this model Berlenga was set as reference level for the variable *Colony*.

2.3. Results

2.3.1. Breeding Parameters

Distance to the nearest nest was significantly higher in both urban colonies, especially in the Porto colony (β = 1.40, $p < 0.001$; Fig. 2.1a), than in the two natural colonies. In the breeding season of 2019, the distance to the nearest nest increased considerably in the natural colony of Berlenga (from an average of 7.4 to 15.5 m; β = 0.88, $p < 0.001$; Table 2.1), and decreased in the urban colony of Porto (from 26.3 to 14.0 m; β = -0.47, $p = 0.04$; Table 2.1). Egg volume and egg length were significantly lower in both urban colonies (Table 2.1), particularly the egg volume in the urban colony of Porto (Fig. 2.1b). Trends in adult body condition were not evident, with both the highest and lowest values being registered in the natural colony of Berlenga (in 2018 and 2019 respectively), and the higher average recorded at the Deserta natural colony (Fig. 2.1c). However, the probability of having a 3 egg-clutch was considerably lower in both urban colonies (Fig. 2.1d). Berlenga and Peniche had significantly higher and lower clutch sizes, respectively (β = 1.52 and -1.23, both with $p < 0.05$; Table 2.1). The hatching success observed in the natural colony of Deserta was similar during 2018 and 2019 (67 and 66%).

However, in the urban colony of Porto this differed between years, showing the lowest (56%, during 2018) and the highest (88%, during 2019) values of hatching success.

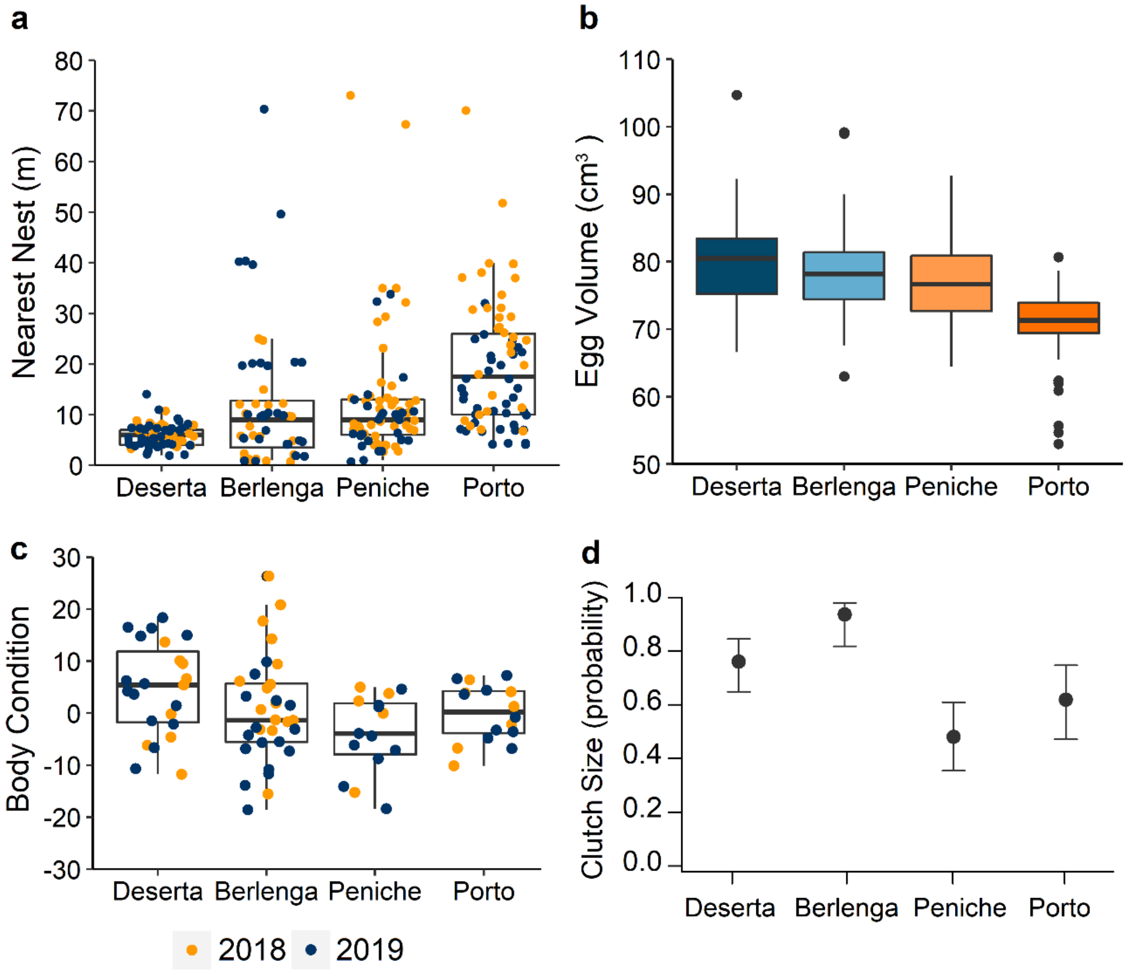


Figure 2.1. *Breeding parameters: (a) distance to the nearest nest (m), (b) egg volume (cm^3), (c) adult body condition (residuals from body mass regressed on wing length) (median, 25-75% percentile range, 1.5*inter-quantile range), and (d) probability of a 3-egg clutch in Yellow-legged gulls' natural (Deserta and Berlenga) and urban (Peniche and Porto) colonies.*

Table 2.1. *Parameter statistics representing the effects of Colony and Year on the Yellow-legged gulls' breeding parameters: distance to the nearest nest, egg dimensions (egg volume, length and width), clutch size and body condition of breeding gulls. Parameter statistics include estimates (β) and standard error (SE). Significant effects (p < 0.05) are in bold and * was included when p ≤ 0.001. Deserta and 2018 were set as reference levels for the variables Colony and Year.*

Parameters	***Nearest Nest***	***Egg Volume***	***Egg Length***	***Egg Width***	***Clutch size***	***Parent Body Condition***
	β ± SE	***β ± SE***	***β ± SE***	***β ± SE***	***value***	***β ± SE***
2019	-0.15 ± 0.18	0.009 ± 0.01	-0.002 ± 0.005	0.005 ± 0.02	0.20 ± 0.31	-0.18 ± 0.10
Berlenga	0.14 ± 0.19	-0.01 ± 0.01	-0.01 ± 0.01	-0.004 ± 0.03	**1.52 ± 0.66**	-0.22 ± 0.12
Peniche	**0.80 ± 0.17***	**-0.03 ± 0.01***	**-0.02 ± 0.01***	-0.01 ± 0.02	**-1.23 ± 0.38 ***	**-0.42 ± 0.15**
Porto	**1.40 ± 0.18***	**-0.12 ± 0.01***	**-0.04 ± 0.01***	-0.04 ± 0.03	-0.67 ± 0.41	-0.22 ± 0.14
2019:Berlenga	**0.88 ± 0.26***	-	-	-	-	-
2019:Peniche	-0.26 ± 0.24	-	-	-	-	-
2019:Porto	**-0.47 ± 0.24**	-	-	-	-	-

2.3.2. Health Parameters – 2019

Adult gulls from all colonies presented significantly lower ESR values when compared to the values of adult gulls from the natural colony of Deserta (Table 2.2; Fig. 2.2a). H/L ratios from adult gulls were also generally lower compared to those observed in the Deserta colony (Fig. 2.2b, 2.3b), but such difference was only significant for the Berlenga natural colony (β = -0.57, p = 0.004; Table 2.2). Adult gulls from the urban colony of Porto tended to have higher H/L ratios compared to adult gulls from Peniche and Berlenga (Fig. 2.2b), but this difference was not significant. WBC counts of adult gulls did not differ between colonies (Table 2.2; Fig. 2.2c), and Hb values were lower in both urban colonies, when compared to the Berlenga natural colony (Fig. 2.2d), but such difference was only significant for the urban colony of Porto (β = -0.11, p = 0.04; Table 2.2).

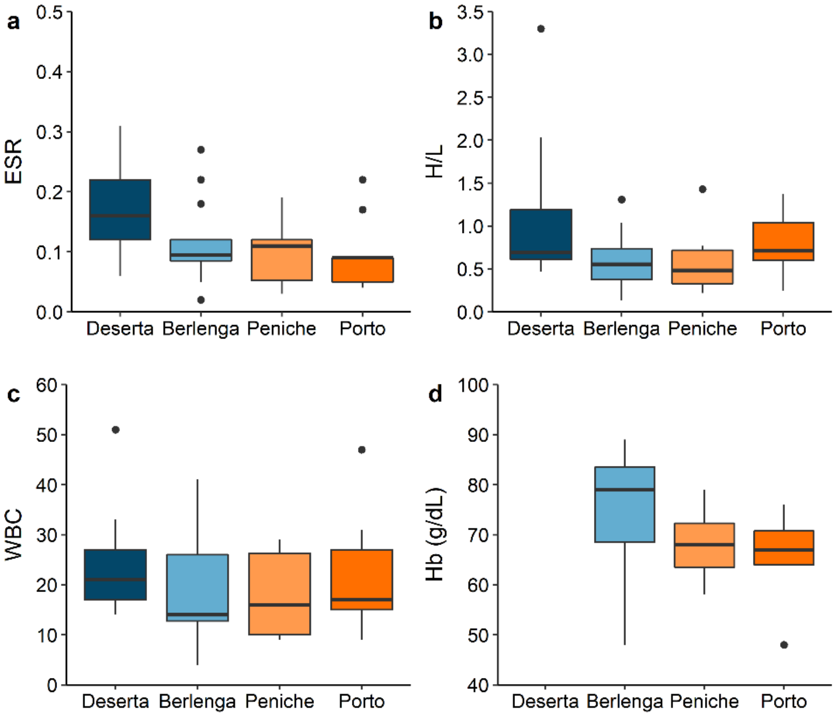


Figure 2.2. *Health parameters for adult Yellow-legged gulls from natural (Deserta and Berlenga) and urban (Peniche and Porto) breeding colonies, during 2019. a) erythrocyte sedimentation rate (ESR), (b) ratio of heterophils/lymphocytes (H/L), (c) white blood cell counts (WBC), and (d) haemoglobin concentration (Hb; g/dl), expressed in median, 25-75% interquartile range, non-outlier range and outliers.*

Chick gulls from the urban colony of Porto exhibited significantly lower values of ESR (β = -0.27, $p < 0.001$), WBC (β = -0.53, $p = 0.04$), and almost significant lower H/L ratios (β = -0.54, $p = 0.06$; Table 2.2, Fig. 2.3a-c), when compared to the same values observed in the natural colony of Deserta. Chicks' Hb did not vary significantly between colonies (Table 2.2). Early linear chick growth was significantly lower in the urban colony of Porto (β = -0.42, $p = 0.001$; Fig. 2.3e), when compared to the natural colony of Deserta, during 2019.

The antioxidant capacity of both adults and chicks did not differ significantly between colonies (Table 2.2; Fig. S2.1), and only adult gulls from the urban colony of Peniche exhibited comparingly higher d-ROM values (β = 0.50, $p = 0.03$; Table 2.2), corresponding to the presence of reactive oxygen metabolites in the plasma.

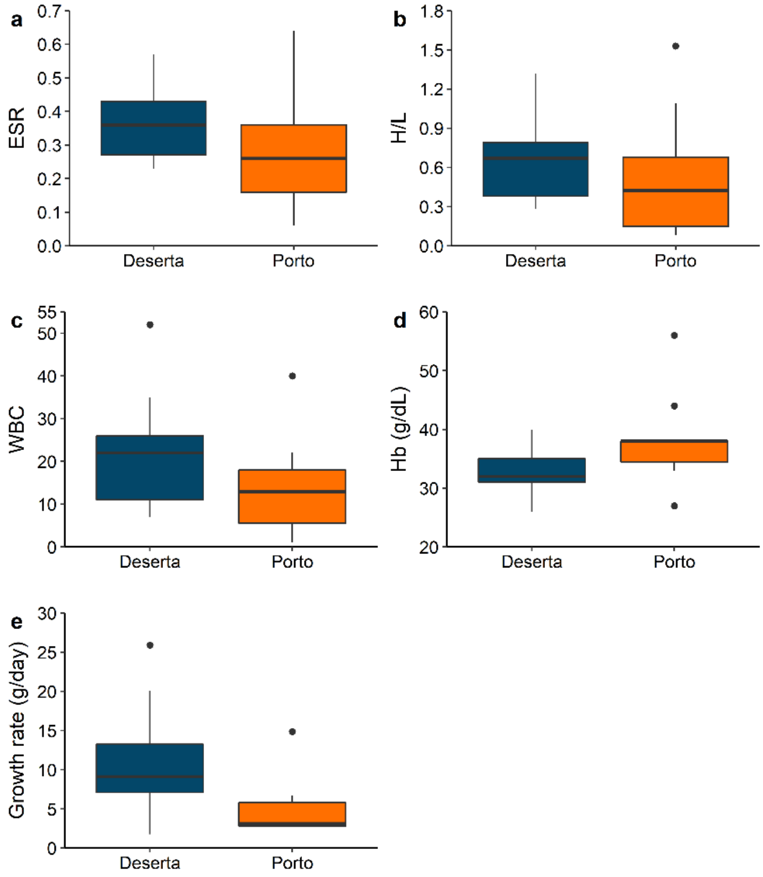


Figure 2.3. *Health parameters for chick Yellow-legged gulls from natural (Deserta) and urban (Porto) breeding colonies, during 2019. (a) erythrocyte sedimentation rate (ESR), (b) ratio of heterophils/lymphocytes (H/L), (c) white blood cell counts (WBC), (d) haemoglobin concentration (Hb; g/dl), and (3) early linear growth rate (g/day); expressed in median, 25-75% interquarkktile range, non out lier range and outliers.*

Table 2.2. *Parameter statistics representing the effects of Colony on adult and chick Yellow-legged gulls' health parameters: erythrocyte sedimentation rate (ESR), ratio of heterophils/lymphocytes (H/L), concentration of haemoglobin (Hb), antioxidant capacity (OXY) and the presence of reactive oxygen metabolites (DROM). Parameter statistics include estimates (β) and standard error (SE). Significant effects ($p < 0.05$) are in bold and * was included when $p \leq 0.001$. Deserta was set as reference levels for the variable Colony.*

Parameters		***ESR***	***H/L***	***WBC***	***Hb***	***OXY***	***DROM***
		β ± SE	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**	**β ± SE**
Adults	Ber	**-0.39 ± 0.18***	**-0.57 ± 0.20**	-0.17 ± 0.18	-	-0.05 ± 0.07	0.21 ± 0.20
	Pen	**-0.55 ± 0.21**	-0.62 ± 0.22	-0.27 ± 0.20	-0.09 ± 0.05	0.02 ± 0.07	**0.50 ± 0.23**
	Por	**-0.54 ± 0.22***	-0.33 ± 0.23	-0.33 ± 0.21	**-0.11 ± 0.05**	-0.01 ± 0.08	0.22 ± 0.24
Chicks	Por	**-0.27 ± 0.16***	-0.54 ± 0.28	**-0.53 ± 0.26**	0.05 ± 0.09	0.14 ± 0.10	-0.59 ± 0.58

2.4. Discussion

Gulls nesting on a novel urban environment seem to face a variety of challenges and important trade-offs between the advantages of breeding in lower density colonies, which offer lower intraspecific negative interactions and a lower probability of disease transmission; and the disadvantages of having an anthropogenic diet usually lower in nutritional value (Pais de Faria et al. 2021a), combined with a higher risk of exposure to hazard materials or other stressors resulting from feeding/nesting on urban structures (Lopes et al. 2020, 2021) and interacting with humans (Pais de Faria et al. 2021b). In addition to these trade-offs, breeding parameters of the most urbanized colony in the rooftops of the Porto city were consistent with the features of a growing population being established by younger unexperienced breeders, such as the increase of nest density over time and generally smaller eggs, which is common to younger female gulls (Coulson 1963).

2.4.1. Breeding parameters

Gulls breeding in the urban colonies exhibited significant differences in most breeding parameters, when compared to gulls breeding in natural colonies, presenting a lower nest density, and lower egg and clutch sizes. Given the structure and topography of buildings within cities, it is common for urban breeders to nest at much lower densities (see Vermeer 1963, Hooper 1988, Vermeer et al. 1988). Nests are commonly physically separated from each other by rooftop structures or just located in different buildings, with just a few nests per rooftop (Kroc 2018). In some cases, a lower nest density is apparently linked to a lower intraspecific aggression, by the surrounding breeding pairs, and a higher breeding success. Vermeer et al. (1988) found this difference in Glaucous-winged Gulls (*Larus glaucescens)* in downtown Vancouver, Canada, where fledging success was much lower for colonial breeders (35%) when compared to solitary breeders (73%). However, this trend was not found in Glaucous-Winged Gulls and American Herring Gulls breeding in the rooftops of Victoria, British Columbia, and Portland, USA, which showed a lower hatching and fledgling success compared to those in the natural insular colonies of Mandarte and Appledore Islands, respectively (Vermeer 1963, Hooper 1988, Perlut et al. 2016). In our case, the urban colony of Porto had an extreme variation in the hatching success from 2018 to 2019 (56-88%), when compared to the steady trend found in the colony of Deserta (67-66%). In fact, the increase in hatching success in the city of Porto occurred in the same year when the distance to the nearest nest reduced considerably (from 26 to 14m) leading to a higher nest density, likely a result of population growth, as suggested by the great increase of peoples' rooftop-nest removal requests to the Porto City Council between 2016 - 2018 (Pais de Faria et al. 2021a). Therefore, our results do not provide a direct support for the idea of a higher nest density causing a reduction in breeding success, here measured as hatching success.

Gulls from both urban colonies also laid smaller eggs, particularly gulls breeding in Porto. Physiological characteristics of avian females seem to play an important role in egg size, with younger females laying smaller eggs due to a still not fully developed oviduct (Coulson 1963, Christians 2002). Indeed, during our work we found a consistent presence of young inexperienced breeders in the city, still exhibiting patterned plumage distinctive from individuals with 2-4 years of age. Gulls from both urban colonies also had a lower probability to produce a 3-egg clutch, which is commonly reported in other roof-nesting gull studies, such as reported by Hooper (1988) when comparing the clutch size of Glaucous-winged Gulls breeding in Victoria, British Columbia, to that in the Mandarte Island (Vermeer 1963, Verbeek 1986); or by Perlut et al. (2016) which observed lower clutch size of urban American Herring Gulls (*Larus smithsonianus*) breeding in Portland, USA, compared to that observed in the Appledore Island. This difference can also be linked with the experience of individuals, as observed in California, where older Western Gulls *Larus occidentalis* presented higher mean clutch size and hatching success, when compared to younger inexperienced individuals (Pyle et al. 1991, Sydeman et al. 1991).

Although, as initially expected, some breeding success parameters were lower or highly variable in urban colonies, such as the production of smaller eggs and extreme variations in yearly hatching success, these seem to be mostly a result of the gulls' experience rather than diet quality. This is also supported by the fact that gulls breeding in urban habitats show a similar body condition to gulls from natural colonies that commonly feed on a higher quality marine diet (Pais de Faria et al. 2021a).

2.4.2. Health Parameters – 2019

Differences in health condition between gulls of natural and urban colonies were more consistent for chicks than for breeding adults. Gull chicks from the urban colony of Porto showed significantly lower ESR and WBC, suggesting a generally lower occurrence of inflammation and lower stimulation of the immune system, although showing a lower early chick growth. Adult gulls from urban colonies showed less consistency in all physiological parameters. Namely, adult gulls from Porto had lower ESR mean values, again showing a lower occurrence of inflammatory processes, but they presented high H/L ratios similar to those observed in Deserta. These might be related with the occurrence of different stressful events from human-gull interactions within the city of Porto (Pais de Faria et al. 2021b), and intraspecific negative interactions common to natural colonies with higher nest density (Soares 2019), such as Deserta, where the transmission of diseases should be enhanced. Adult urban gulls from Porto also showed the lowest Hb values, particularly compared with the Berlenga natural colony, which can be a result of a lower anabolic capacity, with urban gulls expectedly having a lower foraging effort by feeding on predictable anthropogenic resources, together with the lower or absence of migratory movements (Rock 2005); or might be a result of nutritional deficiencies, that also caused a slower early growth of their chicks. Pais de Faria (2021a) found a higher consumption of anthropogenic resources by adult gulls in the city of Porto and the absence of some important omega-3 fatty acids in fledglings of the same colony. In the same study they also report adult gulls feeding their younger chicks with fish, but shifting to anthropogenic items when chicks got older. A fish-based diet of younger chicks could probably explain the higher health condition (higher Hb values) we observed in chicks with 5-10 days old. This also suggests that the lower early chick growth might not be a result of a lower diet quality in the first days of life, but a sign of a lower parent quality expected from younger unexperienced breeders; or even a result of a lower nest density, as suggested by Savoca et al. (2011). They found Herring Gulls breeding on Appledore Island, Maine, in sub-colonies with higher nest density to have higher growth and survival rates than chicks growing isolated from other nests, possibly a result of an increased vigilance and access to food. Data from natural colonies was generally more dispersed, particularly the Hb values from breeding adults of Berlenga. This dispersion could suggest that birds from natural colonies are more heterogenous and probably use a variety of food resources, reflecting a higher individual specialization in foraging strategies (Mendes et al. 2018). Interestingly, besides having low Hb values and generally high H/L ratios, urban adult gulls from Porto did not seem to have the most impaired overall health, as suggested by the absence of significant differences in their body condition. Therefore, our results suggests that urban gulls might be facing a trade-off between the quality of their anthropogenic diet and the avoidance of common colonial stressors, such as intraspecific competition and higher disease transmission probability.

Parameters measuring oxidative stress of adult and chick gulls did not seem to differ consistently between natural and urban colonies, with the higher levels of ROMs in Peniche being possibly a particular characteristic of this colony that we were unable to identify (e.g. exposure to oxidants of an unknown source), which might also be related with the significant lower adult body condition observed in this colony. However, we acknowledge that the number of samples that we were able to collect to measure oxidative stress was small, particularly from chick gulls, and further analysis are required before any firm conclusions.

Our study contributes to the ongoing debate on whether urban nesting is associated with deleterious effects in terms of reproductive and health parameters. The exact location of each urban colony should also be important in explaining the variation in such parameters, also because most urban colonies are located at short distance from coastal areas, where gulls have access to fishing discards, and can provision their young chicks with good quality marine food (Pais de Faria 2021a). Unfortunately, studying urban colonies comes with a variety of challenges, but continuing to study their physiology and breeding biology for longer time periods is pivotal to understand the evolution of urban gull populations, by determining the factors that are allowing the urban populations to grow; and ultimately to aid the design of efficient management measures to deal with established urban gull colonies.

Chapter 3

The importance of marine resources in the diet of urban gulls

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Abstract

The availability of anthropogenic food subsidies has promoted an increase in generalist opportunistic gull species, which currently breed and forage on predictable anthropo genic resources (e.g. landfills). Here we investigated whether marine resources are still important to urban-dwelling gulls. We studied 4 natural and 2 urban Yellow-legged gull *Larus michahellis* colonies and compared (1) diet composition (through pellet analysis) and (2) isotopic niches of adults and chicks, (3) diet delivered to chicks of different ages, and (4) fatty acid (FA) composition of fledglings, in order to assess diet composition, diversity and quality, and the relevance of marine prey for natural and urban gull populations. Adult urban gulls consumed considerably lower proportions of marine prey when compared to gulls from natural colonies; however, they fed their younger chicks (<20 d old) mostly with fish, representing 61−80% of their chick food deliveries. Refuse items were mostly delivered to chicks older than 20 d. Overall, urban isotopic niches were not completely distinct from those of natural colonies, in some cases sharing ca. 50% of their niche space. Fledglings from the most urbanized colony presented overall higher FA concentrations and diversity, but they were lacking some omega-3 FAs relevant to their physiology. Our results highlight the importance of marine resources in the diet of urban gulls, particularly during early chick rearing, the relevance of food sources in the area around the breeding colonies and the fact that urban gulls benefit from year-round reliable anthropogenic food resources.

3.1. Introduction

The modification of natural environments by human activities affects animal physiology and behaviour, causing cumulative impacts across all trophic levels (e.g. Walker 1990, Rosenblatt and Schmitz 2016). Anthropogenic stress factors are known to change the content of proteins in the tissues of primary producers, leading to a lower nutritional intake by consumers (Birnie-Gauvin et al. 2017). Populations with individuals exhibiting higher behavioural plasticity tend to be less affected by human-induced changes (Devictor et al. 2008). In fact, the increase in anthropogenic food subsidies has been promoting an increase in populations of generalist opportunistic species such as gulls, foxes and rats, influencing the functioning of entire ecosystems (Oro et al. 2013). In other cases, the increase in anthropogenic subsidies may represent an ecological trap, such as the reported decrease in the growth rate of Cape gannet *Morus capensis* chicks fed on discards, which are less energetically costly to obtain but have lower nutritional value (Grémillet et al. 2008). Similarly, a decrease in body condition has been reported for juvenile African penguins *Spheniscus demersus* and adult Cape gannets in populations searching for prey in marine regions depleted by fisheries (Grémillet et al. 2016, Sherley et al. 2017).

The Yellow-legged gull *Larus michahellis* (YLG) is a good example of an opportunistic species that has an eclectic diet and the ability to exploit anthropogenic resources such as fisheries discards, landfills or food remains collected within cities (Ramos et al. 2009, Alonso et al. 2015, Navarro et al. 2017, Matos et al. 2018, Parra-Torres et al. 2020), with a consequent increase in population numbers of this species in recent decades (Thibault et al. 1996, Vidal et al. 1998, Duhem et al. 2008). Populations of several gull species have been increasingly exploring urban areas, causing conflicts and negative interactions with humans (e.g. Belant 1997, Rock 2005, Huig et al. 2016).

Such increasing presence in urban areas together with the abundance of anthropogenic items in the diet of urban gulls raises the question as to whether urban gulls are completely independent from the sea. Most of the cities highly populated by gulls are located near the coast (e.g. Huig et al. 2016, Spelt et al. 2019). This proximity may suggest some dependency on marine resources, which could be naturally preyed on or could be obtained from frequent interactions with fishing vessels (Matos et al. 2018, Romero et al. 2019). Duhem et al. (2003) showed that YLGs from colonies close to refuse dumps on the French Mediterranean coast, commonly have a diet composed largely of refuse items but also consistently consume small amounts of fish and other marine prey. Other gull species, such as the Lesser Black-backed gull *L. fuscus*, seem to switch their foraging strategies from terrestrial to marine habitats during the chick-rearing season, to provide higher-quality food to their younger chicks (Isaksson et al. 2016). However, very few studies have analysed in detail the diet of urban gulls throughout the year, which is important to determine whether the inclusion of marine resources in their diet is casual or constant.

Biochemical methods have been widely used to study avian diets to complement analyses of pellets, which only reflect the indigestible parts of a previous meal (Barrett et al. 2007). For instance, terrestrial invertebrates like earthworms are known to be included in the diets of gulls (Coulson and Coulson 2008, Pennycott et al. 2020), but due to their high digestibility they are unlikely to be detected by pellet ana- lysis. In marine ecosystems, nitrogen isotope ratios ($\delta^{15}N$) in animal tissues increase at each trophic level in a predictable manner, and carbon isotope ratios ($\delta^{13}C$) are also known to vary between marine and terrestrial food webs. Thus, their values may be used to represent trophic levels and foraging habitats of birds, and consistency in trophic ecology over time, when analysing diverse tissues with different turnover rates (Inger and Bearhop 2008, Ceia et al. 2014). Isotopic niches obtained from $\delta^{13}C - \delta^{15}N$ biplots are also valuable tools to provide insights into the trophic redundancy between colonies and trophic diversity within each colony, by using several dispersion metrics proposed by Layman et al. (2007). Because most fatty acids (FAs) are acquired through the diet, determining FA composition in different tissues has also been used to characterize and assess the quality of bird diets (e.g. Iverson et al. 2007). The highly unsaturated FAs (HUFAs) and the polyunsaturated FAs (PUFAs), containing omega-3 and omega-6 FAs, are particularly important to bird physiology and are obtained mainly by feeding on aquatic prey (e.g. fish; Gladyshev et al. 2009).

In this study, we compared diet diversity, isotopic niches and FA composition of YLGs from natural and urban colonies, and assessed the importance of marine resources for urban breeding gulls. Specifically, we investigated: (1) the occurrence of marine prey in the diet of natural and urban gulls using pellet analysis; (2) isotopic niches between natural and urban gulls through the analysis of carbon and nitrogen stable isotope ratios in different tissues, and their consistency over time; (3) the occurrence of marine prey delivered to chicks in the most urbanized colony in relation to chick age; and (4) FA composition between fledglings raised in natural and urban colonies, which provides information on the quality and diversity of their diet. We expected gulls from natural colonies to feed mostly on marine prey with little to no refuse in their diet (Calado et al. 2018, 2020, Matos et al. 2018), and gulls from urban colonies to have a refuse-dominated diet with a small but constant consumption of marine prey (Duhem et al. 2003, Méndez et al. 2020), particularly during the chick-rearing period when they tend to feed their chicks with marine (higher quality) prey (Alonso et al. 2015, Isaksson et al. 2016). In addition, because gulls from urban colonies explore different feeding opportunities in the cities (Méndez et al. 2020), we expected them to have a more diverse composition of FAs and isotopic values, reflecting a wider foraging niche with lower temporal consistency, when compared to individuals from natural colonies.

3.2. Methods

3.2.1. Study areas

Data were collected in 4 natural colonies (Deserta, Pessegueiro, Berlenga and Sálvora Islands) and 2 urban colonies (within the cities of Peniche and Porto, Portugal) (Table S3.1). Deserta is a sand-barrier island in the south of Portugal, with approximately 1400 YLG breeding pairs; Pessegueiro is a smaller island located 300 m from the southwest Portuguese coast with about 500 breeding pairs (J. A. Ramos pers. obs.). Berlenga Island lies ~12 km from the Peniche coast and is the largest YLG colony in Portugal, with about 8500 breeding pairs (Instituto da Conservação da Natureza e das Florestas [Nature Conservation Institute and Forestry] unpubl. data). Sálvora Island is part of Galicia National Park, Spain; ca. 3600 YLG pairs were counted on this island in 2019 (Mar de Aves Portal 2019). The exact gull population of both urban colonies is unknown, but in Porto we detected ~150 breeding individuals in the area where we worked, and in Peniche, some individuals bred on rooftops, and a small colony of about 30 pairs bred in an abandoned part of a fortress. Both urban colonies are close to fishery landing areas: (1) Porto, a large urban centre, has ca. 215 000 inhabitants (INE 2018) and is located at the mouth of the Douro River, with nearby extensive riverside and coastal residential areas, and a major fishing harbour; and (2) Peniche, which has ca. 26 500 inhabitants (INE 2018), is a small city with a fishing harbour.

3.2.2. Diet composition of natural and urban gulls throughout the year

To quantify recent diets of the gulls, we collected pellets in all study areas (n = 398 pellets in natural colonies and 349 in urban colonies; Table S3.1) during 3 periods of the 2018 breeding season (pre-breeding: January−March, n = 133 and 93, respectively, for natural and urban colonies; breeding: April−August, n = 133 and 129; post-breeding: September−December, n = 132 and 127). The pellets from the pre-breeding and breeding periods only represent the diet of breeding gulls. However, the post-breeding pellets may represent the diet of both adult breeding and immature gulls, because during this period, the territorial behaviour of individuals tends to be lower, with adult and immature gulls observed resting in the same areas (J. Pais de Faria pers. obs.). The pellet content was identified and grouped into marine (mostly otoliths and other fish bones), refuse (animal bones and artificial materials such as plastic, glass, metallic pieces) or terrestrial (mostly vegetation matter) categories. We assessed the presence or absence of each food category in gull pellets, and categories were then summed and converted to a percentage; the large majority of pellets had only one food category.

3.2.3. Trophic ecology of adults and chicks using SIA

Samples of blood (1 ml from the tarsal vein), the tip of the first primary (P1) and eighth secondary (S8) feathers, and 3 breast feathers (Br) were collected from adult breeding gulls during the incubation period of 2018 in Porto (n = 33), Berlenga (n = 69), Peniche (n = 28), Pessegueiro (n = 44) and Deserta (n = 35; Table S3.1) using traps over gull nests. Since different tissues have different turnover rates, analysis of their isotopic values provides information on different periods during the life cycle. According to the moult phenology of gulls, the P1 and S8 feathers represent the previous breeding and non-breeding seasons, respectively, and Br feathers, which are less time specific, represent the period of body moult in the previous year, i.e. the late-breeding or early pre-breeding period (Hobson and Clark 1993, Ramos et al. 2011). Blood samples can be used to provide information on the assimilated diet of 3−4 previous weeks (using red blood cells; RBCs), or the previous week (using plasma; Bearhop et al. 2004, Inger and Bearhop 2008). During the chick-rearing period, we also collected growing Br samples from chicks > 2 weeks old, which represent the diet provided by their parents. These samples were collected in all study areas except Peniche and Sálvora.

In the field, blood samples were separated into plasma and RBCs, using a portable centrifuge, and were stored frozen after data collection. Prior to isotopic analysis, several rinses with a 2:1 chloroform: methanol solution were used on plasma to extract lipids and on feathers to clean surface lipids and contaminants. Feathers were cut into small fragments, and blood samples were dried at 60°C to a constant mass. We weighed 0.32–0.38 mg of each sample into a tin cup, which was crimped for combustion. Nitrogen and carbon isotope ratios (presented in δ notation, expressed as ‰) were obtained using a continuous flow isotope ratio mass spectrometer, following the equation:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{sample} / R_{standard}) - 1]$$

where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$, respectively. International standards were atmospheric nitrogen (N_2) for $\delta^{15}N$ and Vienna-PeeDee belemnite (V-PDB) for $\delta^{13}C$. Replicate measurements of internal laboratory standards indicated a precision of < 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

3.2.4. Chick food delivery by breeding urban gulls

Chick feeding behaviour was documented in a rooftop breeding area, where a total of 22 nests were monitored during the chick-rearing periods of 2018 (for ca. 20 days each year over the period 15 May to 30 June) (n = 9) and 2019 (n = 13) in Porto, the most urbanized colony. Chick age was determined from the date of egg hatching and grouped into 4 age interval categories (0−5, 6−10, 11−20 and > 20 d old). Chick feeding events were registered for the 22 nests that were followed; based on the last day that each chick was observed, the number of chicks in each age class was 22, 20, 16, and 9, respectively, for chicks of 0−5, 6−10, 11−20 and > 20 d old. The items provided by parents to the chicks were identified using binoculars (Olympus 8×42 EXPSI) and a telescope (Swarovski ATX 20–60 × 95). The observations were conducted for 1 h in the morning/mid-day (between 10:00 and 13:00 h) and 1 h in the afternoon/evening (between 14:00 and 18:00 h). The observations were made from higher public buildings, distanced far enough away from the birds so that the observer was never visible to them or cause any apparent disruption to their behaviour.

3.2.5. Diet quality assessment of fledglings using FA analysis

Blood samples for FA profiles were collected in July 2018 from chicks approximately 3 weeks of age. Chick age was estimated from regular monitoring of nests, with 10 chicks sampled in the natural colony of Berlenga and 11 chicks from the urban colony of Porto (Table S3.1). Samples were collected from physically separated nests (separate rooftop structures or different buildings) in urban areas, and nests ca. 30 m apart from each other in the natural colony, to ensure that chicks were not from the same broods. Samples were centrifuged in the field, using a portable centrifuge, and the plasma was stored in a −80°C freezer. The extraction of total lipids and FA methyl esters (FAMEs) was performed according to the methodology described by Gonçalves et al. (2012). The separation and quantification of FAMEs was performed by comparison with the mass spectrum and the standard Supelco® 37 component FAME mix (Sigma-

Aldrich). The FA methylnonadecanoate C19:0 was added as an internal standard for further quantification. Determination of FAMEs was achieved by gas chromatography−mass spectrometry using a Thermo Scientific Trace 1310 Network. This equipment has a 0.32 mm internal diameter (i.d), 0.25 μm film thickness and a 30 m long Ton refrigeration free fatty acid phase (TR- FFAP) column. The injector port was lined with a splitless glass liner with 4.0 mm i.d. A Thermo Scientific ISQ 7000 Agilent Network Mass Selective Detector was also used with 70 eV electron impact mode, and the *m /z* range of 40−500 was scanned in 1 s cycles in full scan acquisition mode. The initial oven temperature was 80°C followed by 3 ramps of linear temperature increase: 25°C min^{-1} until 160°C; 2°C min^{-1} until 190°C; 40°C min^{-1} until 230°C (maintained for 5 min). The carrier gas used was helium at a flow rate of 4.4 ml min^{-1} and 2.66 psi of column head pressure.

3.2.6. Data analysis

After identifying pellet contents, we ran generalized linear mixed models with binomial family distribution and logit link function, with the ‘lme4’ package (Bates et al. 2015) in R version 3.6.0 (R Core Team 2019), to test the effect of the type of colony (natural and urban) and breeding period (pre-breeding, breeding and post-breeding) on the probability of occurrence of marine, refuse and terrestrial items in the pellets. Sampling location was set as random effect, to control for within-colony variability, and the interaction between the colony type and breeding period was included as a fixed factor in the model selection. The best models were selected based on the lowest Akaike’s information criterion (AIC) and results of likelihood ratio tests comparing the candidate models, with both methods favouring the same models. When the addition of variables did not significantly improve the AIC values, we kept the most parsimonious models.

Layman dispersion metrics (NR: δ^{15}N range; CR: δ^{13}C range; TA: convex hull area; CD: mean distance to centroid; NND: mean nearest neighbour distance; Layman et al. 2007), characterizing isotopic niches of each colony from a given sampled tissue, were generated using the R package SIBER (Jackson et al. 2011). Pairwise Euclidian distances between niche centroids (bivariate means of δ^{15}N and δ^{13}C for each colony/tissue) were obtained using the 'dist' function in the stats built-in R package (R Core Team 2019). SIBER was also used to obtain standard ellipse area, corrected for small sample sizes (SEAc), containing 40% of observations, and ellipses containing 95% of observations. The extent of shared isotopic niches for each season was determined by the overlap of standard and 95% ellipses areas between colonies, using the 'maxLikOverlap' function within SIBER, which is based on the maximum likelihood fitted ellipses.

We used linear models evaluated with a randomized residuals in a permutation procedure (RRPP; Collyer and Adams 2018) to test differences in δ^{15}N and δ^{13}C values; niche dispersion metrics; pairwise centroid distances; pairwise absolute CD and NND differences; and standard and 95% overlap areas. The RRPP is recommended when dealing with distance matrices or high-dimensional data (Turner et al. 2010, Collyer and Adams 2018). In all models, Z-scores and probability distributions (p-values) were obtained from 10 000 random permutations of residuals using the function 'lm.rrpp' within the RRPP package in R (Collyer and Adams 2018), and significance was determined when $p \leq 0.05$. To test differences in δ^{15}N, δ^{13}C and isotopic dispersion metrics between colonies, we ran individual models for each sampled tissue, with colony as the dependent variable. To test for seasonal differences in niche dispersion metrics, we additionally performed a full linear RRPP model for each parameter, with colony (or colony pairs when testing pairwise metrics) and tissue sample (P1, S8, Br or RBC, representing different seasons) as dependent variables in a nested model design.

Dispersion niche metrics and pairwise metrics from chick samples were tested separately. Consistency in trophic level ($\delta^{15}N$) and habitat used ($\delta^{13}C$) were estimated by regressing the isotopic values present in P1 on those present in S8 for long-term consistency, and regressing the isotopic values present in plasma on those present in RBC for short-term consistency. Because carbon isotopic ratios also have a trophic component, we used the residuals of $\delta^{13}C$ plotted against $\delta^{15}N$ to determine $\delta^{13}C$ without this trophic effect.

From our field observations, only chicks from Porto were fed with anthropogenic items; therefore, we performed a general linear model with a binomial distribution only for the Porto colony, to test the effect of chick age (0−5, 6−10, 11−20 and > 20 d) on the presence of anthropo- genic items delivered to them.

The variation in FA profiles was analysed via non- metric multidimensional scaling (NMDS) plots using data converted into similarity triangular matrices through Bray-Curtis resemblance measures using the PRIMER-6 software.

3.3. Results

3.3.1. Diet composition of natural and urban gulls throughout the year

Pellet analysis indicated that gulls from natural colonies ingested a significantly higher amount of marine prey (69.0%, $\chi^2_2 = 314.8$, $p < 0.001$) when compared to other food categories (21.2% terrestrial and 9.8% refuse; Fig. 3.1), and gulls from urban colonies ingested a significantly higher amount of refuse items (42.1%, $\chi^2_2 = 21.8$, $p < 0.001$), but also considerable amounts of marine prey (30.6%) and terrestrial items (27.3%; Fig. 3.1). Marine items were mostly fish and crustaceans, especially in samples from Berlenga Island, where crustaceans represented more than 50% of the diet (Fig. 3.1). Terrestrial items were composed mainly of plant seeds, and refuse items often included small bones (mostly chicken) mixed with regurgitated artificial items (e.g. plastic, glass, metallic pieces).

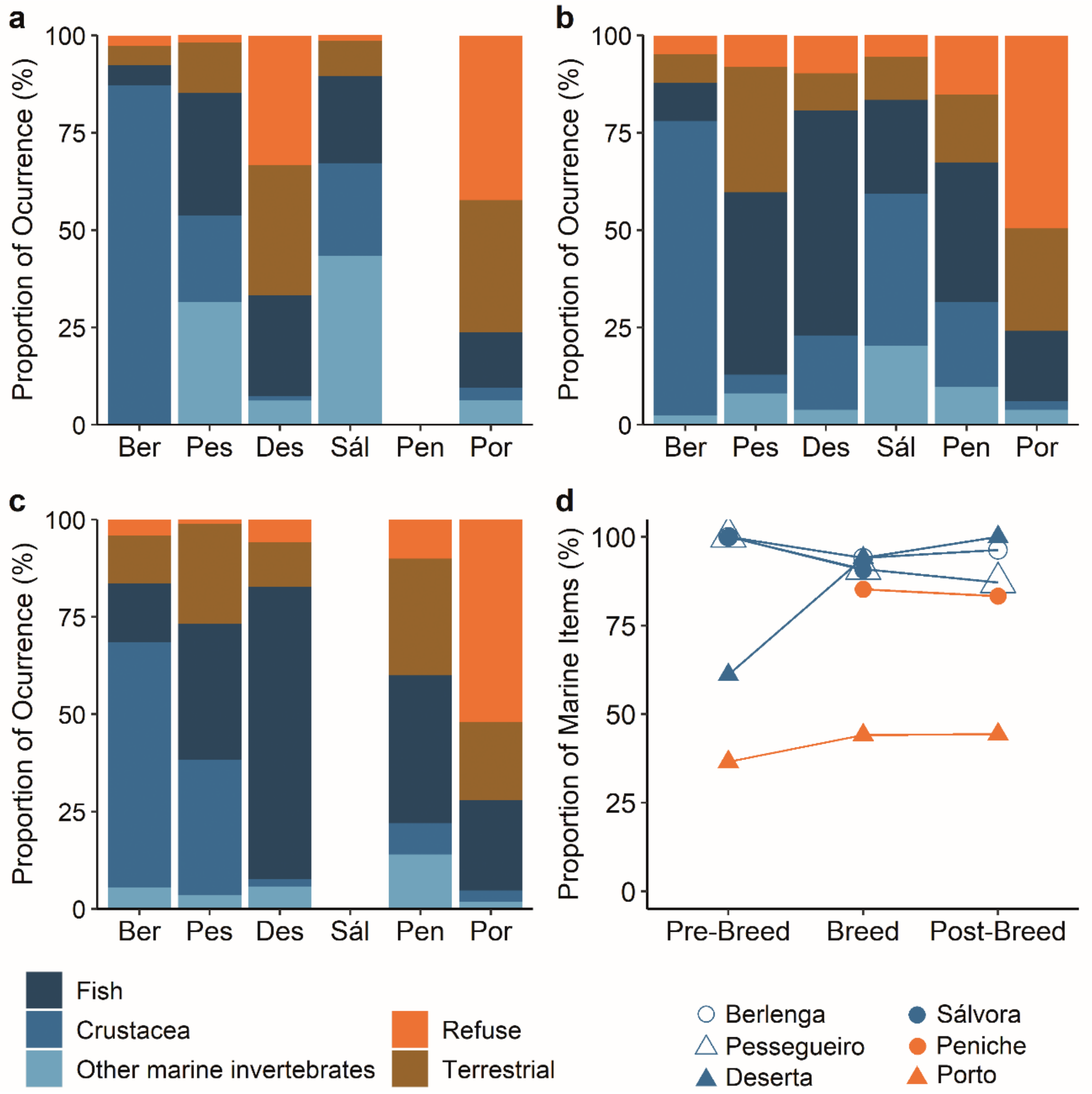

Figure 3.1. *Proportional occurrence of items of different origins (marine, refuse and terrestrial) within pellets collected in several yellow-legged gull colonies, during the (a) pre-breeding, (b) breeding and (c) post-breeding periods of 2018, and (d) variation in the proportion of marine prey occurrence between seasons. Natural colonies are Ber: Berlenga (N = 124), Pes: Pessegueiro (N = 98), Des: Deserta (N = 109) and Sál: Sálvora (N = 67); urban colonies are Pen: Peniche (N = 91) and Por: Porto (N = 258).*

The interaction between colony type and season had a significant influence on refuse consumption (χ^2_2 = 18.29, $p < 0.001$; Table S3.2), particularly during the pre-breeding season, when refuse consumption was considerably lower in urban colonies (β = −2.53, $p < 0.001$; odds ratio = 12.5; Table 3.1). Colony type only influenced the consumption of marine prey and refuse items, with gulls from urban colonies showing a diet with a higher number of refuse items (β = 3.86, p = 0.005; odds ratio = 47.46; Table 3.1) and a lower number of marine prey items (β = −2.07, p = 0.001; odds ratio = 7.9; Table 3.1), when compared with gulls from natural colonies.

Table 3.1. *Parameter statistics representing the effects of each parameter on the probability of occurrence of marine, refuse and terrestrial items in the Yellow-legged gulls' diet from pellet analysis. Parameter statistics include estimates (β) and standard error (SE). Significant effects ($p < 0.05$) are in bold. Post-breeding and Natural were set as reference levels for the variables Period of gulls' life cycle and Colony type.*

Model	***Parameters***	β	***SE***	***Pr (>|z|)***
Marine	Intercept	**2.74**	**0.43**	**<0.001**
	Colony (Urban)	**-2.07**	**0.65**	**<0.01**
	Period (PreBreeding)	-0.45	0.24	0.06
	Period (Breeding)	-0.01	0.24	0.98
Refuse	Intercept	**-3.56**	**0.85**	**<0.001**
	Colony (Urban)	**3.86**	**1.38**	**<0.01**
	Period (PreBreeding)	**2.00**	**0.47**	**<0.001**
	Period (Breeding)	**1.03**	**0.49**	**0.03**
	Colony (Urban) * Period (PreBreeding)	**-2.53**	**0.64**	**<0.001**
	Colony (Urban) * Period (Breeding)	-0.40	0.66	0.55
Terrest.	Intercept	**-1.34**	**0.38**	**<0.001**
	Colony (Urban)	0.87	0.60	0.15
	Period (PreBreeding)	**0.74**	**0.20**	**<0.001**
	Period (Breeding)	0.06	0.19	0.74

3.3.2. Trophic ecology of adults and chicks using SIA: Isotopic niches

Adult RBCs, which represent the incubation period, had overall lower mean stable isotope values than other tissues, particularly for the urban gulls (Fig. 3.2a,b). Within this period, gulls in the Peniche urban colony had significantly lower δ^{13}C values ($Z_{Peniche}$ = 4.19, $p \leq 0.05$; Table S3.3; Fig. 3.2a), suggesting the intake of fewer marine resources, and gulls in the Porto urban colony had significantly lower δ^{15}N values (Z_{Porto} = 5.85, $p \leq 0.05$; Table S3.3; Fig. 3.2b), indicating a lower trophic level diet. During this period, the isotopic niches were particularly segregated, especially for gulls from Porto when compared to the isotopic niche of gulls from Berlenga (dist = 2.18, $p \leq 0.05$; Table S3.4) and Pessegueiro (dist = 2.06, $p \leq 0.05$; Table S3.4, Fig. 3.3d).

Adult P1 feathers, which represent the breeding season, had significantly lower δ^{15}N values for gulls from both the Pessegueiro natural colony and the Porto urban colony ($Z_{Pessegueiro}$ = 3.58 and Z_{Porto} = 3.39, both with $p \leq 0.05$; Table S3.3; Fig. 3.2b), indicating that gulls from these 2 colonies were foraging at a lower trophic level. The more dispersed isotopic niche for gulls from the Deserta natural colony and the Porto urban colony, with significantly higher CD and NND values ($CD_{P1\text{-}Deserta}$ = 1.46, $NND_{P1\text{-}Porto}$ = 0.72, both with $p \leq 0.05$; Table S3.5, Fig. 3.3c), respectively, indicate an overall varied diet for gulls from these 2 colonies. The greatest differences in the isotopic niche dispersion were observed between the Berlenga and Deserta natural colonies ($|CD_{Berlenga} - CD_{Deserta}|$ = 0.86, $p \leq 0.05$; Table S3.4), and between the Berlenga natural colony and the Porto urban colony ($|NND_{Berlenga} - NND_{Porto}|$ = 0.48, $p \leq 0.05$; Table S3.4). All colony pairs presented some degree of niche overlap during the breeding season, except for the Pessegueiro vs. Berlenga natural colonies (Table S3.4). Gulls from Pessegueiro and the Porto urban colony shared the largest standard niche area (standard overlap area = 1.11, $p \leq 0.05$;

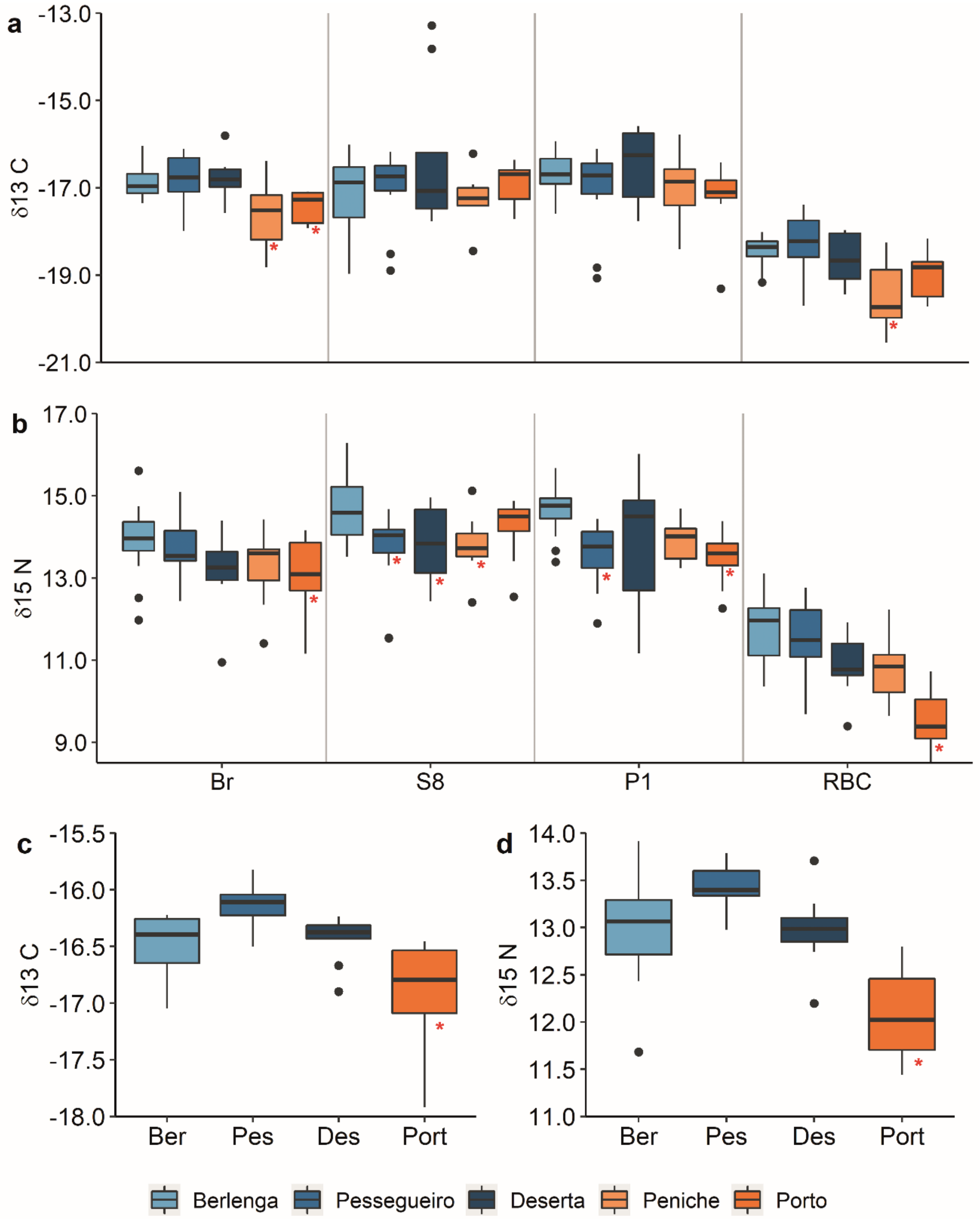

Figure 3.2. *The (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values (median, 25-75% percentile range, 1.5*inter-quantile range, and outliers) in the different tissues of adult Yellow-legged gulls, representing diet assimilated during different time periods (Br = breast feathers, as general indicators of the previous year; S8 = eighth secondary feather, for the non-breeding season; P1 = first primary feather, for the breeding season, and RBC = red blood cells, for the incubation period), and (c) $\delta^{13}C$ and (d) $\delta^{15}N$ in the chicks' breast feathers, in natural (Berlenga, Pessegueiro, Deserta) and urban (Peniche, Porto) colonies. Significant differences between colonies are marked with the red star under the boxplots, Berlenga was set as reference level for the variable colony.*

Table S3.4), which suggests the consumption of prey with similar isotopic composition.

The stable isotope values of adult S8 feathers, which represent the non-breeding season, showed the widest isotopic niche for gulls from Deserta (Fig. 3.3b), with significantly higher values for all dispersion metrics, except for δ^{15}N range and NND ($CR_{S8} = 4.48$; $TA_{S8} = 8.28$; $CD_{S8} = 1.60$, $SEAc_{S8} = 5.28$, all with $p \leq 0.05$; Table S3.5), and had a significantly higher pairwise CD difference, when paired with both urban colonies ($|CD_{Deserta} - CD_{Peniche}| = 0.88$, $|CD_{Deserta} - CD_{Porto}| = 0.85$, both with $p \leq 0.05$; Table S3.4). The greatest overlap in niche areas (containing 95% of samples) was also obtained during the non-breeding season, between the 2 natural colonies of Deserta and Berlenga (95% overlap area = 11.09, $p \leq 0.05$; Table S3.4). A lower but significant overlap was observed with the P1 data, i.e. within the breeding season, between the natural colony of Pessegueiro and the urban colony of Porto (95% overlap area = 6.83, $p \leq 0.05$; Table S3.4).

Adult Br samples, as general broad indicators of assimilated diet during the previous year, exhibited significantly lower δ^{13}C mean values for both urban colonies (δ^{13}C; $Z_{Peniche} = 3.38$; $Z_{Porto} = 2.58$, both with $p \leq 0.05$; Table S3.3; Fig. 3.2a), suggesting a diet generally lower in marine resources.

Chicks in the Porto urban colony consumed prey with significantly lower δ^{13}C and δ^{15}N values ($Z_C = 2.50$, $Z_N = 3.60$, both with $p \leq 0.05$; Table S3.3; Fig. 3.2c,d), also indicating a lower marine resources-based diet obtained at a lower trophic level. These differences in the chick samples were reflected in the higher distances between niche centroids, particularly between the urban colony of Porto and the natural colony of Pessegueiro, although this was not significantly different from zero (dist = 1.54, p = 0.11; Table S3.4).

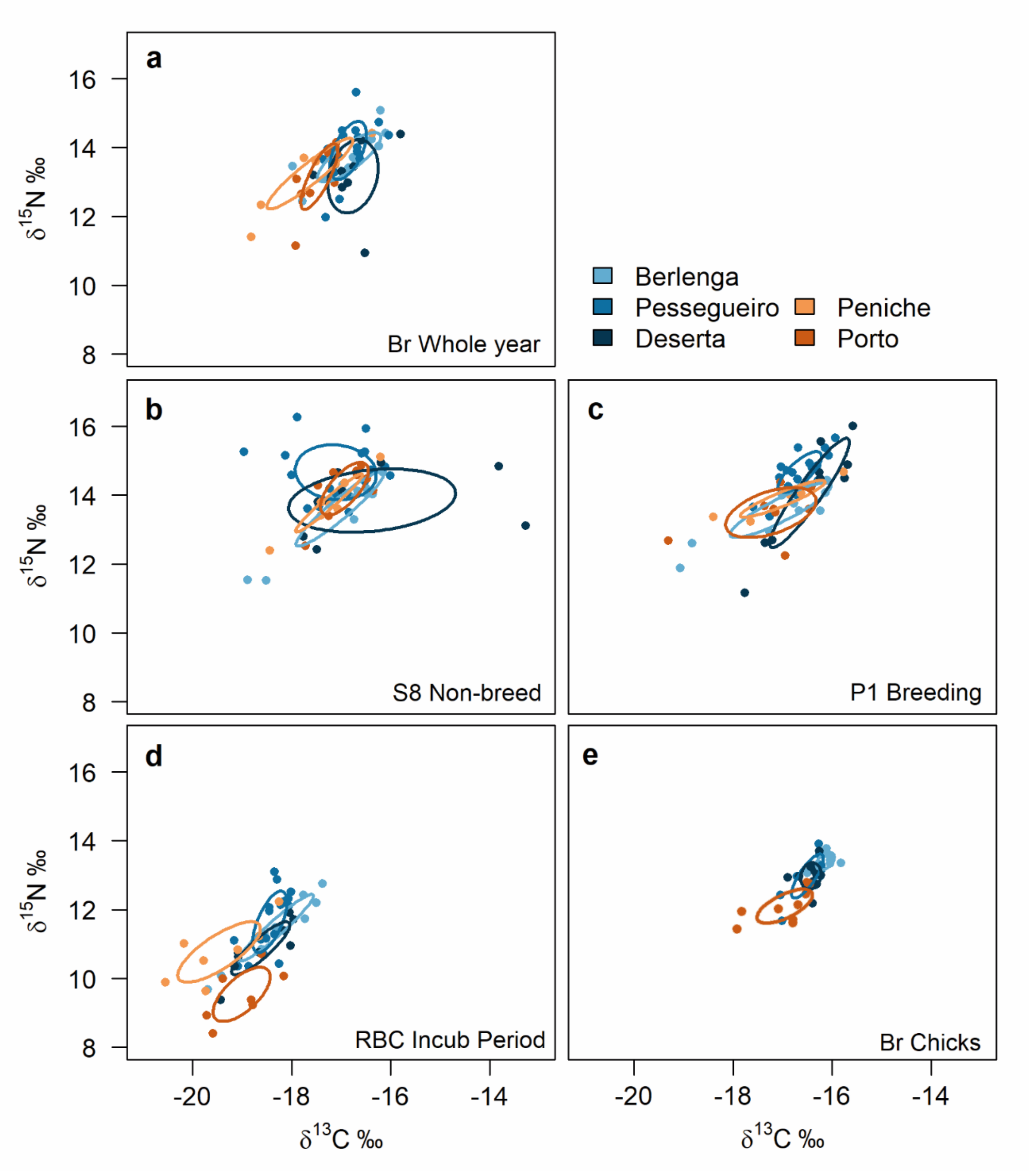

Figure 3.3. *Isotopic niches for different time periods, expressed as standard ellipses containing 40% of individual $\delta^{13}C$ and $\delta^{15}N$ measurements (dots), from Yellow-legged gull adult (a) breast feathers, as general indicators of the previous year, (b) eighth secondary feathers, for the non-breeding season, (c) first primary feathers, for the breeding season, (d) red blood cells, for the incubation period and (e) chicks' breast feathers, representing the chicks' diet during the chick-rearing period, from natural (Berlenga, Pessegueiro, Deserta) and the urban colonies (Peniche and Porto).*

3.3.3. Short- and long-term trophic consistency

Short-term consistency, obtained by regressing the isotopic values in plasma on those in RBC, was present in both colony types for trophic level (natural δ^{15}N $\beta = 0.70$, $R^2 = 0.47$, $F_{1,35} = 31.04$, $p < 0.001$; urban δ^{15}N $\beta = 1.02$, $R_2 = 0.61$, $F_{1,12} = 18.87$, $p < 0.001$; Fig. 3.4a) and habitat use (natural δ^{13}C $\beta = 0.90$, $R_2 = 0.30$, $F_{1,35} = 15.25$, $p < 0.001$; urban δ^{13}C $\beta = 0.62$, $R_2 = 0.30$, $F_{1,12} = 5.22$, $p = 0.04$; Fig. 3.4b).

Long-term consistency, obtained by regressing the isotopic values present in P1 on those present in S8, was observed in both colony types, but only for trophic level (natural δ^{15}N $\beta = 0.55$, $R_2 = 0.28$, $F_{1,35} = 13.9$, $p < 0.001$; urban δ^{15}N $\beta = 0.50$, $R_2 = 0.39$, $F_{1,13} = 8.35$, $p = 0.013$; Fig. 3.4c).

There was no long-term consistency in habitat use in gulls from both colony types (natural $\delta\ ^{13}$C $\beta = 0.21$, $R_2 = 0.10$, $F_{1,35} = 3.86$, $p = 0.06$; urban $\delta\ ^{13}$C $\beta = 0.48$, $R_2 = 0.18$, $F_{1,13} = 2.85$, $p = 0.115$; Fig. 3.4d).

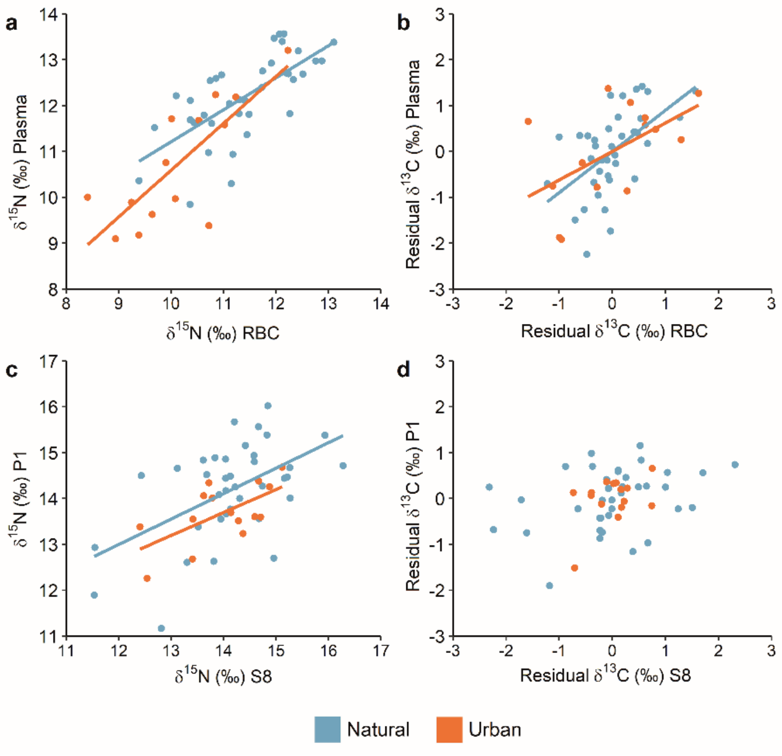

Figure 3.4. *The isotopic values (δ^{15}N and residuals of δ^{13}C plotted against δ^{15}N) of blood (RBC = red blood cells and plasma) and feather samples (P1 = first primary and S8 = eighth secondary feathers) of Yellow-legged gulls form Natural and Urban colonies, representing short (a-b) and long-term (c-d) consistency in the trophic level (δ^{15}N) and used habitat (δ^{13}C).*

3.3.4. *Chick food delivery by breeding urban gulls*

A total of 116 provisions were registered in both years, although we were only able to identify items being delivered to chicks in 66% of provisions. Marine prey represented 80, 61, 69 and 35% of items delivered to chicks < 5, 6−10, 11−20 and > 20 d old, respectively (Fig. 3.5). The proportion of marine prey ingested by chicks > 20 d old differed significantly from that ingested by chicks in younger age classes, showing a particularly strong negative effect ($\beta = -1.99$, $p < 0.05$). Anthropogenic items were mostly delivered to older chicks, > 20 d old, representing 65% of their diet (Fig. 3.5), which included processed meat (e.g. ham, prepared chicken breasts) and human meal leftovers (e.g. cooked meat, pasta).

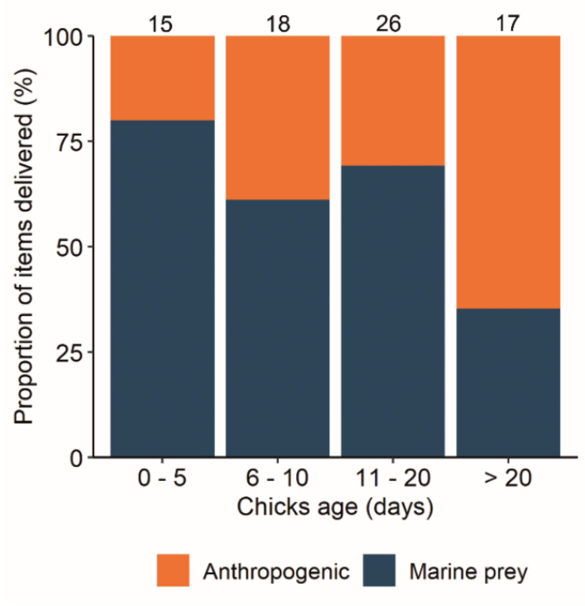

Figure 3.5. *Proportion of anthropogenic (e.g. ham, chicken, cooked pasta) and marine prey items delivered by Yellow-legged gull parents to their chicks of different age categories (in days), from the monitored rooftop nests (N = 22) in the Porto colony, during the breeding season of 2018 and 2019. Items delivered to chicks were only possible to identify in 66% of all 116 provisions. In the top of columns are the number of deliveries where the items were possible to be identified, for each chick age class.*

3.3.5. *Diet quality assessment of fledglings using FA analysis*

Saturated FAs (SFAs) had higher mean concentration in fledgling samples from both natural (Berlenga) and urban (Porto) colonies, especially from latter (natural mean = 416.2 $\mu g\ g^{-1}$, urban mean = 1181.8 $\mu g\ g^{-1}$; Fig. 3.6). HUFAs had lower mean concentrations in both colonies (natural mean = 68.3 µg g^{-1}, urban mean = 41.1 µg g^{-1}; Fig. 3.6). Variation in the number of FAs per bird was higher in the natural colony (N range = 6−13; Table S3.6) compared to the urban colony (N range = 9−13; Table S3.6). FA similarity within the natural colony (average similarity = 46.17; Table S3.7) was lower than within the urban colony (average similarity = 61.76; Table S3.7). The SFAs C18:0 and C16:0, which had the highest mean concentrations, contributed most to the similarities within the 2 colonies (ca. 39% of cumulative contribution for the natural colony, and ca. 35% of cumulative contribution for the urban colony; Table S3.7) (Fig. 3.6). C16:0 and C18:0, in conjunction with C14:0, C22:00 and C20:3n6, contributed most, up to 56%, to the dissimilarities between natural and urban colonies (average dissimilarity = 48.73; Table S3.8), with samples from the urban colony presenting much higher mean concentrations (Fig. 3.6).

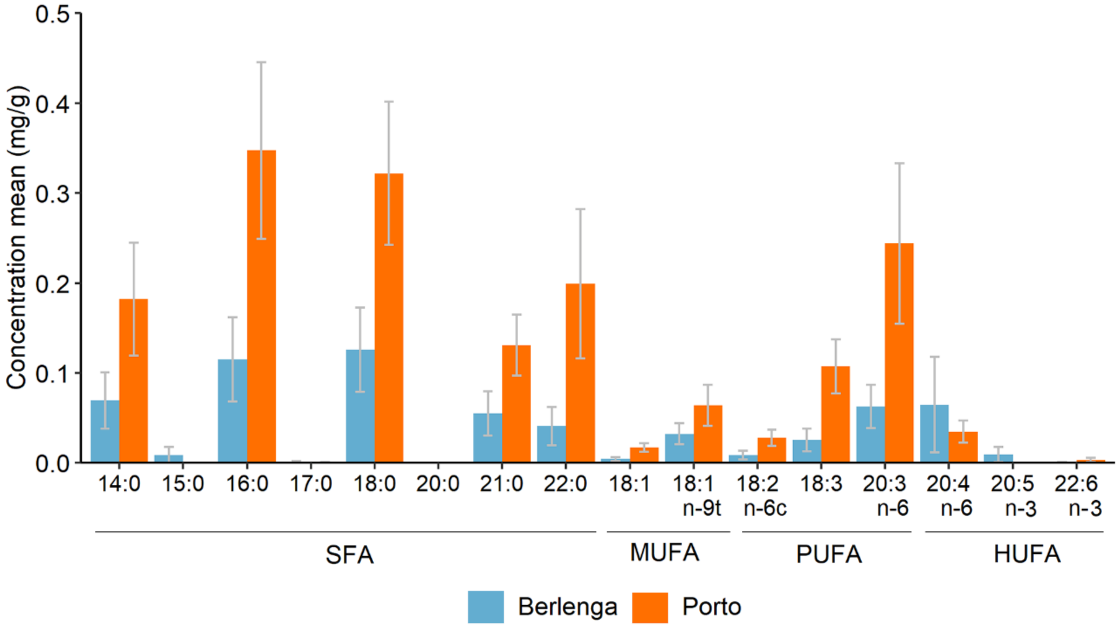

Figure 3.6. *Concentration (mean ± SE) of major saturated (SFA), monounsaturated (MUFA), polyunsaturated (PUFA) and highly unsaturated (HUFA) fatty acids in the plasma of Yellow-legged gull fledglings from a natural (Berlenga N = 10) and an urban (Porto; N = 11) colony.*

Similarities in the FA profiles of both colonies were also identified in the NMDS; however, samples from the natural colony were generally more dispersed (Fig. S3.1). Overall, we found no major variations in the FAs from chicks in the urban colony (Fig. S3.1), exhibiting higher concentrations of all FA groups than chicks from the natural colony, except for the HUFAs (Table S3.6). In all urban samples, there was a total absence of the SFA C15:0, the PUFA C20:2 and the HUFA C20:5n3 (eicosapentaenoic acid) (Table S3.6).

3.4. Discussion

We used several approaches to evaluate adult YLG diets, adult and chick trophic ecology, composition of FAs in fledglings from natural and urban colonies and chick food provisioning by gulls breeding in a highly urbanized colony. We found that urban gulls regularly consumed marine resources throughout the year, which seemed especially important when adults fed their younger chicks (< 20 d old). In both colony types, gulls presented short-term and long-term consistency in their trophic levels, but no long-term consistency in their habitat use, which might reflect their higher foraging plasticity throughout the year.

Although it remained constant throughout the year, the consumption of marine prey was considerably lower in urban colonies than in natural colonies. Anthropogenic items are commonly found in the diet of several gull species (Seif et al. 2018, Pennycott et al. 2020), and in some cases, gulls actually show higher breeding success while feeding on anthropogenic resources. For instance, 90% hatching success was reported in lesser black-backed gulls having a diet mostly based on terrestrial and refuse items (Gyimesi et al. 2016); and Herring Gulls *Larus argentatus* feeding on domestic refuse and fishery discards during the chick-rearing period had higher fledgling success (van Donk et al. 2017). In our study, seasonality was particularly evident in the natural colony of Deserta Island, with adult gulls increasing their consumption of refuse during the pre-breeding season, up to similar proportions as those in Porto, the most urbanized colony. Such an increase in the diet diversity could explain the wider isotopic niche of gulls from Deserta Island during the non-breeding season. In contrast, gulls from the urban colony of Peniche mainly consumed marine prey, in similar diet proportions of natural colonies, possibly due to their proximity to the coast or some dependency on fishing discards from the nearby fishing harbour. Zorrozua et al. (2020) reported that the distance to the nearest fishing harbour had a strong effect on the diet of YLG chicks from the Bay of Biscay, and this was more relevant in explaining the diet of gulls than the distance to the nearest landfill. Romero et al. (2019) found that YLGs from Madeira Island foraged within 5 km of the coast, and a high proportion of their trips to the sea involved interactions with fishing boats; they also fed their chicks mostly with fish, likely from fishing discards.

Overall, we found some trophic similarities between gulls from natural and urban colonies, sometimes sharing ca. 50% of their isotopic niches. However, gulls from natural colonies exhibited higher mean $\delta^{15}N$ and $\delta^{13}C$ values, which stresses that gulls were feeding at a higher trophic level and mainly on marine resources (Peterson and Fry 1987, Lopezosa et al. 2019). Differences between colony types were particularly evident during the incubation period, when isotopic niches representing the trophic level and foraging habitats used by gulls from Porto were particularly segregated. These differences, along with the absence of long-term consistency in habitat use ($\delta^{13}C$), could be explained by gulls foraging in specific nearby resources during this period, not only to maximize their energy intake (Schoener 1971), but also because they were more constrained by breeding duties. Altogether, gulls from urban colonies do not seem to have a distinct foraging pattern compared to gulls from natural colonies. As generalists, YLGs are expected to adapt their foraging strategies according to the nearest available resources (Calado et al. 2020, Zorrozua et al. 2020), regardless of their breeding grounds (natural or urban). Thus, gulls from the same colony type with similar breeding grounds will not necessarily behave alike, and gulls from distinct breeding grounds but with similar nearby resources (e.g. fishing harbours near natural and urban colonies), would probably have similar diets. The presence of anthropogenic items in the diet of older chicks from Porto could be the reason why they exhibit a distinct isotopic niche, with a lower trophic level and likely a diet less based on marine resources. Overall, the proportion of marine prey seemed considerably higher in the items delivered to younger chicks, compared to the items found within pellets from adult gulls in the same colony. This suggests a dietary shift from terrestrial to marine prey, probably to feed younger chicks with higher-quality marine prey. This is a particularly well documented behaviour observed in several gull species, especially in natural insular colonies (e.g. Annett and Pierotti 1989, Isaksson et al. 2016), but it does not seem to always be the case. At Berlenga Island, YLG adults are known to include terrestrial items in their diet but feed their chicks with marine items (Alonso et al. 2015). Further, the stomach contents of urban YLG chicks from Barcelona, Spain, mainly comprised terrestrial birds (e.g. pigeons) and demersal marine resources, probably obtained when visiting the nearby fishing harbour (Méndez et al. 2020). Méndez et al. (2020) also found an increase in demersal and pelagic marine resources in the stomach content of older chicks (ca. 4−5 weeks old), and the presence of anthropogenic items in all chick ages. In natural insular colonies in northern Spain, Moreno et al. (2010) found refuse items (chicken and pork) in the diet of ca. 2−3 weeks old YLG chicks, and Lenzi et al. (2019) found that kelp gulls *L. dominicanus* from an insular colony in Uruguay progressively fed their chicks with larger refuse items. This variation in the items delivered to chicks of different ages in different colonies seems to reveal the dependency of gulls on available nearby resources, especially during the chick- rearing phase.

The most abundant FAs in fledgling samples from both Berlenga and Porto were C16:0 and C18:0, as expected since both are a common released product from the de novo FA biosynthesis pathway (Dalsgaard et al. 2003). These SFAs, along with C14:0, C22:0 and the PUFA C20:3n6, were found at particularly high concentrations in the urban colony. The abundance of long-chain SFAs (e.g. C22:0) and the deficiency of omega-3 HUFAs, as observed in Porto fledglings, are both common indicators of terrestrial food webs (Dalsgaard et al. 2003, Taipale et al. 2015, Twining et al. 2018), which is in agreement with the observed anthropogenic items being delivered to chicks from Porto. The HUFA group, containing omega-3 fatty acids important to physiology (Dalsgaard et al. 2003, Gladyshev et al. 2009), was the only group presenting a comparatively higher concentration in the natural colony, which is consistent with a diet based on marine resources.

The generally higher FA concentration and diversity in urban fledglings suggest that urban gulls might be fulfilling the nutritional needs of their growing chicks. They could be benefiting from reliable and predictable food sources (Real et al. 2017), either by interacting with fishing boats and feeding on marine species of higher nutritional value (EFSA NDA Panel 2014), or by feeding on human meal leftovers collected from trash containers or landfills (Huig et al. 2016, Egunez et al. 2018). Items found in human meal leftovers, although usually rich in fat and proteins which allow for a greater energy intake (Patenaude-Monette et al. 2014), might be deficient in essential nutrients. Several studies have shown breeding costs related to a decrease in marine prey in the diet of several gull species, such as the reported decrease in chick weight of laughing gulls *L. atricilla* from New Jersey, USA (Dosch 1997), or the decrease in egg quality of Herring Gulls breeding on the Laurentian Great Lakes (reviewed by Hebert et al. 2020). Although exploring predictable resources would allow gulls to reduce energetic costs incurred by foraging, urban environments are also commonly associated with an increased exposure to several contaminants (e.g. Isaksson 2018, Zapata et al. 2018, Sorais et al. 2020) and pathogens (Alm et al. 2018, Smith et al. 2020), potentially jeopardizing their health condition. Nevertheless, we acknowledge the relatively small number of samples used for FA analysis, which prevented a more robust interpretation of our results.

Overall, we found that urban gulls had a highly diverse diet, but still relied on marine resources, especially when feeding their younger chicks. These marine items could be obtained either by foraging in the open ocean, or by feeding on fishery discards. To understand if urban gulls are efficiently exploring urban areas, tracking studies would be recommended to identify the most-used foraging locations, where gulls could be obtaining the identified food items. Such studies are important to complement the dietary data and minimize limitations from diet analysis methods (e.g. overestimation of hard remains within pellets; physiological processes influencing FA composition; and the requirement of sampling hypothesized prey for a more detailed FA and stable isotopic analysis; Barrett et al. 2007, Williams and Buck 2010). Because breeding gulls are particularly constrained by distance to resources during the breeding season (e.g. Zorrozua et al. 2020), the assessment of breeding success and general health condition of these urban populations could also be a valuable complementary tool to understand the effects of an anthropogenic diet.

Chapter 4

Seasonal variation in habitat use, daily routines and interactions with humans by urban-dwelling gulls

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Abstract

The effects of growing urbanization have caused an increase in human-wildlife interactions in urban areas. Human-gull conflicts have been particularly studied during the breeding season when gulls cause an obvious nuisance in urban areas. However, with many gulls being present in urban areas throughout the year, stakeholders need knowledge of seasonal effects on local human-gull interaction dynamics. Here we present a comprehensive study on spatial and temporal variation of urban habitat use and human interactions with urban gulls, *Larus* spp., in Oporto, Portugal. The work combined: (1) a large-scale study, using year-round monthly surveys to quantify gulls' behaviour and their use of multiple urban habitats, with (2) a small-scale study, using 10-hour daily urban surveys to capture gulls' daily routines and interactions with humans during the winter and breeding seasons. We found a strong temporal effect in the number of gulls and human-gull interactions occurring in urban areas, with both highly increasing during winter. Habitats with higher urbanization intensity were mainly used by adult gulls and the number of breeding-related conflicts reported by the human population peaked during the chick-rearing period. Still, during winter, several adult gulls kept occupying their rooftop nesting grounds, and the number of individuals foraging and interacting with humans in city-squares increased, and was mostly triggered by humans feeding birds. Therefore, when designing urban management landscape measures, seasonal variations of the urban gulls' behaviour and habitat-use should be considered, as well as anthropogenic activities and human behaviour.

4.1. Introduction

Humans and nature have been co-existing and interacting for centuries, with some wildlife interaction records dating from ancient Egypt (Dixon 1989). Several studies addressed human-nature interactions, mostly focusing on the negative outcomes for both humans and nature (e.g. Oro et al. 2013; Cox and Gaston 2018; Newsome et al. 2015). However, human-nature interactions and associated dynamics are highly complex (Soga and Gaston 2020; Gaston et al. 2018a) and can exhibit spatial and temporal dynamism or depend on socio-economic factors, with all the attributes and dimensions of such interactions showing complex relationships (Soga and Gaston 2020).

From a human perspective, negative human-nature interactions were always common in rural areas, particularly between farmers and wildlife (e.g. Horgan and Kudavidanage 2020; Sangay and Vernes 2008; Conover 1998). However, with the increase of the human population and growing urbanization, natural habitats are progressively reduced and fragmented, amplifying the human habitat-related pressures on several ecosystems (e.g. Gosling et al. 2017). These new pressures consequently led to an increase in the use of urban areas by opportunistic species and an increase in human-wildlife conflicts (Soulsbury and White, 2015), with urban areas being more prone to human-avian conflicts (von Döhren and Haase, 2015). Humans may also benefit from positive human-nature interactions related with the provision of several cultural ecosystem services (Gaston et al. 2018b) and mental health benefits associated with nature experiences (Barnes et al. 2019; Cox et al. 2017a), although these tend to be less common in urban areas (Cox et al. 2017b).

Birds have been adjusting to urban environments, especially species with higher phenotypic and behavioural plasticity, and in some cases changing migratory patterns, breeding timings and phenotypic traits (Garcia et al. 2017; Hensley et al. 2019). A bigger part of human-bird interactions is associated with the intentional or unintentional food provisioning by humans and the increase of food subsidies available in urban areas (Oro et al. 2013; Newsome et al. 2015; Cox and Gaston 2018). The intentional provision of food is commonly a response to the ‘extinction of experience’, when people seek to increase the currently rare nature experiences in urban areas (Cox and Gaston 2016; Soga and Gaston 2016). However, these experiences can rapidly progress to negative human-bird interactions with opportunistic species, which increased their human tolerance through a habituation process (e.g. Kumar et al. 2019).

Several gull species are generalist and have the ability to adapt and exploit novel food (Carmona et al. 2021; Lopes et al. 2020, 2021) and nesting site opportunities provided by human-modified environments, leading to the worldwide increase of their populations over the past decades (Belant 1997; Vidal et al. 1998; Rock 2005; Ross-Smith et al. 2014; Huig et al. 2016; Winton and River 2017). Such increase of opportunistic gull species in urban areas has caused human-gull interactions and conflicts worldwide. These can be related to the rooftop-nesting behaviour, leading to damages of urban structures, nuisance and aggressive behaviour near the nests, or related to the foraging behaviour, such as foraging in trash containers and stealing food from people in parks or restaurants (Belant 1997; Huig et al. 2016). Urban areas do not only provide predictable anthropogenic food subsidies, which are usually less energetically costly to obtain (van Donk et al. 2019), but also provide several breeding-related advantages, such as less intraspecific aggression due to the lower ‘rooftop-nest’ density (Rock 2005). Landfills nearby urban areas are a significant source of predictable food subsidies for opportunistic species such as gulls (Real et al. 2017; Alm et al. 2018), hence the movement of gulls to urban areas may constitute a public health concern (Carroll et al. 2015).

The management of areas where humans and wildlife co-exist usually aims at increasing the positive interactions (e.g. eco-tourism), while minimizing the effects and reducing the number of negative human-wildlife interactions (e.g. nuisance, animal attacks or transmission of zoonotic diseases). This can sometimes be highly challenging when dealing with higher plastic opportunistic species, which tend to grow habituation to the implemented management measures (e.g. urban gulls; Cook et al. 2008). Besides, each city has its own features (e.g. construction type, food resources, human behaviour) with numerous factors influencing human-nature interactions (Soga and Gaston 2020). Nevertheless, the knowledge of local human-gull interaction dynamics is still limited to allow an efficient management of gull-related conflicts. Most management of human-gull conflicts in urban areas, such as the removal of nests or the prevention of breeding in certain areas is carried out isolated from an understanding of seasonal variation in habitat use and daily routines of gulls in urban areas (Rock 2005).

The use of urban habitats by gulls has been increasingly studied in the last years, but mostly at a broad scale perspective with the use of tracking technology (e.g. Isaksson et al. 2016; Maynard and Ronconi 2018). Spatial and temporal local dynamics of human-gull interactions are still poorly known, with few existing studies usually conducted during the breeding season. For instance, Spelt et al. (2019) found that Lesser Black-backed gulls (*Larus fuscus*) nesting in Bristol, UK, selected terrestrial over marine foraging areas during the entire breeding season. Huig et al. (2016) quantified human-gull interactions for the Lesser Black-backed and Herring (*Larus argentatus*) gulls breeding in traditional colonies, but visiting the city of The Hague, Netherlands, during the breeding season, causing several nuisance events, especially during the chick-rearing period. Zelenskaya (2019) reported a comparingly higher breeding productivity of Slaty-backed gulls (*Larus schistisagus*) nesting in roofs and discussed the influence of several factors on the selection of urban nesting grounds, such as the existence of rooftop structures and the degree of roof attendance by humans. Kroc (2018) also observed gull nests isolated on rooftops or structures, to be physically separated and less susceptible to intra-specific aggression.

In this study, we focused on spatial and temporal dynamics of urban habitat use and human interactions with urban gulls, to understand the main driving factors promoting human-gull conflicts in urban areas. We quantified seasonal variation in the use of urban habitat types by Yellow-legged adult gulls (*Larus michahellis*) and *Larus* spp. immature gulls, registered their foraging/resting/breeding behaviours per habitat type and characterized all human-gull interactions occurring in urban areas throughout the day during the breeding season and winter to address the following main questions: (1) How gulls from different age classes use urban habitats? (2) Is there a monthly variation in their habitat-use? (3) How gulls behave in different urban habitat types? (4) Is there a variation in the number and type of human-gull interactions between seasons? (5) Do gulls have any foraging daily routines matching human routines within the city? From these questions, we expect to find the number of gulls using urban habitats to increase during the breeding season, especially the number of adult breeding gulls. Human-gull conflicts should be higher during the breeding season, when gulls tend to be more territorial around the rooftop-nests and constrained to forage in nearby areas due to breeding duties. Because in winter, gulls no longer have breeding related duties, we expect an increase in the use of natural coastal habitats in the vicinity of urban areas, and a consequent decrease of human-gull interactions within the city. We also expect the number of foraging gulls within the city to increase when the number of humans is higher, with main interactions being related to intentional or unintentional bird feeding.

4.2. Methods

4.2.1. Monthly use of urban habitat types

Monthly surveys were conducted in Oporto, Portugal and surrounding areas for one year (November 2017 – October 2018). The study area was selected due to the proximity to a major fishery landing area (Matosinhos), intertidal feeding grounds and urban areas near rooftop-nests. Six types of urban habitats were defined along a gradient of increasing urbanization intensity (Fig. 4.1), and sampled in 3-8 different areas: 1) coastal areas bordered by buildings and pedestrian paths (22 ha), located up to 6-10 km from Oporto city centre; 2) river and riverside areas within the city, situated near bridges, touristic urban areas and fluvial beaches (64.8 ha); 3) large green parks, characterized by large vegetation patches of different heights and different sized lakes (7.8 ha); 4) highly urban city squares, located near buildings and high traffic roads (1.27 ha); 5) small gardens within urban city areas, characterized by small vegetation areas, trees and public garden benches (2.85 ha); 6) rooftops of highly urban building areas within the city, visible from higher location points and usually characterised by rooftop-nesting (22.93 ha). Each habitat-type was monitored in 5-8 different locations within the city of Oporto and surrounding regions, except for large green parks, that were monitored in 3 different locations. The number of adults of Yellow-legged gulls, *Larus michahellis,* (LMA) and immatures, *Larus* spp, (LI) were counted in all areas, and the number of gulls was converted to density (gulls.ha^{-1}) for each habitat type. The number of humans in each sampling area was also recorded and converted to density. To minimize the effect of external environmental drivers, surveys were conducted in similar weather conditions. To avoid human disturbance during surveys, binoculars (Olympus 8x42 EXPSI) and telescope (Swarovski ATX 20-60 x95) were used to count birds in rooftops, coastal and riverside areas. The behaviour of gulls was also registered and categorized into 3 main types which were easily perceptible to the observer (resting, breeding, feeding/foraging), and the number of gulls in each behavioural type was then converted to density.

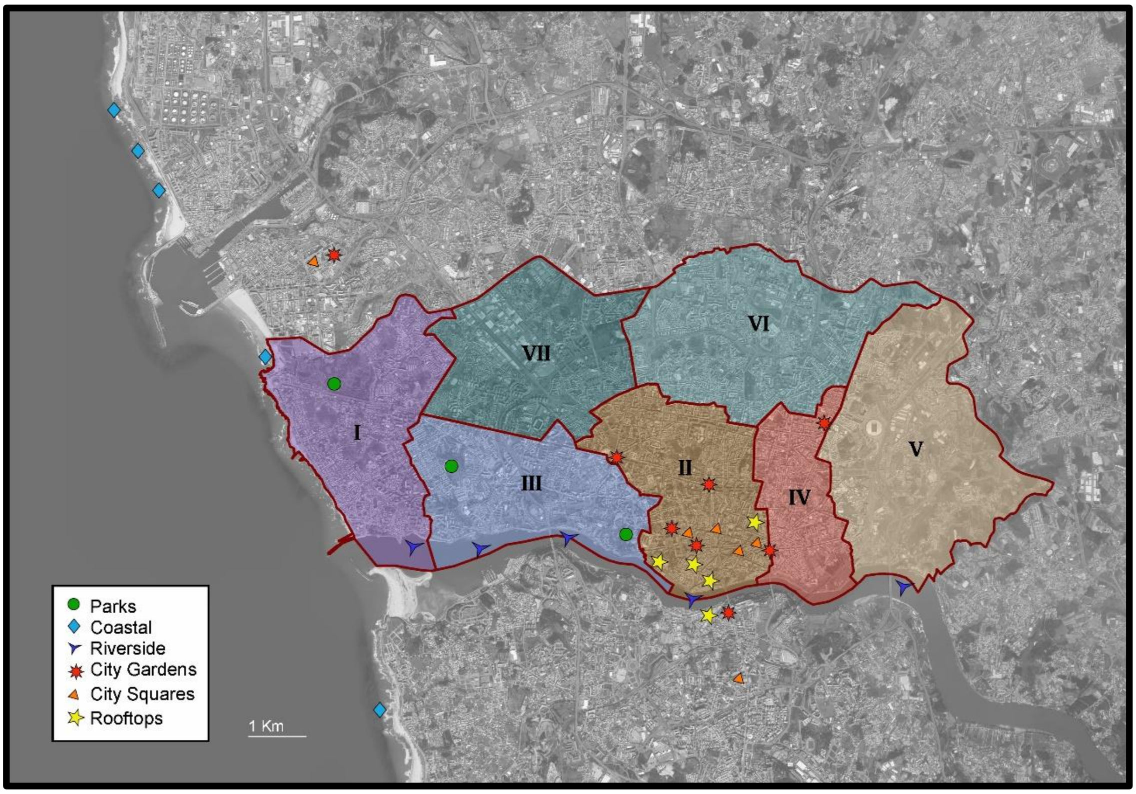

Figure 4.1. *Map of study area with survey location points of all six urban habitat types with different symbols (parks in green circle; coastal in light blue diamond; riverside in dark blue 3-pointed star; city-gardens in red 8-pointed star; city-squares in orange triangles; rooftops in yellow 5-pointed star) and city district areas of Oporto city. The city district code refers to the most recent union of Oporto districts, which include (I) Aldoar, Foz do Douro and Nevogilde; (II) Cedofeita, St. Ildefonso, S. Nicolau, Sé, Miragaia and Vitória; (III) Lordelo do Ouro and Massarelos; (IV) Bonfim, (V) Campanhã, (VI) Paranhos and (VII) Ramalde. The map was performed by Quantum GIS 3.0.0. with ESRI maps included in the plugin QuickMapServices.*

4.2.2. Human-gull interactions: Intervention requests

A database of the interventions requested by humans during 2016-2018 was provided by the Oporto City Council which only keep records of the interventions related to the removal of nests and animals. The database was categorized by year (2016-2018), intervention type (gull or nest removal), season (Winter: December – March; Breeding: April - August, and Migration: September – November) and city district (I-VII).

4.2.3. Human-gull interactions in city-squares

Human-gull interactions were also assessed using 10-hour day observations in two central touristic city-squares in Oporto (Batalha and Clérigos city squares) for 20 days equally spread across winter and breeding seasons, from the same observational points. Observation days were selected based on weather conditions (no rain, average temperatures) to minimize the effect of external environmental drivers. To account for differences in human social behaviour during non-working days, which may affect human-gull interactions, ca. 30% of observational days were conducted at weekends. All interactions were recorded throughout the day and the number of gulls and humans were recorded using instant counts every 15 minutes. Four major interaction types were considered: (1) Focal Group Attraction (FG), characterized by a sudden attraction of several gulls into a specific point, usually related with food provided by humans, (2) Steal/Prowl (SP), when gulls stole or attempted to steal food from humans, sometimes chasing and flying over people's heads, (3) Hygiene/Structures (LS) defined by gulls landing on near-food structures, such as restaurant tables and chairs, which may compromise the hygiene and human health and (4) gulls foraging on trash containers (FT). To maximize the number of daylight hours observed while keeping the same number of hours in both seasons, a time window of 10 hours was considered for each season depending on the sunset time. The 10-hour daytime window was then divided into 8 periods of 75 minutes duration, and data were converted into the mean number of gulls and mean number of interactions for each 75 min daytime period.

4.2.4. Statistical Analysis

To quantify urban gulls' habitat-use and behaviour we performed Zero-Inflated models with Negative Binomial distribution (ZINB). These models have a count component with a negative binomial distribution (hereafter presented as the conditional component) and a separated component with all the zero outcomes (hereafter presented as the zero component), therefore they are ideal to account for the excess of zeros and the overdispersion of the data (Zeileis et al. 2008). ZINB models were performed using the *glmmTMB* package (Brooks et al. 2017) in R version 3.6.0 (R Core Team 2019). We firstly performed two base models with gulls density (number of gulls.ha^{-1}) as the dependent variable: a) a count base model with *month*, *habitat* type, gull *age* class (immature, adult) and *human density* as explanatory variables, and b) a behaviour base model with these variables and also a categorical *behaviour* variable with two levels (resting and feeding/foraging). Breeding behaviour was excluded from the statistical analysis, because it occurred only at rooftops. Base models were validated using *performance* (Lüdecke et al. 2019) and *DHARMa* packages (Hartig 2019) to check collinearity among predictors, overdispersion, residual patterns and observed *versus* fitted values evaluation. A set of all possible model combinations from both base models were generated using the *dredge* function within *MuMIn* package (Bartoń 2019) and the best count and behaviour models were selected based on the lowest corrected Akaike's information criterion for small sample sizes (AICc). This evaluation included combinations with the location of the counting point as a random effect, to control for within habitat variability. To quantify urban gulls' habitat-use and behaviour, three model selection procedures were conducted: (1) a count model selection including the interaction *habitat*age*, to address our first study question; (2) a count model selection including the interaction *habitat*month*, to address our second question and (3) a behaviour model selection including the interaction *habitat*behaviour*, to address our third question. Parameter estimates (*β)* were then obtained by averaging the top Δ6AICc counting and behavioural models, as suggested by Grueber et al. (2011) and Richards (2008).

To test for differences in the number of intervention requests by year, season and city district, we performed a Generalized Linear Model using *glmmTMB* package (Brooks et al. 2017) with an assumed negative binomial distribution to account for overdispersion. The *number of requests* was set as the response variable and explanatory variables were: *year* (2016-2018), *season* (winter, breeding and migration) and *city district* (I-VII; Fig. 4.1). The best model was selected based on the lowest AICc criteria.

The factors driving gulls to city-squares during the 10-hour day observations were analysed using generalized linear autoregressive moving average (GLARMA) models (within *glarma* package; Dunsmuir and Scott 2015) which detect and account for serial dependence. The mean *number of gulls* counted in each period was set as the dependent variable with a negative binomial distribution, and the fixed terms used were: *number of humans, season* (winter or breeding), *weekend* (week or weekend days), mean of each event *interaction type* (FG, SP, LS and FT interaction types by daytime period) and *minutes until the end* of the 10-hour daytime window. Due to differences in light hours and sunset time between seasons, this last variable was added as a daylight time measure that would fit both seasons. Response distribution was validated via the probability integral transformation, and the ARMA parameters were selected considering the estimated autocorrelation of the residuals from a generalized linear model regression. The best model was selected based on the lowest AICc and the lowest log-likelihood.

4.3. Results

4.3.1. Monthly use of urban habitat types

Rooftops were mainly used by *L. michahellis* adults (LMA; Fig. 4.2a, representing 40.9% of their habitat use with a mean density of 13 gulls/ha. LMA also used coastal (23.9%) and riverside areas (11.4%) with an average of 7 and 4 gulls.ha^{-1}, respectively. *Larus* sp. immatures (LI) used mainly coastal areas (16 LI/ha), riverside areas (15 LI/ha) and parks (13 LI/ha) (Fig. 4.2b), representing 36.8%, 29.2% and 15.7% of total LI density. City squares had on average 4 gulls/ha of both age groups and represented 12.8% of LMA and 9.9% of LI. City gardens were equally used by both age groups (ca.5%), with a mean density of 1-2 gulls/ha.

From the first count model selection, the most supported model (w = 0.93, Table 4.1) included the interaction *habitat*age* term, the random slope for location *point* and month in the zero component of the model. A second supported model (ΔAICc = 5.53, w = 0.07; Table 4.1) included the same variables, but with *month* and the interaction term only in the conditional part of the model, and the *habitat* main effect was only in the zero model component (Table 4.1).

From the second count model selection, the most supported model (w = 0.75, Table 4.1) included the interaction *habitat*month, age* and *habitat* main effect in the zero component of the model, and a random slope for location *point* in both components. A second supported model (ΔAICc = 2.10, w = 0.25; Table 4.1) included the same variables in the same components, except *age* which was not included. Overall, the majority of individuals were immature gulls (LI), with adults (LMA) presenting a negative averaged effect in the conditional component (β = -0.81, $p < 0.001$; Table 4.2). The overall density of gulls decreased along the breeding season, but particularly during the chick-rearing period, i.e. June and July (Fig. 4.2a-b), showing a strong averaged effect in the zero

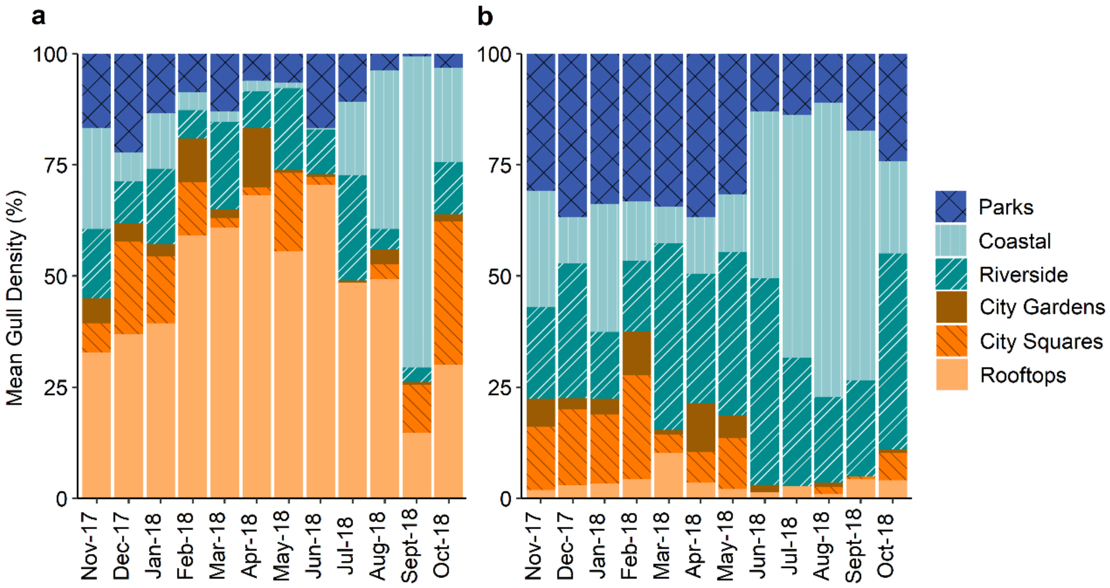

Figure 4.2. *Mean gull density percentage in the six different urban habitat types from November 2017 to October 2018. (a)* Larus michahellis *adult gull, (b)* Larus *spp. immature gulls.*

component (June β= 2.40, p < 0.001 and July β = 1.76, p < 0.001, Table 4.2). Some of the highly urbanized habitats were mostly used by adult gulls (LMA), particularly rooftops and city-squares (β = 2.98 and 0.82, respectively, both with p < 0.05, Table 4.2). When compared to coastal areas, both city-gardens and city-squares had a great number of zero counts in some months and a generally lower gull density (Fig. 4.2a-b), showing positive effects in the zero component in both averaging procedures (Tables 4.2 and S4.1), and negative effects in the conditional component, in the first averaging procedure (Table 4.2). Interestingly, rooftops had significant negative effects in the conditional component of the first averaging (β = -0.81, p > 0.001; Table 4.2) but also in the zero component of the second averaging procedure (β = -2.22, p > 0.05; Table S4.1), probably because the density of gulls in rooftops is extremely low, especially the density of immature individuals (LI; Fig. 4.2b), but was rarely zero. The use of coastal areas increased during

Table 4.1. *Summary statistics for Zero-Inflated models representing the gull habitat use and factors influencing the probability of* Larus *spp. immature gulls and* Larus michahellis *adult gulls to be present in the study area. Df = degrees of freedom, logLik = loglikelihood ratio statistic, AICc = Akaike's information criterion corrected for small sample size, ΔAICc = difference in AICc relative to the lower AICc model,* w_i *= Akaike weight, Δ* w_i *= difference in Akaike weight relative to the lower AICc model. Only supported models (ΔAICc < 6) are shown, from the first and second model selection procedures including different interaction terms.*

	Conditional Component	***Zero Component***	***df***	***logLik***	***AICc***	***ΔAICc***	w_i	Δw_i
1st selection	Habitat*Age+ (1|point)	Habitat*Age+ Month+(1|point)	38	-4125.27	8330.51	0	0.93	0.93
	Habitat*Age+ Month+ (1|point)	Habitat+(1|point)	32	-4134.52	8335.84	5.33	0.06	0.99
2nd Selection	Habitat*Month+ Age+(1|point)	Habitat+(1|point)	82	-4186.31	8556.00	0	0.75	0.75
	Habitat*Month+ (1|point)	Habitat+(1|point)	81	-4188.64	8558.10	2.10	0.24	0.99

the late summer months (Fig. 4.2a-b), reaching a mean density of 41 LI/ha during August and 34 LMA/ha during September. These movement of gulls to the coastal areas during the late chick-rearing period and at the end of the breeding season was generally reflected by the negative effects obtained from the second averaging procedure, particularly: city-gardens during July, August and September (β = -1.74, -1.52 and -2.37; all with $p < 0.05$; Table S4.1); city-squares during August (β = -2.00, $p < 0.05$; Table S4.1); riverside and rooftops, both during September (β = -1.54 and -1.77, both with $p < 0.05$; Table S4.1). During winter, there was a general increase in the use of all habitats, when compared to the use of coastal areas (Fig. 4.2a-b). This was reflected by the positive significant effects obtained from the second averaging procedure, particularly city-gardens, city-squares, rooftops, and riverside areas during February (β = 1.35, 1.42, 1.42, 1.44, respectively, all with p < 0.05; Table S4.1). Parks were mostly used by LI also during winter months, with a mean density increasing to 20 LI/ha during January and decreasing to 7 LI/ha during August ($\beta = -2.07$, $p < 0.05$; Table S4.1).

In all habitats, except city gardens, resting was the predominant behaviour, representing more than 50% of gull density at each habitat type (Fig. 4.3a-b). The density of gulls foraging on human-provided items was higher at city-gardens (50% of LMA and 37.38% of LI) and city-squares (23.24% of LMA and 29.43% of LI). Foraging/feeding on natural and unknown items were mainly observed at city-gardens (19.30% of LMA and 35.98% of LI) and coastal areas (28.35% of LMA and 26.35% of LI). The best competing behavioural models (ΔAICc < 6AIC) predicting gull density included the variables *month*, *age*, the interaction *behaviour*habitat* term and random slope for location *point* (Table 4.3). *Human density* was also included in the last three best models, although it had no significant averaged effect (Table 4.4). Therefore, the best count and behavioural models suggest that *month* and gull *age* are important variables to explain gull density in each urban habitat, and the gull's most common behaviour depends on the habitat-type.

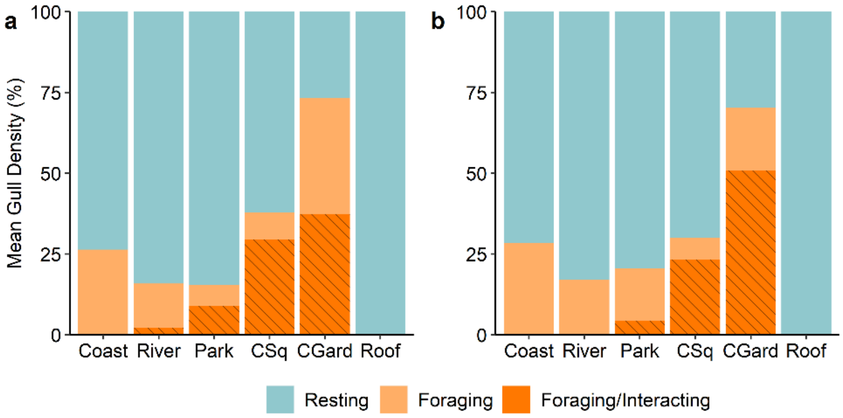

Figure 4.3. *Percentage of mean gull density resting or foraging/feeding in the six urban habitat types. (a)* Larus michahellis *adult gull, (b)* Larus *spp. immature gulls, (1) Foraging/Feeding on items from natural and unknown source, (2) Foraging/Feeding on items provided by humans feeding wild birds.*

4.3.2. Human-gull interactions: Intervention requests

A total of 900 requests were registered during 2016-2018. All three variables were important to explain the number of intervention requests (Table S4.2). The number of intervention requests increased throughout the years, particularly during 2018 ($\beta = 0.36$, $p = 0.001$; Table 4.5; Fig. 4.4a-c). Most requests were registered during the breeding season, which showed a strong main effect in the selected model ($\beta = 1.47$, $p < 0.001$; Table 4.5) and represented 72.2% of all season requests, particularly during the chick-rearing period months (i.e., June/July; Fig. 4.4a-c). The most common request type was "gull removal" (e.g. injured and dead gulls or chicks that fell from rooftop-nests), which represented 80.9% of requests during the breeding season ($\chi^2_2 = 241.8$, $p < 0.001$), 98.2% of requests during the migration season ($\chi^2_2 = 111.1$, $p < 0.001$) and 100% of requests during winter (Fig. 4.4a-c). In all seasons the city district II, which is in the city centre, registered the highest intervention requests ($\chi^2_8 = 643$, $p < 0.001$; Fig. 4.4d) representing 39.2% of total requests and a strong main effect ($\beta = 2.27$, $p < 0.001$, Table 4.5) in the selected model. The city district V, the most distant from the sea, was the city district with the lowest intervention requests (Fig. 4.4d), representing 3.6% of all requests.

Parameters	***β***	***SE***	***Pr(>|z|)***
City District (I)	**1.24**	**0.24**	**<0.001**
City District (II)	**2.27**	**0.23**	**<0.001**
City District (III)	**0.99**	**0.25**	**<0.001**
City District (IV)	**1.16**	**0.25**	**<0.001**
City District (VI)	0.41	0.25	0.12
City District (VII)	**079**	**0.13**	**<0.001**
Year (2017)	0.15	0.13	0.25
Year (2018)	**0.36**	**0.16**	**0.01**
Season (Migration)	-0.21	0.13	0.18
Season (Breeding)	**1.47**	**0.24**	**<0.001**

Table 4.5. *Parameter statistics of the best Generalized Linear Model, representing the effects of each parameter on the number of intervention requests. Parameter statistics include estimates (β) and standard error (SE)). Significant effects (p < 0.05) are in bold. Winter and the city district V were set as reference levels for the variables season and city district, respectively.*

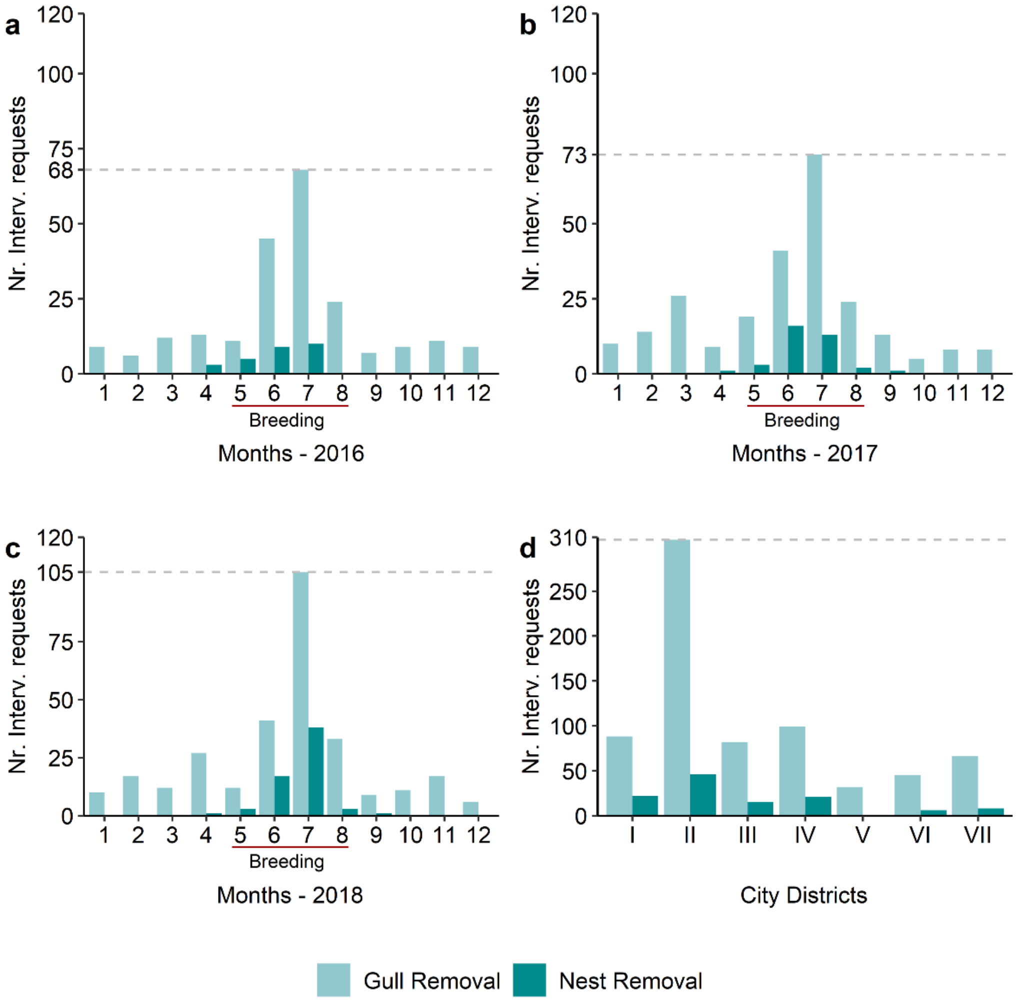

Figure 4.4. *Number of monthly interventions requested by the human population of Oporto from 2016 to 2018 (a-c), and the total number of intervention requests from the three years in the seven city districts (d), depending on the intervention type.*

4.3.3. Human-gull interactions in city-squares

A total of 301 events were registered during the 210 hours total of 301 events were registered during the 210 hours of daily observations. These events were differently distributed along event categories ($\chi^2_4 = 213.54$, $p < 0.001$), with Focal Group (FG) attractions representing 60.1% of the total events, landing on near-food structures (LS) representing 20.9%, Steal and Prowl (SP) representing 14%, and Foraging on Trash (FT) representing 5.0% of total events. Excepting FG, the number of events varied significantly along daytime periods (FTχ^2_8 = 34.60, LSχ^2_8 = 53.19, SPχ^2_8 = 25.05, all these with $p < 0.001$; Fig. 4.5a-b), especially during breeding season with 77.8% of FT, 51.7% of LS and 56.3% of SP occurring at the last daytime period, from 19:15 h to 20:30 h (Fig. 4.5b).

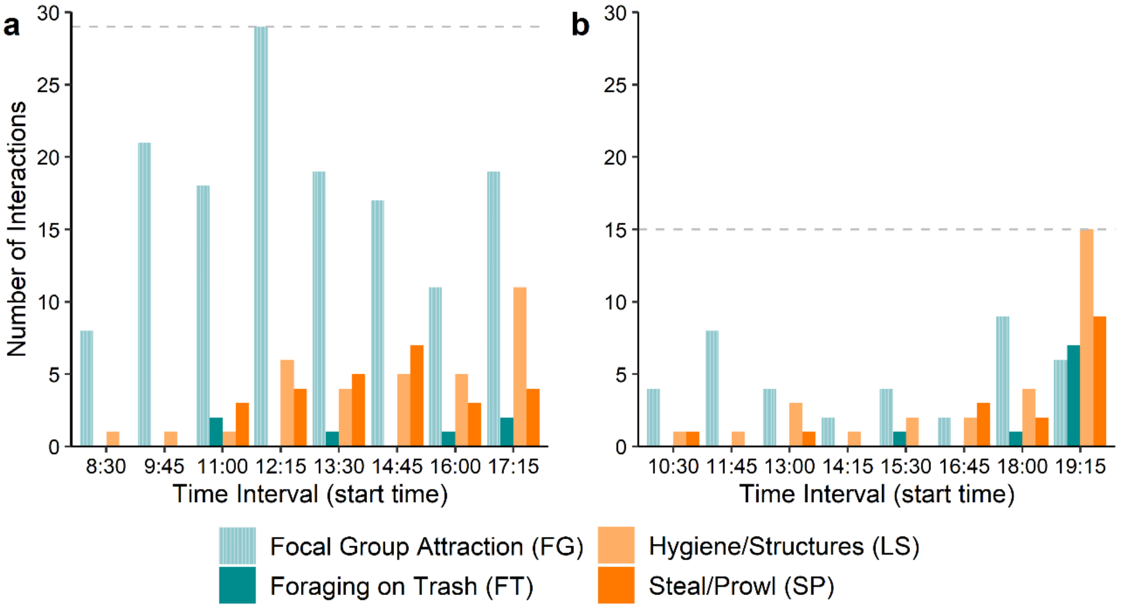

Figure 4.5. *Number of human-gull interactions during the 10-hour day observations in two central city-squares during winter (a) and breeding season (b) along the daytime periods, depending on the interaction type.*

Only FG differed significantly between seasons (χ^2_2 = 58.61, $p < 0.001$), increasing up to 78.5% during winter (Fig. 4.5a). The mean number of gulls differed between seasons (χ^2_2 = 986.07, $p < 0.001$), with winter representing 84.7% of gulls, and between daytime periods within each season (χ^2_8Winter = 54.96 and χ^2_8Breeding = 28.16, both with $p < 0.001$). The highest mean gull numbers were observed at the 3rd daytime period during winter, from 11:00 h to 12:15 h (Fig. 4.6a), and at the last daytime period during the breeding season, from 19:15 h to 20:30 h (Fig. 4.6b).

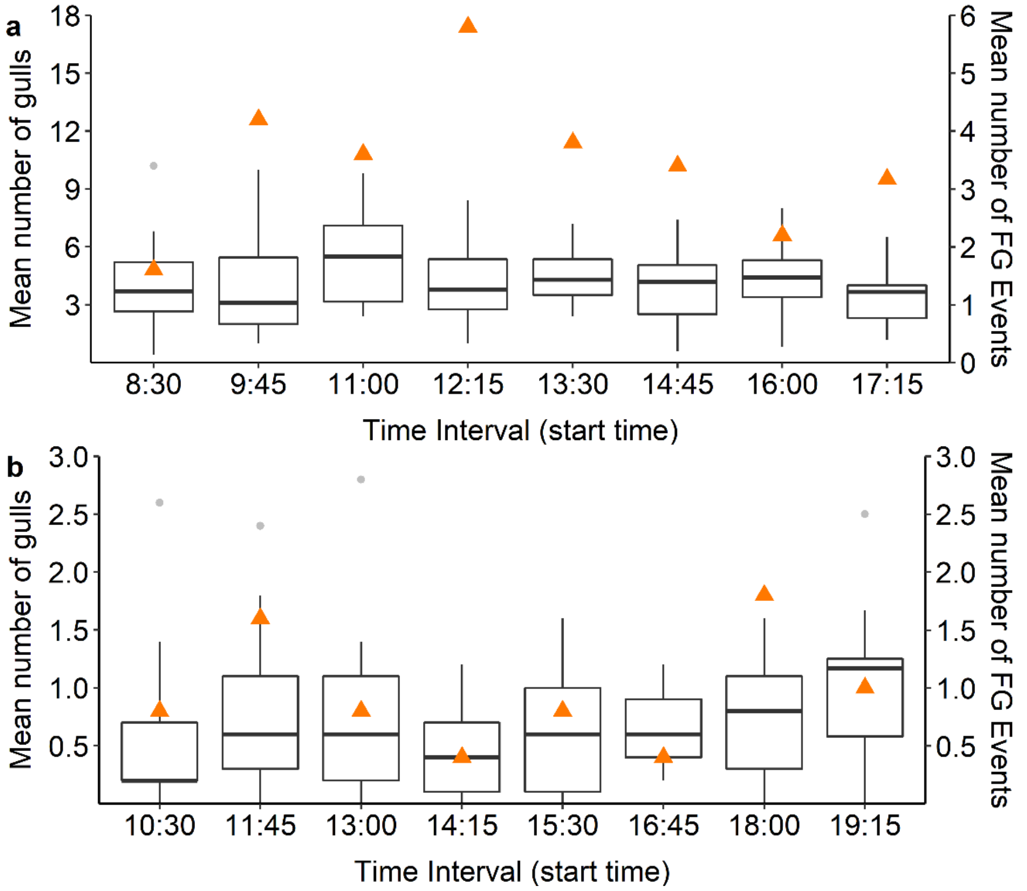

Figure 4.6. *Mean number of gulls (box plots) and mean number of Focal Group attraction events (FG; yellow triangles) counted in the 10-hour day city square observations at different daytime periods, during winter (a) and breeding season (b). Gulls were counted every 15 minutes and FG events were registered continuously; both were transformed to the mean of each 75-minute daytime period. Box plots represent the distribution of all gull daytime period means and the triangles are the sum of FG daytime period means. The lower and upper hinges from the box plots correspond to the 25th and 75th percentile, respectively, the line in the middle of the box represents the median, the upper and lower whisker represent 1.5*the inter-quantile range and grey points represent outliers outside the previous intervals.*

Overall the selected GLARMA model successfully detected the mean gull variation, except for extreme values (Fig. S4.1). The likelihood ratio test and Wald test indicated a fit improvement when compared with the generalized linear model. The probability integral transform diagnostic plot indicate that the assumed negative binomial distribution and the inclusion of serial correlations were adequate. The main variables explaining the mean number of gulls attracted to city squares were season ($\beta = -1.35$, p <

0.001; Table 4.6) and the mean number of FG events (β = 0.31, $p < 0.001$; Table 4.6), especially during the breeding season, when the increase in FG events was always followed by an increase in the number of gulls (Fig. 4.6b). The mean number of FT events was also related with the number of gulls (β = 0.08, $p < 0.001$; Table 4.6). The number of gulls attracted to city squares did not change significantly with the number of humans within city squares and between weekdays and weekends, as these variables did not improve our selected model (Table S4.3).

Parameters	***β***	***SE***	***Pr (>|z|)***
Season	**-1.35**	**0.190**	**<0.001**
FG	**0.31**	**0.056**	**<0.001**
LS	0.05	0.052	0.319
FT	**0.08**	**0.039**	**0.029**
Glarma			
Phi_3	**0.197**	**0.051**	**<0.001**
Phi_4	**0.181**	**0.065**	**0.005**
Phi_6	**0.156**	**0.054**	**0.004**
Negative Binomial			
Alpha	**3,06**	**0,49**	**<0.001**

Table 4.6. *Parameter statistics of the selected GLARMA model, representing the effects of each parameter on the number of gulls Larus spp. attracted to city squares. Parameter statistics include estimates (β) and standard error (SE). Significant effects (p < 0.05) are in bold.*

4.4. Discussion

Gulls from different age classes were differently spatially distributed across the urban habitat types, with some seasonal variations. Aquatic and green urban areas close to water bodies were mainly used by immature gulls for resting and foraging, and the highly urbanized habitats within the city were mostly used by *Larus michahellis* (LM) adult gulls as breeding, resting and foraging grounds. We found a strong temporal effect in the number of gulls and human-gull interactions in urban areas, asboth increased strongly during the winter season. Seasonality and the occurrence of interactions associated with humans intentionally or unintentionally feeding birds, were the most important factors driving the variation of gull numbers within the city squares, throughout the day. The resident human population of Oporto requested the intervention of the City Council to deal with gull nuisance problems throughout the year, but such requests peaked during the chick-rearing period, when the existence of a rooftop nest is most noticeable.

4.4.1. Gull abundance and human-gull interactions in urban habitats

Rooftops were the only urban habitat almost exclusively used by adult gulls during the entire year. Rooftops were particularly important for nesting, where gulls were usually observed in pairs, even during the winter season. This suggests that some nesting gulls keep occupying their valuable nesting grounds during the entire year as an advantaged strategy compared to other migrant/dispersing breeding gulls, which will only select and defend nesting areas after arriving from migration. In Bristol, UK, this behaviour was also observed in urban breeding gulls (Rock 2005) with an estimated 22% of Lesser Black-backed (*Larus fuscus*) adult gulls returning extremely early or not migrating at all.

Larus spp. immatures mainly used natural habitats such as coastal and riverside areas. These lower disturbed areas are sometimes used by several migratory species, such as *L. fuscus* (Marques et al. 2009), leading to the increase of *Larus* spp. immatures during winter. Besides coastal and riverside areas, lakes within large parks were also abundantly used to rest. This selection of larger freshwater roosting areas near the last daytime location by *Larus* spp., was also found by Clark et al. (2016), when tracking gulls from Massachusetts, USA. Because large parks in our study area were always near urban or intertidal feeding areas, roosting in parks could reduce the energetic costs spent by travelling between foraging and roosting habitats. More urbanized habitats, such as city squares and city gardens, were mainly used during winter and incubation periods by both adult and immature gulls. Gulls counted in these habitats were mostly resting or foraging on human provided food. Presently *L. michahellis* is the only urban breeding gull species in Oporto, but *L. fuscus* adults were also seen in urban areas during winter, exhibiting a similar foraging behaviour to *L. michahellis* adults (*pers. obs*). Thus, urban areas could be increasingly attracting other non-urban breeding gull species that are becoming more comfortable with the human presence. For example, migratory Herring Gulls (*Larus argentatus*) from natural colonies in eastern North America were seen using urban habitats during winter (Anderson et al. 2019).

The absence of *Larus* spp. immatures in urban areas during the chick-rearing period could be partly explained by the strong territorial behaviour of breeding gulls nearby their rooftop nests. Also, during this period it is common to observe a dietary switch of breeding gulls for higher nutritional marine prey to feed their chicks (Annett and Pierotti 1989; Isaksson et al. 2016; Pais de Faria et al., 2021a), leading to a decrease in foraging-related conflicts in urban areas. However, not all urban gulls present this behaviour; Lesser Black-backed gulls breeding in Bristol rooftops did not forage on marine habitats during the entire breeding season, suggesting that urban gulls could adapt their foraging strategies depending on the costs and benefits of foraging in different habitats (Spelt et al. 2019). Oporto rooftop nests are only 7 km distant from the closest fisheries port, and can be visited easily by gulls to feed their chicks with higher quality marine prey with a relatively low energetic cost.

The human population intervention requests increased along the years, which could be a result of people general awareness of the problem or could indicate an increase of the Oporto urban gull population. The intervention requests registered by Oporto City Council were only related with nest removal or injury/dead gull captures. As expected, these types of requests were higher during the breeding season, when gulls are more aggressive defending their nests, leading to the increase in nest removal requests. From our observations, nests that were more visible to humans caused more human-gull aggressive interactions and were more frequently removed. Because most of the nests are inaccessible and not visible to humans, the number of nest removal requests were relatively low when compared with the number of gull removal requests. This was especially high during June, when young chicks are more mobile and prone to fall from the nest.

As expected, central historic riverside areas (city district II) known by their rooftop nest abundance, had the larger number of intervention requests. This area is characterized by old, abandoned buildings and traditional building types, with rooftop structures that offer weather protection and are capable of supporting gull nests (e.g. tiles and chimneys). These types of structures seem to be preferred by urban nesting gulls (Rock 2005), allowing a decrease in intra-specific aggression given the existence of a physical separation between breeding birds. In Vancouver, British Columbia, Canada, gull nests are also commonly seen individually in an isolated rooftop or structures (e.g. 73 from the 102 monitored urban nests of Glaucous-winged gulls, *Larus glaucescens*; Kroc 2018).

In our study gulls using city squares did not present strong daily routine patterns, however their numbers tend to increase at lunch time during winter, and at dinner time during summer. During meal hours the number of humans eating in restaurants and city gardens increase, attracting small groups of foraging gulls. However, the most important factor promoting the increase of gulls in city squares was the occurrence of Focal Group Attraction (FG) events. These events are usually characterized by humans feeding birds, sometimes only intentionally feeding pigeons, but attract large number of foraging flying gulls, described as “feeding frenzies” by Huig et al. (2016). This pattern seems stronger during the breeding season, when adult gulls are constrained with breeding duties, only leaving the nest and using nearby city squares in the presence of strong stimulus.

Overall, excepting FG, all interaction types increased during the last daytime periods, especially interactions related with landing near human food and stealing food attempts. At the end of the day city squares are more used by humans leaving their workplace and commonly eating while walking or having a meal on street esplanades of restaurants and pastries. From our observations, both cases are common targets of foraging flying gulls. In some situations, we observed territorial behaviour to defend best waiting spots, usually traffic lights, where gulls stand and wait to steal humans crossing the street carrying food after visiting nearby pastries. This type of behaviour, characterized by birds learning human habits and adapting accordingly their foraging strategies, was also observed by Spelt et al. (2020) in Bristol, UK, where the foraging patterns of gulls, *Larus* spp., matched the timing of school breaks and opening hours of a waste centre. At Kabushima Island, Japan, Black-tailed gulls *Larus crassirostris* seem to visit specific feeding grounds at discrete times of the day, especially those areas related with anthropogenic activities, such as fishery or meat-processing plants or markets (Yoda et al. 2012).” This type of behaviour is common to several other urban species, for example, carrion crows (*Corvus corone*) from Japan place walnuts in the street near traffic lights, so cars can crush and open the walnuts, when the traffic light turned into green (Nihei and Higuchi 2001).

Furthermore, human habits of feeding birds in cities, although it may not represent the major gull food source, promotes human-gull interactions, allowing gulls to be more comfortable and confident when approaching humans (e.g. stealing food, landing in street restaurant tables, attacks near rooftop nests). This was observed particularly during the winter season, when the number of gulls and FG interactions occurring in urban locations were higher. During this season, urban dispersing and resident gulls are no longer constrained by breeding duties and territorial breeding behaviour, and are thus more able to explore foraging opportunities within the city. Several factors may influence human-gull interactions (Soga and Gaston 2020), such as social and educational knowledge (e.g. lack of knowledge on the ecological consequences of feeding wildlife) or economic factors, with gulls preferring to build their nests in older and less maintained rooftop buildings which are rarely visited by humans. Personal orientation to engage with nature may also be an important factor. From our observations, human feeders were mainly older citizens, or in some cases homeless sharing their food. This could be related with a particular orientation and predisposition to feed and take care of the 'most needed ones', while in some extent humanizing birds and concerning about bird health (Cox and Gaston 2016; Soga and Gaston 2020), or a consequence of likely being the two social groups that most suffer from loneliness, that will most frequently subconsciously seek for the psychological benefits of interacting with nature (Barnes et al. 2019; Cox and Gaston 2016; Cox et al. 2017a).

4.4.2. Management considerations

Although it is appealing to focus management efforts during the gulls' breeding season, when the number of human population complaints and intervention requests are higher, the conflicts and interactions occurring during winter should also not be neglected. During winter we observed gulls to learn and adapt their foraging behaviour according to human habits, such as perching and waiting on a lower traffic light for people leaving pastries carrying food. This underlines the need of considering human activities, routines and behaviour when designing management measures that aim to decrease human-gull conflicts in cities. It is also apparent that such measures should be specific to each human-gull local dynamics and consider seasonal variations of each location. For example, the number of humans feeding gulls in city squares was considerably lower during the breeding season, although some gulls were observed feeding in the trash, food remains and hunting pigeons, especially at the end of the day. Bird feeding was much higher during winter; this variation in human behaviour may be related with an increase of general awareness of the problem during the breeding season, when gulls are more territorial or simply because there are fewer gulls using city squares during this season. Feeding wild animals is forbidden by the Oporto Municipal Regulation Code (article C-3/16º; CRMP, 2019), but a total of 90 confirmed feeding events were registered during our observations, most of them attracting large number of gulls. Thus, environmental education and promoting social awareness is essential when managing urban bird populations. However, since urban bird feeding is known to increase mental and social health in humans seeking closer nature experiences (Cox and Gaston 2016; Cox et al. 2017a), its discouragement can be challenging. For example, Clark et al. (2015) had limited effect on the number of gulls foraging on parking lots, after educating human feeders with educational posted signage and direct verbal approach, with some humans repeating the behaviour after being approached.

Roosting habitats usually aggregate a large number of birds, which tend to select large water bodies (e.g. lakes within parks or reservoirs), near the last daytime location (Clark et al. 2016). Gulls using these roosting sites commonly feed on landfills (Alm et al. 2018) and act as nutrient and pathogens vectors, leading to the eutrophication of freshwater bodies (Winton and River 2017) and dissemination of pathogens and zoonotic infections (Carroll et al. 2015; Alm et al. 2018). Therefore, detecting all these roosting sites and designing management measures that prevent the use of important water bodies by this large group of gulls is required. Since urban gulls have shown to be resilient to several avoidance techniques (Cook et al. 2008), and tend to roost near their last daytime location, targeting at the same time nearby foraging locations is crucial.

In addition to the negative human-gull interactions and public health concerns, the widespread of opportunistic gull species are known to threat other seabird species, including some international important populations, through kleptoparasitism (Spencer et al. 2017) and predation of seabirds' eggs, chicks and adults (Matias and Catry 2010). Gulls' predatory behaviour is also known to affect mammals, as reported by Camphuysen et al. (2010) that found 44.7% of Lesser Black-backed gull food samples to be composed by mammalian prey, in the Netherlands. Spencer et al. (2017) observed kleptoparasitism in *Laridae* birds, in the UK, to occur more frequently in urban habitats comparing to coastal habitats. This could be an adaptation of gulls' foraging strategies when facing different environmental pressures in novel habitats.

In several countries management measures have been attempted, some of them aimed to i) disperse gulls (using pyrotechnics, hand-held distress calls, falcons or ammunitions; Cook et al. 2008); ii) reduce the amount of predictable food subsidies available (e.g. closing open-air landfills; Payo-Payo et al. 2015; Steigerwald et al. 2015); iii) prevent gulls to roost in important water bodies (Clark et al. 2013) or iv) land and nest in rooftops (Rock 2015). However, most of them showed to be sometimes highly costly to the city and long-term inefficient or to introduce further complications, by simply relocating gulls breeding efforts (Rock 2013). Other measures, such as egg oiling, aim to reduce breeding success and stabilizing gull population. Unlike other techniques, egg oiling does not seem to cause the abandonment of the colony, which could lead to the movement of breeding-related problems to other locations (DeVault et al. 2014). However, for the sake of effectiveness, egg oiling should be done for several consecutive seasons, since gulls are long-lived and highly philopatric species. It is also important to have in mind that although some measures may seem efficient, each one when solely implemented will be only targeting one specific problem. For example, the decrease of hatching success caused by egg oiling, will be only reducing the noisy and aggressive behaviour that is commonly higher during chick-rearing, while foraging related interactions caused by the present gull population will continue.

Given the complexity of this problem, it is important to understand all the local human-gull interaction dynamics within all seasons, without neglecting the conflicts generated in important roosting locations. This is pivotal to then implement integrated global efficient long-term management measures, which should include all parties involved in the problem, such as. the City Council, human population, private and public related industries, among others).

Chapter 5

General discussion

Part of this chapter was published as:
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5.1. Overview of the thesis and main results

The research work conducted within this PhD project was pioneer in providing a complete study of urban gulls' ecology and assessment of human-gulls interactions, particularly in the city of Porto, Portugal. Such understanding of gulls' urban life quality, through the study of their diet quality, breeding success and general health condition, combined with the insights on the major human-gull conflicts occurring in the city, is crucial to design efficient management measures targeting the different types of human-gull conflicts.

The major findings of this thesis highlight: (1) the importance of human activities to create desirable conditions for the establishment of new urban gull colonies, while at the same time contribute for the deterioration of traditional natural colonies; and the importance of conducting long-term monitoring studies that capture the evolution of urban gull populations (Chapter 1); (2) the importance that marine prey still have in the diet of urban gulls, particularly for younger chicks (Chapter 2); (3) the trade-offs that gulls seem to be facing between the advantages of breeding in urban colonies with lower nest density, where the transmission of diseases is less prone to occur, and the disadvantages linked to a lower quality 'anthropogenic-derived' diet (Chapter 3); and lastly, (4) the importance of the winter season in the use of urban habitats by gulls and the occurrence of human-gull interactions, which tend to increase during this season in city-squares and mostly triggered by humans feeding birds (Chapter 4). Considerations regarding the management of human-gull conflicts are presented at the end of this chapter.

5.2. Evolution of urban gull populations and related triggers

The history of gull colonization of urban areas in the British Isles and North America (Chapter 1) underline the importance of human activities in shaping gull populations. The movement of gulls to urban areas can be either promoted through the deterioration of conditions in natural traditional colonies, such as the overexploitation of natural marine prey (Calado et al. 2020, 2021), or the reduction and fragmentation of breeding habitats; but also, at the same time, through the provision of desirable conditions that will attract gulls to urban areas. Colonized urban areas usually provide nearby predictable and abundant food resources (e.g. landfills and fishery discards, Zorrozua et al. 2020); less disturbed breeding conditions, with less inter-specific competition and predation (Monaghan 1979); warmer temperatures and shelter from extreme weather conditions by rooftop structures (Rock 2005). However, the movement of gulls to urban areas might also be promoted by space constrains in natural colonies, forcing younger unexperimented breeders to seek for nesting opportunities elsewhere (Monaghan and Coulson 1977). Independently of the triggers leading gulls to move to urban areas, gulls do not seem to return to the previous colony even if conditions in their original colony improve considerably, suggesting that urban locations could be providing enough quality resources. This was analysed in Chapters 2 and 3 when assessing the diet quality, health condition and breeding success of gulls breeding in the city of Porto. Here, the goal was to understand if urban habitats truly provide long-term optimal conditions to sustain gull populations or if they represent an ecological trap with immediate benefits (e.g. higher breeding success) but with long-term consequences (e.g. poorer health condition possibly reducing their life-time).

Since urban and traditional natural colonies seem to be tightly linked by the use of similar resources (as discussed in the next section) and the inter-colony migrations, it is important to monitor and study all surrounding colonies. This larger scaled monitoring would allow an understanding of the factors influencing the conditions of both natural and urban areas, and to implement broader-scale management measures to improve conditions in natural habitats and diminish the desirable conditions in urban habitats (e.g. less availability of anthropogenic subsidies and nesting locations), in order to discourage new movement of gulls to urban areas and to reduce the increase of current urban populations.

5.3. Assessment of urban gulls' health status

5.3.1. Diet composition and the importance of marine prey in urban gulls' diet

The diet composition of gulls analysed in the Chapter 2 highlight the importance of marine food resources to the diet of urban gulls breeding in the city of Porto, particularly when it comes to feed their younger chicks. Although the diet of adult gulls was mostly composed by terrestrial and refuse items (Fig. 5.1), they kept regularly consuming marine prey. Younger growing chicks were mostly fed with fish, but as they become older (> 20 days of age) refuse items were progressively introduced in their diet. It is common to observe a dietary shift from terrestrial to marine based sources during the chick-rearing period (Alonso et al. 2015), however the presence of terrestrial and refuse items is also common in the diet of chicks from different ages and colony types, but mostly in older chicks (2-5 weeks old) (Moreno et al. 2010, Méndez et al. 2020), likely because they will ingest larger anthropogenic items more easily. Adult urban gulls however seem to partly explore similar trophic resources to those of natural colonies, which is well visible in the fact that they may share 50% of their isotopic niche, except during the incubation period, when gulls breeding within the city of Porto presented a particularly segregated isotopic niche, indicating a distinct diet from that of the other colonies. This distinction combined with the absence of a long-term consistency in habitat-use observed in this chapter, suggest the use of nearby resources during this period, not only to maximize the energy intake (Schoener 1971), but also because during this period gulls are more constrained with breeding duties. As generalist species, gulls are expected to adapt their foraging behaviour to explore the nearby resources, with the distance to fisheries/fishing ports and landfills having a great impact in their diet composition (Calado et al. 2020, Zorrozua et al. 2020).

Figure 5.1. *Adult Yellow-legged gulls and* Larus *spp. immature gulls trying to feed on artificial objects and urban pigeons.*

Overall, urban gulls seem to have a highly varied diet, with some similarities to the diet observed in natural colonies, but also with a strong presence of anthropogenic items ingested by adult gulls and delivered to older chicks. This diversity was reflected in the higher diversity of fatty acids (FA) observed in fledglings from the Porto colony compared to natural traditional colonies, although they were lacking some ω-3 FA important for an adequate growth and physiological status, and usually obtained only by feeding on aquatic prey (e.g. fish; Gladyshev et al. 2009). Nevertheless, studies with a greater number of samples to the FA analysis are required to allow a more robust conclusion regarding the nutritional status of urban gulls. In this chapter it was still not clear whether gulls from Porto were fulfilling their nutritional needs and whether the urban breeding grounds could be providing higher quality conditions compared to those from natural traditional grounds.

5.3.2. Reproductive quality and general health status of rooftop breeding gulls

Reproductive and physiological parameters analysed in the Chapter 3 suggest that urban gulls breeding in rooftops of Porto city are facing important trade-offs between the advantages of breeding in lower density colonies with lower intraspecific negative interactions, and the disadvantages of having an anthropogenic diet usually lower in nutritional value. The first aspect apparently resulted in a higher hatching success and a lower probability of disease transmission (reflected in the general lower occurrence of inflammatory events), and the second aspect resulted in a lack of important ω-3 FA in fledglings, as detected in Chapter 2, lower Haemoglobin (Hb) concentration in adult gulls and lower early chick growth rate. Low levels of Hb concentration might also be a result of a lower anabolic capacity, as a consequence of gulls travelling less far and expectedly having a lower foraging effort by feeding on highly predictable anthropogenic resources; combined with short-distance or even absent migratory movements observed in urban colonies (Rock 2005). In other studies a lower early chick growth was associated with the lack of experience of young breeders in feeding their chicks combined with less competitive pressure in colonies with lower nest density (Savoca et al. 2011). This seems to be the most plausible explanation for the lower early chick growth of gulls from Porto, because adults from Porto were feeding their chicks mostly with fish (Chapter 2), which was then reflected by the chicks' better health condition compared to chicks from the natural colony of Deserta Island (Algarve). The lack of breeding experience from gulls breeding at Porto rooftops was evident, not only by direct observation of several individuals still showing feathers common to immature gulls, but also by the breeding parameters' results, such as the laying of less and smaller eggs and a highly variable hatching success between years.

In summary, urban gulls breeding at Porto, although facing some negative effects from an anthropogenic novel environment, do not seem to exhibit a particularly impaired health, showing lower occurrence of inflammatory events and similar adult body condition to those observed in natural traditional colonies. Additionally, the Porto urban gull population appears to be increasing in numbers, with the nest density growing considerably with passing years. Such population growth however could be the result of an input of foreign individuals moving from other natural colonies that could be reaching saturation levels, and not necessarily a result of the quality of urban breeding grounds. For this reason, it is pivotal to continue to study urban gulls' physiology and breeding biology together with the long-term monitoring of urban and surrounding natural colonies, to better understanding the evolution of urban gull populations and the factors triggering the movement of gulls to the city, as well as the actual long-term advantages and effects of an urban lifestyle. The monitoring of urban colonies should also consider anthropogenic activities and human society behaviour that will certainly influence the success of urban gull populations. In the next section, we discuss the findings from the Chapter 4 that addressed more closely the dynamics of human-gull interactions.

5.4. Urban habitat-use and human-gull interactions

The seasonality of gulls' use of urban habitats and local human-gull interaction dynamics was addressed in Chapter 4. Although the majority of human complains to the

City Council related with gulls tend to increase during the breeding season, particularly during the chick-rearing period, when gulls display a more aggressive territorial behaviour and chicks commonly fall from the rooftops, the actual number of gulls observed within the city and interacting with humans was considerably higher during the winter season. It is also clear that a great part of breeding gulls no longer migrate and keep occupying their nesting grounds the entire year. An age segregation in habitat-use was observed, with the less urbanized areas near water bodies (riverside, coastal areas and lakes) being mostly used by immature individuals to rest or forage on intertidal prey, and the highly urbanized areas within the city being mostly used by adult individuals to rest and breed on rooftops or to forage in city gardens and city-squares, where the majority of interactions with humans occurred. The decrease in the number of gulls and the number of human-gull interactions in city-squares during the breeding season seemed to be a result of a higher territorial behaviour of breeding gulls defending their nests and surrounding areas, combined with the probable shift in the use of foraging areas during the chick-rearing period, as suggested in Chapter 2. Porto rooftop nests are relatively close to a main fishery landing area that could be easily visited by gulls to feed their chicks with predictable marine prey at a relatively low energetic cost, resulting in less gulls foraging in the city centre during this period.

The number of intervention requests by human population has been increasing along the years, supporting the idea that the gull population breeding in city of Porto is increasing, a fact that is also supported by the increase in nest density registered in the Chapter 3. It would be expected that with this increase the general people awareness to the problem would also increase, however the interactions that are initiated by humans (i.e. feeding birds; Fig. 5.2), are still extremely frequent, and represent the majority of human-gull interactions registered in our observations. Although the food provisions

Figure 5.2. *Groups of gulls* Larus *spp. feeding on items provided directly by humans in the city of Porto and Matosinhos, Portugal.*

from this interaction would not be able to sustain an entire population, they will allow gulls to be progressively more comfortable and confident in approaching humans (Fig. 5.3), leading to other interactions such as landing near food structures (e.g. tables and covers of pastries/ restaurants), comprising the hygiene of those places, prowling and stealing food from humans feeding in outside restaurant tables, and nuisance caused by gulls foraging on trash containers spreading the garbage on the street. Additionally, the nesting conditions in the central historic riverside area, which registered the higher number of intervention requests, also seem to have favourable conditions to sustain urban gull populations, particularly characterised by old, less-attended buildings and traditional building construction, with common desirable features to gulls construct their nests (structures that will sustain and protect their nests, such as chimneys and water drainage open tubes).

Figure 5.3. *Group of gulls, Yellow-legged adult gull and* Larus *spp. immatures, confidently approaching human who is feeding all birds in the city of Porto, Portugal.*

Thus, the dynamics and complexity of human-gull interactions should be considered when managing urban gull populations, given its close relationship and mutual inter-dependence, particularly the important role of human activities and human behaviour in shaping the faith of urban gull populations. The next section discusses more deeply the complexity of these interactions and the efficiency of several management measures attempted in other countries.

5.5. Management of human-gull conflicts

Human-nature interactions and associated dynamics can be highly complex (Gaston et al. 2018b, Soga and Gaston 2020), exhibiting spatial and temporal variation and being commonly associated with socio-economic factors (Soga and Gaston 2020). The same complexity is applied when it comes to human-gull interactions. A great part of direct human-gull interactions is associated with the intentional and unintentional provisioning of food subsidies in urban areas (Oro et al. 2013, Newsome et al. 2015, Cox and Gaston 2018). The intentional provision of food is commonly a response to the ‘extinction of experience’, where people feed wildlife to experience a relationship with nature in urban areas - resulting in a positive interaction with several psychological benefits (Cox and Gaston 2016, Soga and Gaston 2016). However, these positive interactions can rapidly progress to negative ones, with opportunistic species increasing their human tolerance through a habituation process, and humans losing control over the interactions that they initially initiated (e.g. Kumar et al. 2019).

Several aspects may influence direct human-gull interactions (Soga and Gaston 2020), such as social and educational factors (e.g. lack of knowledge about the ecological consequences of wildlife feeding) or socio-economic factors, with gulls in some cases preferring to build their nests on older buildings with lower human disturbance levels (Reynolds et al. 2019), as observed in the Chapter 4. Humans intentionally feeding wildlife may be often elderly and lonely citizens sharing their food (Fig. 5.4). This could be related to a particular orientation and/or predisposition to feed and, ultimately, take care of the ‘most vulnerable ones’ (Cox and Gaston 2016, Soga and Gaston 2020), or a consequence of both being from social groups that suffer the most from loneliness, and will most frequently and subconsciously seek psychological benefits of interacting with nearby wild animals, such as gulls (Cox and Gaston 2016, Cox et al. 2017b, Barnes et al. 2019).

The complexity of human-gull interactions underlines the need to consider the local activities, routines and behaviour of humans, and their seasonality (Chapter 4), when designing management measures aiming to decrease human-gull conflicts within cities. But changing human behaviour can be extremely challenging. Clark et al. (2015) observed people repeatedly feeding gulls in parking lots after being approached during awareness campaigns, and suggested the use of community-based social marketing techniques as a possible and more efficient approach. Contrarily, the Litter Free Coast and Sea "Don’t Feed the Locals" Campaign (DFLC 2017) that occurred in Weymouth, UK, seemed to be very successful in engaging the local community, tourists and local

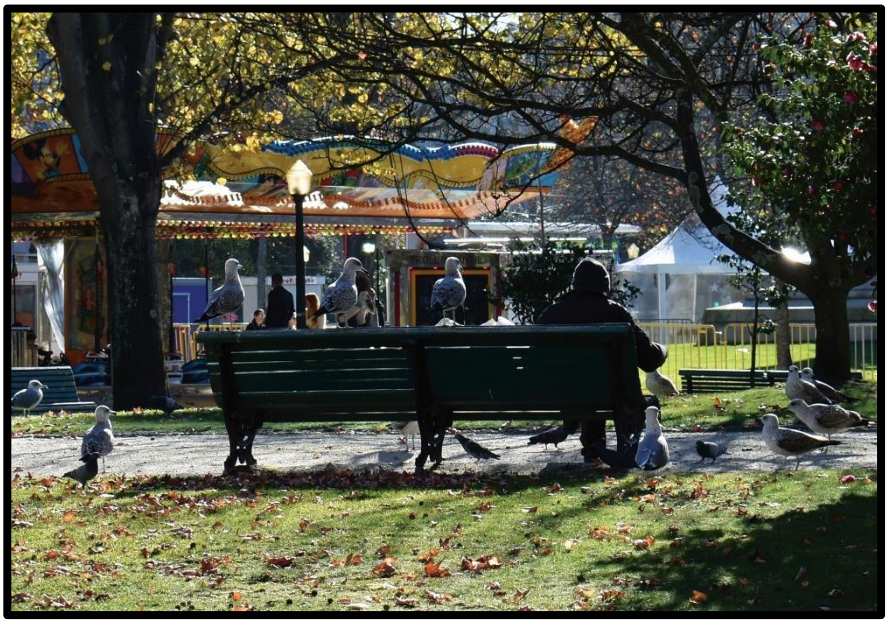

Figure 5.4. *Citizen sharing his food with a group of gulls,* Larus *sp., in a city park within the city of Porto, Portugal.*

business on several activities that aimed to educate people about the reasons why they should not feed gulls.

Several management measures that have been attempted aim to: disperse gulls (e.g. pyrotechnics, broadcast of gull distress calls, blank ammunitions, hazing by trained raptors; Cook et al. 2008, Rock 2013, Thieriot et al. 2015); prevent gulls from roosting in important water bodies (Clark et al. 2013); prevent gulls from constructing their nests on roof-tops (e.g. application of wires, spikes and roof netting); and to reduce the availability of anthropogenic food subsidies (e.g. the use of gull-proof litter bins or closing open-air landfills; Payo-Payo et al. 2015, Steigerwald et al. 2015). However, due to gulls' extreme resilience, most of the applied measures were inefficient in the long-term, and, in some cases simply relocated gulls, and their related conflicts, to new locations (Rock 2005, 2013). The general use of scaring devices is probably one of the least efficient techniques when it comes to dispersing gulls from roosting or nesting roof-top locations, with gulls commonly observed to nest next to these devices (Rock 2013, Kroc 2018a). Roof netting or wiring, on the other hand, could prevent gulls from nesting on roof-tops, but only if mesh size and wire spacing is correctly considered to match the gulls' size and behaviour (Rock 2005, 2013; Louise K. Blight, personal observation). The use of a similar technique showed to be highly effective at preventing Ring-billed Gulls from roosting in wastewater treatment tanks in Millbury, USA, where single-strand stainless-steel piano wires (1 mm in diameter) were spaced at 0.9 - 3.3 m with a 136 kg tensile strength (Clark et al. 2013). On landfills, the use of trained falcons to scare and disperse foraging gulls also seems to be effective (Thieriot et al. 2015), especially when combined with other techniques to reduce gulls' habituation to a single method (Cook et al. 2008). But again, all these measures aiming to disperse gulls, even if highly effective, could just be moving the problem elsewhere. Measures aimed at reducing breeding success, such as egg oiling, do not seem to lead to the abandonment of the colony or the movement to new locations (DeVault et al. 2014), but the management effort required is high, with campaigns being conducted during several consecutive breeding seasons, as gulls are long-lived and highly philopatric species, meaning that the loss of a couple of seasons in productivity does not affect population size.

Overall, changes in the availability of anthropogenic food resources can affect major population trends at breeding sites (Oro et al. 2004, Duhem et al. 2008, Camphuysen 2013). In some cases, these changes may affect the gulls' average body mass, egg volume and clutch size (Pons and Migot 1995, Steigerwald et al. 2015). Although information on worldwide urban-nesting gull population trends is generally lacking, it has been shown for Europe that gulls nesting in roof-top areas forage both in landfills (Spelt et al. 2019) and fishing ports (Méndez et al. 2020). Therefore, combining measures that reduce the availability of predictable anthropogenic subsidies and those that aim to reduce urban gulls' breeding output, along with environmental education and social awareness campaigns to minimize direct human-gull conflict within cities, could potentially increase effectiveness of managing increasing urban gull populations.

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Supplements

Table S2.1. *Number of samples used for the analysis of each breeding and health parameters in natural (Deserta and Berlenga) and urban (Peniche and Porto) colonies, for adult and chick Yellow-legged gulls, during 2018 and 2019.*

		Nearest Nest		***Egg measures***		***Clutch size***		***Parent Body Condition***		***ESR, HL, WBC***	***Hb***	***OXY, DROM***
	Colony	***2018***	***2019***	***2018***	***2019***	***2018***	***2019***	***2018***	***2019***	***2019***	***2019***	***2019***
Adults	Deserta	30	40	30	39	30	39	9	14	13	-	12
	Berlenga	25	31	30	15	30	15	16	18	16	11	15
	Peniche	45	26	34	27	31	27	7	10	10	8	10
	Porto	30	38	25	20	24	20	7	9	9	8	9
Chicks	Deserta	-	-	-	-	-	-	-	-	15	8	7
	Porto	-	-	-	-	-	-	-	-	8	7	5

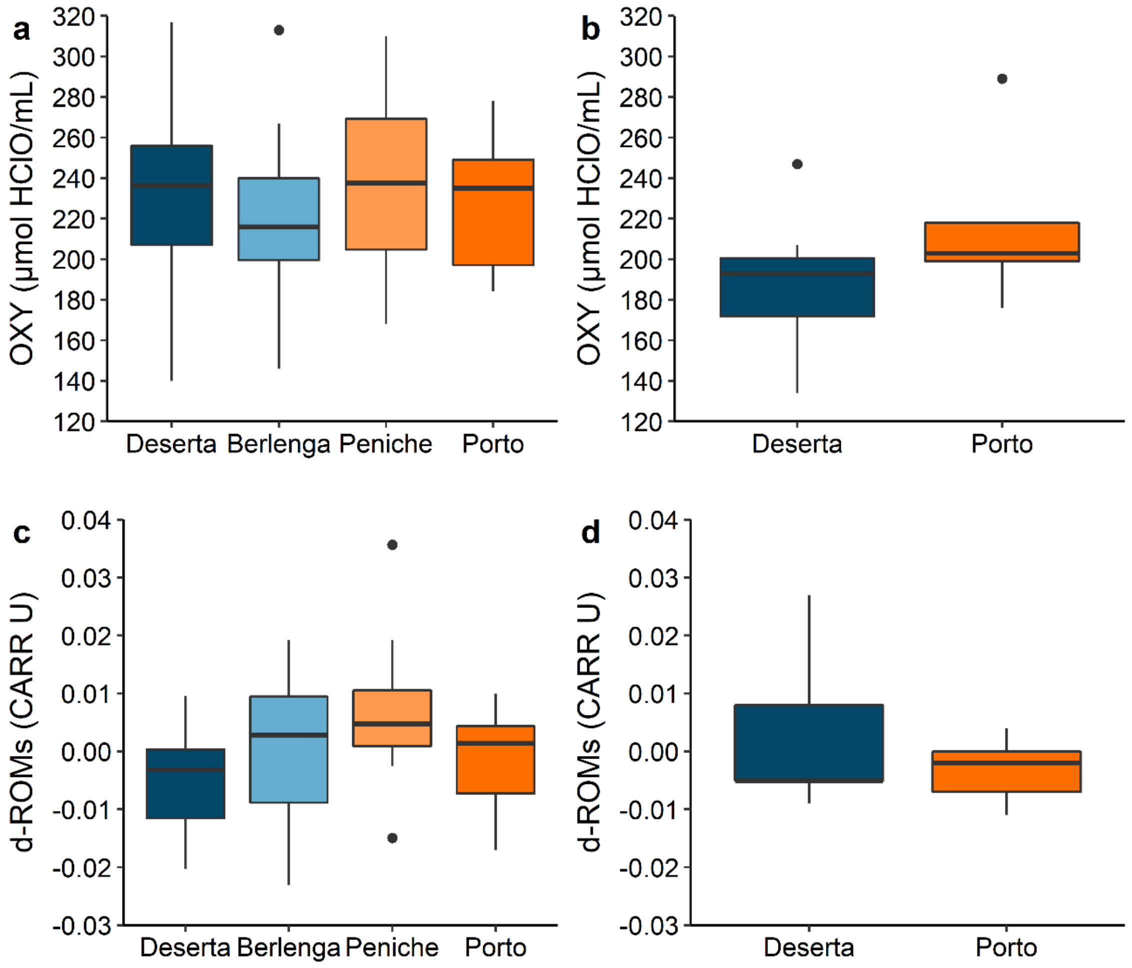

Figure S2.1. Parameters measuring the oxydative stress, antioxidant capacity (OXY; µmol HClO/mL) and the presence of reactive oxygen metabolites (d-ROMs; CARR U), in natural (Deserta and Berlenga) and urban (Peniche and Porto) colonies from adult (a,c) and chick (b,d) Yellow-legged gulls.

Table S3.1. *Number of samples collected for pellet analysis, Stable Isotope Analysis (SIA), urban nests observations (Obs) and Fatty Acid analysis, in natural (Berlenga, Pessegueiro, Deserta, Sálvora) and urban colonies (Peniche and Porto), during pre-breeding (PreB), breeding (Breed) and post-breeding periods (PostB). Br-Ad = adults' breast feathers; Br-Ck = chicks' breast feathers; S8 = eighth secondary feathers; PI = first primary feathers and RBC = red blood cells.*

	Berlenga	***Pesseg***	***Deserta***	***Sálvora***	***Peniche***	***Porto***
Pellet						
PreB	36	26	36	35	-	93
Breed	34	33	34	32	61	68
PostB	54	39	39	-	30	97
SIA						
Br-Ad	17	11	8	-	7	9
Br-Ck	10	10	10	-	-	9
S8	17	11	9	-	7	9
P1	18	11	9	-	7	8
RBC	17	11	9	-	7	7
Obs	-	-	-	-	-	22
FA	10	-	-	-	-	11

Table S3.2. *Summary statistics for the tested Generalized Linear Models (GLMM) representing the probability of occurrence of marine, refuse and terrestrial items in the Yellow-legged gulls' diet from pellet analysis, including fixed terms, random terms, df = degrees of freedom, AIC = Akaike's Information Criterion, ΔAIC = difference in AIC, BIC = Bayesian Information Criterion, logLik = loglikelihood ratio statistic, Dev = deviance,* χ^2 *= chi-square statistics comparing the candidate models. Significant differences (*$p \leq 0.05$*) are in bold.*

Model	***Fixed Terms***	***Rand. Terms***	***df***	***AIC***	***ΔAIC***	***BIC***	***logLik***	***Dev***	χ^2	***p*** (>χ^2)
Marine										
1a	Colony + Period	1|Site	5	667.0	0	690.1	-328.5	657.0	0.39	0.82
1b	Colony * Period	1|Site	7	670.6	3.6	702.9	-328.3	656.6		
Refuse										
2b	**Colony * Period**	**1|Site**	**7**	**528.4**	**0**	**560.8**	**-257.2**	**514.4**	**18.29**	**<0.001**
2a	**Colony + Period**	**1|Site**	**5**	**542.7**	**14.3**	**565.8**	**-266.3**	**532.7**		
Terrest.										
3a	Colony + Period	1|Site	5	916.87	0	940.0	-453.4	906.9	4.01	0.13
3b	Colony * Period	1|Site	7	916.86	0.01	949.2	-451.4	902.9		

Table S3.3. *Parameter statistics for the linear RRPP models representing the $\delta^{13}C$ and $\delta^{15}N$ values in the Yellow-legged gull breast (Br), eighth secondary (S8), and first primary (P1) feathers, red blood cells (RBC), and chicks' breast feathers (Br - chicks) from different colonies. Statistics were obtained from 10.000 random permutations of residuals and include coefficient vector lengths (d = distance) with the observed values, Z-scores and p-values. Berlenga was set as reference level and significance was determined when $p \leq 0.05$.*

		$\delta^{13}C$			$\delta^{15}N$		
		d	***Z-score***	***P(>d)***	***d***	***Z-score***	***P(>d)***
Adult gulls	**Whole year (Br)**						
	Pessegueiro	0.01	-1.21	0.9387	0.19	-0.43	0.5930
	Deserta	0.10	-0.74	0.7227	0.75	1.84	0.0549
	Peniche	**0.77**	**3.38**	**0.0040**	0.67	1.35	0.1063
	Porto	**0.58**	**2.58**	**0.0184**	**0.75**	**1.99**	**0.0468**
	Non-Breeding (S8)						
	Pessegueiro	0.08	-0.97	0.8202	**1.06**	**3.55**	**0.0027**
	Deserta	0.73	1.76	0.0625	**0.82**	**2.23**	**0.0308**
	Peniche	0.14	-0.81	0.7539	**0.89**	**2.16**	**0.0354**
	Porto	0.17	-0.61	0.6693	0.48	0.71	0.2215
	Breeding Season (P1)						
	Pessegueiro	0.39	0.83	0.1962	**1.10**	**3.58**	**0.0032**
	Deserta	0.20	-0.30	0.5390	0.60	1.20	0.1258
	Peniche	0.34	0.31	0.3297	0.78	1.65	0.0715
	Porto	0.58	1.57	0.0817	**1.17**	**3.39**	**0.0039**
	Incubation Period (RBC)						
	Pessegueiro	0.13	-0.52	0.6301	0.17	-0.67	0.6928
	Deserta	0.18	-0.26	0.5266	0.77	1.51	0.0908
	Peniche	**1.02**	**4.19**	**0.0007**	0.87	1.64	0.0757
	Porto	0.57	1.73	0.0682	**2.10**	**5.85**	**0.0001**
Chick gulls	Pessegueiro	0.36	1.78	0.06120	0.43	1.18	0.1345
	Deserta	0.07	-0.76	0.73430	< 0.001	-1.35	0.9995
	Porto	**0.46**	**2.50**	**0.01820**	**0.88**	**3.60**	**0.0021**

Table S3.4. *Pairwise isotopic niche dispersion metrics for different tissues of adult Yellow-legged gulls, representing different time periods, and for chicks' breast feathers, from natural (1 = Pessegueiro, 2 = Berlenga, 3 = Deserta) and urban (4 = Peniche and 5 = Porto) colonies. Presented metrics include dist = Euclidian distances between centroids; absolute value of the difference between the means distances to centroid (CD); absolute value of the difference between the nearest neighbor mean distances (NND); Standard (containing 40% of observations) and 95% ellipses overlap, based on the maximum likelihood fitted ellipses (presented in raw area and proportion). In bold are the parameters with significant effects (p ≤ 0.05) in the linear RRPP full nested models with colony and sample tissue as dependent variables in a nesting model design (*), and RRPP individual models per tissue with colony as dependent variable (**).*

					Standart Overlap		***95% Overlap***	
		dist	$\|CD_1-CD_2\|$	$\|NND_1-NND_2\|$	***Area***	***Prop (%)***	***Area***	***Prop (%)***
Adult gulls	***Whole year (Br)***							
	1 - 2	0.20	0.04	0.04	0.56	45.76	3.51	49.40
	1 - 3	0.56	0.09	0.26	0.68	32.08	4.82	40.16
	1 - 4	0.93	0.29	0.20	0.27	14.28	4.04	45.96
	1 - 5	0.82	0.07	0.03	0.22	14.65	2.84	38.79
	2 - 3	0.75	0.13	__0.30**__	0.57	26.17	5.03	44.56
	2 - 4	__1.03**__	__0.32**__	0.24	0.26	14.48	3.18	34.66
	2 - 5	__0.95**__	0.11	0.07	0.10	6.52	2.91	42.97
	3 - 4	0.87	0.19	0.07	0.18	6.11	4.13	28.72
	3 - 5	0.68	0.02	0.24	0.09	3.48	3.93	32.96
	4 - 5	0.21	0.22	0.17	0.44	28.82	3.01	34.01
	Non-Breeding (S8)							
	1 - 2	1.07	0.02	0.08	0.28	9.42	3.98	25.69
	1 - 3	0.69	0.55	__0.44**__	0.93	17.01	6.08	18.89
	1 - 4	__0.28**__	0.33	0.27	0.14	9.26	2.98	43.60
	1 - 5	0.59	0.30	0.11	0.36	20.82	3.85	45.10
	2 - 3	1.10	0.57	0.35	0.92	14.19	__11.09*__	33.32
	2 - 4	0.90	0.31	0.18	0.23	9.36	2.28	16.73
	2 - 5	0.51	0.28	0.03	0.71	29.65	5.19	39.02
	3 - 4	0.87	__0.88*/**__	0.17	0.49	9.15	3.11	9.85
	3 - 5	0.66	__0.85*__	0.32	__0.85*__	15.73	5.72	18.12
	4 - 5	0.52	0.02	0.16	0.34	30.14	2.43	37.91
	Breeding (P1)							
	1 - 2	1.17	0.41	0.17	0.00	0.00	1.78	19.50
	1 - 3	0.77	0.45	0.09	0.555	23.26	3.83	27.81
	1 - 4	0.33	0.22	0.09	0.403	26.04	3.89	49.80
	1 - 5	__0.21**__	0.16	0.31	__1.114*/**__	49.80	__6.83**__	51.56
	2 - 3	0.64	__0.86*__	0.27	0.064	2.95	2.43	22.28
	2 - 4	0.85	0.19	0.26	0.029	2.42	1.60	27.49

Table S3.4. *continued*

					Standart Overlap		***95% Overlap***	
		dist	$|CD_1\text{-}CD_2|$	$|NND_1\text{-}NND_2|$	***Area***	***Prop (%)***	***Area***	***Prop (%)***
Adult gulls	***Breeding (P1) (continued)***							
	2 - 5	1.31	0.24	**0.48***	0.056	2.17	2.60	19.70
	3 - 4	0.57	0.67	0.01	0.249	11.83	2.18	18.30
	3 - 5	0.97	**0.62***	0.22	0.680	22.14	5.31	30.93
	4 - 5	0.46	0.05	0.22	0.568	25.85	3.94	31.20
	Incubation Period (RBC)							
	1 - 2	0.21	0.10	0.16	0.33	28.33	2.30	34.12
	1 - 3	0.68	0.15	0.02	0.39	35.27	3.51	63.87
	1 - 4	1.35	0.05	0.37	0.09	3.60	3.62	32.41
	1 - 5	**2.06*/****	0.13	0.17	0.00	0.00	2.22	22.54
	2 - 3	0.79	0.05	0.14	0.25	19.40	2.68	41.76
	2 - 4	1.35	0.15	0.53	0.11	4.42	3.64	32.35
	2 - 5	**2.18*/****	0.03	0.33	0.00	0.00	1.99	19.51
	3 - 4	0.85	0.20	0.39	0.06	2.65	4.06	37.60
	3 - 5	1.39	0.02	0.19	0.02	0.88	3.07	33.82
	4 - 5	1.31	0.18	0.20	0.00	0.00	2.99	19.96
Chick gulls	**1-2**	0.56	0.30	0.14	0.05	0.10	0.76	0.29
	1-3	0.52	0.08	0.05	0.01	0.03	0.60	0.32
	1-5	1.54	0.36	0.11	0.00	0.00	0.37	0.08
	2-3	0.07	0.22	0.09	0.22	0.45	1.40	0.50
	2-5	0.99	0.06	**0.03****	0.07	0.07	1.57	0.30
	3-5	1.02	0.28	0.06	0.00	0.00	1.13	0.23

Table S3.5. *Layman isotopic niche dispersion metrics for different tissues of adult Yellow-legged gulls, representing different time periods, and for chicks' breast feathers, from natural and urban colonies. Presented metrics include both isotopes range (δ^{15}NR and δ^{13}CR) = distance between samples with maximum and minimum isotopic values, TA = convex hull area, CD = mean distance to centroid, NND = mean nearest neighbor distance and SEAc = Standard Ellipse Area, corrected for small sample sizes. In bold are the parameters with significant effects ($p \leq 0.05$) in the linear RRPP full nested models with colony and sample tissue as dependent variables in a nesting model design (*), and RRPP individual models per tissue with colony as dependent variable (**).*

		δ^{15}NR	***δ^{13}CR***	***TA***	***CD***	***NND***	***SEAc***
Adult gulls	***Whole year (Br)***						
	Nat (Pessegueiro)	2.65	1.88	1.94	0.76	0.36	0.93
	Nat (Berlenga)	3.63	1.32	2.19	0.72	0.32	0.85
	Nat (Deserta)	3.45	1.77	2.92	0.85	**0.63****	1.88
	Urb (Peniche)	3.02	2.44	1.47	**1.04****	0.56	1.22
	Urb (Porto)	3.01	0.84	1.19	0.83	0.39	0.77
	Non-Breeding (S8)						
	Nat (Pessegueiro)	3.14	2.72	2.12	1.05	0.32	1.12
	Nat (Berlenga)	2.76	2.96	5.21	1.03	0.40	2.13
	Nat (Deserta)	2.53	**4.48***	**8.28***	**1.60***	0.76	**5.28***
	Urb (Peniche)	2.71	2.23	0.66	0.72	0.59	0.52
	Urb (Porto)	2.33	1.36	1.46	0.74	0.43	0.96
	Breeding Season (P1)						
	Nat (Pessegueiro)	2.54	**2.97****	2.19	1.01	0.41	1.27
	Nat (Berlenga)	2.28	1.66	1.55	0.60	0.24	0.55
	Nat (Deserta)	4.85	2.18	2.58	**1.46*/****	0.51	1.67
	Urb (Peniche)	1.45	2.63	0.78	0.79	0.50	0.68
	Urb (Porto)	2.12	2.89	3.27	0.84	**0.72*/****	**2.09****
	Incubation Period (RBC)						
	Nat (Pessegueiro)	3.07	**2.32****	1.29	0.94	0.38	0.74
	Nat (Berlenga)	2.74	1.15	1.93	0.84	0.21	0.76
	Nat (Deserta)	2.52	1.47	1.21	0.79	0.35	0.76
	Urb (Peniche)	2.59	2.29	2.31	0.99	**0.74****	1.73
	Urb (Porto)	2.32	1.56	1.62	0.81	0.54	1.28
Chick gulls	*Nat (Pessegueiro)*	**0,81****	0,68	0,26	0,26	0,16	0,81
	Nat (Berlenga)	2,23	0,83	0,73	0,56	0,30	2,23
	Nat (Deserta)	1,51	0,66	0,50	0,34	0,21	1,51
	Urb (Porto)	1,36	1,46	0,99	0,62	0,27	1,36

Table S3.6. *Fatty acid concentration from plasma samples of Yellow-legged gulls from natural and urban colonies (SFA – Saturated Fatty Acids, MUFA – Monounsaturated Fatty Acids, PUFA – Polyunsaturated Fatty Acids, HUFA – Highly Unsaturated Fatty Acids)*

	Fatty Acids (µg/g)	***A***	***B***	***C***	***D***	***E***	***F***	***H***	***I***	***J***	***K***
Natural colonies	C14:0	1.0	30.7	156.9	311.2	72.0	0.6	5.5	41.2	74.4	0.4
	C15:0	0.5	88.2	-	-	-	-	-	-	-	-
	C16:0	24.0	-	156.8	308.7	63.2	3.9	10.3	109.9	437.9	35.4
	C17:0	1.1	-	-	-	-	0.2	0.4	-	9.1	1.3
	C18:0	38.0	78.7	131.7	240.6	46.7	5.1	17.2	172.8	490.0	40.1
	C20:0	1.2	-	-	-	-	-	-	-	-	-
	C21:0	4.8	69.6	-	21.4	51.7	0.5	5.3	98.2	255.6	39.7
	C22:0	1.4	7.7	171.4	-	-	0.4	1.8	48.4	159.6	17.7
	TOTAL SFA	**71.9**	**274.9**	**616.9**	**881.9**	**233.7**	**10.7**	**40.4**	**470.4**	**1426.7**	**134.6**
	C18:1	-	4.7	-	-	6.9	0.1	-	7.2	18.6	2.2
	C18:1n9t	2.6	20.5	55.4	5.9	43.9	0.5	-	61.7	99.5	12.5
	TOTAL MUFA	**2.6**	**25.1**	**55.4**	**5.9**	**50.8**	**0.6**	**-**	**68.8**	**118.1**	**14.7**
	C18:2n6c	-	8.0	-	-	4.8	-	-	35.3	29.8	3.9
	C18:3	9.7	27.3	-	-	30.2	2.2	4.8	38.2	118.2	9.9
	C20:3n6	3.2	47.2	211.2	-	113.6	0.6	5.9	72.5	109.7	14.5
	C20:4n6	2.0	-	40.0	488.3	30.1	0.3	1.2	-	20.5	2.0
	TOTAL PUFA	**14.9**	**82.6**	**251.2**	**488.3**	**178.8**	**3.2**	**11.8**	**146.0**	**278.2**	**30.3**
	C20:5n3 (EPA)	4.8	4.5	-	-	-	-	-	-	83.2	-
	C22:6n3 (DHA)	-	4.4	-	-	-	-	-	2.2	-	-
	Total HUFA	**4.8**	**8.9**	**-**	**-**	**-**	**-**	**-**	**2.2**	**83.2**	**-**
	N	**13**	**12**	**7**	**6**	**10**	**11**	**9**	**11**	**13**	**12**

Table S3.6. *continued*

	Fatty Acids (µg/g)	***L***	***M***	***N***	***O***	***P***	***Q***	***R***	***S***	***T***	***U***	***V***
Urban colonies	C14:0	49.9	10.0	6.2	5.6	108.1	374.1	538.1	545.3	201.3	57.2	107.6
	C16:0	189.2	41.0	76.4	40.7	121.6	854.9	685.2	911.3	444.1	203.6	251.9
	C17:0	3.4	1.0	-	-	-	-	-	-	-	-	-
	C18:0	215.8	45.7	247.5	41.0	64.7	709.3	604.1	767.2	416.3	245.9	183.8
	C20:0	-	-	-	-	-	-	-	-	-	1.2	-
	C21:0	162.1	20.8	9.2	20.5	23.5	290.9	102.8	284.5	263.6	189.8	72.1
	C22:0	51.9	11.7	5.8	11.5	108.9	150.0	682.3	774.0	272.8	-	121.0
	TOTAL SFA	**672.3**	**130.1**	**345.2**	**119.3**	**426.7**	**2379.1**	**2612.6**	**3282.3**	**1598.1**	**697.7**	**736.4**
	C18:1	50.9	1.9	-	1.7	30.8	31.6	11.9	17.8	9.0	41.1	7.1
	C18:1n9t	15.6	9.2	-	10.7	-	260.3	84.8	147.3	110.0	20.4	95.6
	TOTAL MUFA	**66.5**	**11.1**	**-**	**12.4**	**30.8**	**292.0**	**96.7**	**165.1**	**119.0**	**61.5**	**102.7**
	C18:2n6c	18.5	2.6	-	3.8	12.4	99.1	23.2	72.0	56.3	16.0	28.5
	C18:3	48.2	13.1	104.8	45.4	20.1	194.2	321.3	276.8	114.1	56.7	79.5
	C20:3n6	89.0	11.2	8.4	5.5	108.5	529.7	784.6	858.1	305.5	79.6	133.4
	C20:4n6	11.8	-	3.6	4.8	30.0	69.7	130.0	96.2	28.1	17.6	23.0
	TOTAL PUFA	**167.5**	**27.0**	**116.8**	**59.5**	**171.0**	**892.8**	**1259.1**	**1303.2**	**504.0**	**169.8**	**264.4**
	C22:6n3 (DHA)	9.6	-	1.6	1.2	-	24.5	-	-	-	-	-
	TOTAL HUFA	**9.6**	**-**	**1.6**	**1.2**	**-**	**24.5**	**-**	**-**	**-**	**-**	**-**
	N	**13**	**11**	**9**	**12**	**10**	**12**	**11**	**11**	**11**	**11**	**11**

Table S3.7. *Results of SIMPER analyses showing average similarity of fatty acids (FA) content within the natural colony of Berlenga (N = 10) and the urban colony of Porto (N = 11), according to non-metric multidimensional scaling (n-MDS) analysis.*

MDS Group	***FA***	***Av. Abund***	***Av. Sim***	***Sim/SD***	***Contrib. %***	***Cum. %***
Natural	**C18:0**	0.31	10.55	3.04	22.86	22.86
	C16:0	0.27	7.44	1.54	16.12	38.98
	C20:3n6	0.19	4.87	1.26	10.55	49.54
	C21:0	0.18	4.82	1.27	10.45	59.99
	C14:0	0.20	4.66	1.30	10.09	70.07
	C18:3	0.12	3.65	1.12	7.90	77.98
	C18:1n9t	0.14	3.58	1.27	7.75	85.73
	C22:0	0.14	2.43	0.89	5.27	91.00
Urban	**C18:0**	0.52	11.06	2.93	17.90	17.90
	C16:0	0.53	10.52	3.62	17.04	34.94
	C18:3	0.31	6.71	2.80	10.87	45.81
	C20:3n6	0.42	6.43	2.01	10.41	56.22
	C21:0	0.32	6.36	2.49	10.30	66.52
	C14:0	0.35	5.64	2.12	9.13	75.65
	C22:0	0.35	4.75	1.42	7.69	83.34
	C18:1n9t	0.21	2.88	1.18	4.66	88.00
	C20:4n6	0.16	2.66	1.71	4.31	92.30

Table S3.8. *Results of SIMPER analyses showing average dissimilarity of fatty acids (FA) content between the natural colony of Berlenga (N = 10) and the urban colony of Porto (N = 11), according to non-metric multidimensional scaling (n-MDS) analysis.*

MDS Group	***FA***	***Av.Abund.***	***Av.Abund***	***Av.Diss***	***Diss/SD***	***Contrib%***	***Cum.%***
	C16:0	0.27	0.53	6.34	1.71	13.01	13.01
	C18:0	0.31	0.52	5.64	1.41	11.57	24.58
	C20:3n6	0.19	0.42	5.45	1.53	11.18	35.76
Natural	C22:0	0.14	0.35	5.09	1.5	10.46	46.21
vs	C14:0	0.2	0.35	4.84	1.52	9.93	56.14
Urban	C21:0	0.18	0.32	4.19	1.55	8.59	64.74
	C18:3	0.12	0.31	4.06	1.59	8.32	73.06
	C20:4n6	0.14	0.16	3.17	1.01	6.5	79.56
	C18:1n9t	0.14	0.21	3.07	1.54	6.3	85.87
	C18:2n6c	0.06	0.15	2.25	1.63	4.62	90.48

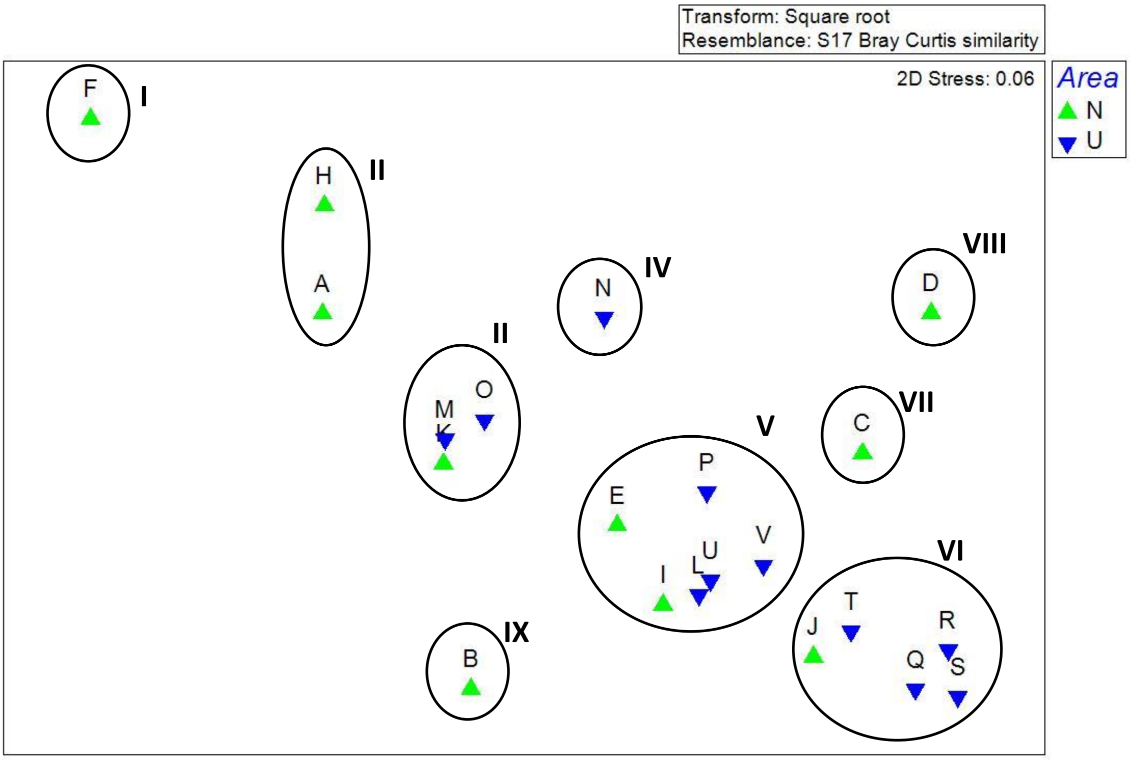

Figure S3.1. *Two-dimensional non-metric MDS ordination plot of FA content of Yellow-legged gulls from natural (green, from A to K) and urban (blue, from L to V) colonies. From I to VIII represent distinct groups at the MDS plot according to FA profile.*

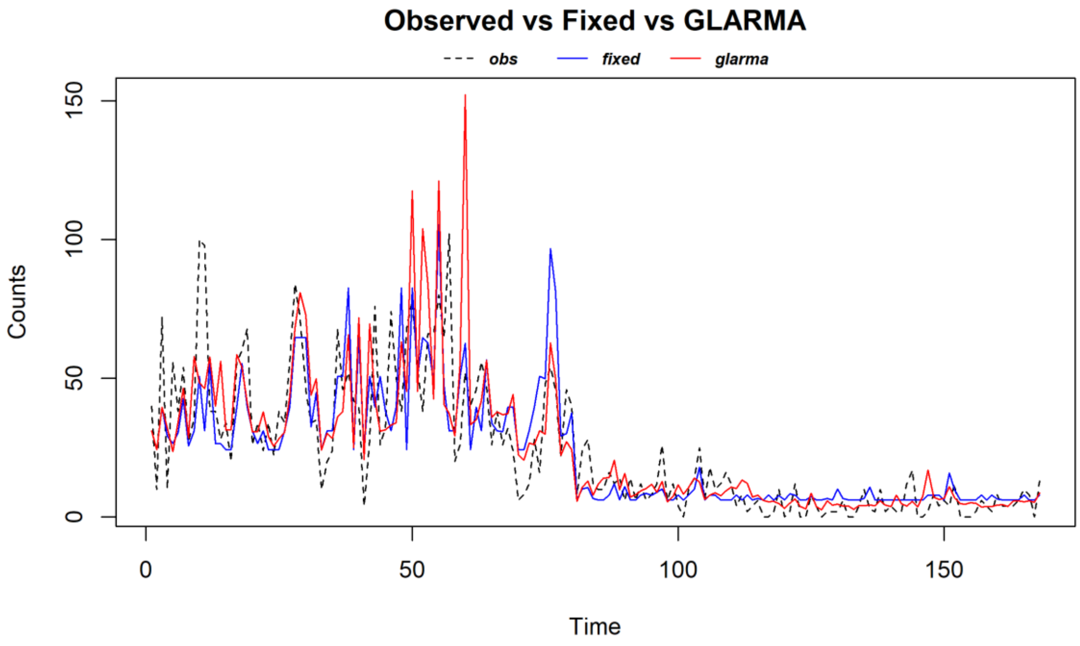

Figure S4.1. *Representation of GLARMA model fit vs observed data vs fixed effects for the mean number of gulls counted in the 10-hour day observations in two central city squares within our study area. The dashed black line represents actual observations, blue line represents fixed effects and red line represents the GLARMA model fit.*

Table S4.1. *Parameter statistics of Conditional and Zero model components after averaging the supported models (ΔAICc < 6) from the second model selection, including the interaction habitat*month, representing the effects of each parameter on the probability of* Larus *spp. immature (LI) gulls and* Larus michahellis *adult (LMA) gulls to be present in the study area. Parameter statistics include estimates (β) and standard error (SE). Significant effects (p < 0.05) are in bold. Months are represented by the respective numbers. Coastal and January were set as reference levels for the variables habitat and month, respectively, and LI was set as reference level for the variable age.*

	Conditional Component			***Zero Component***		
Parameters	***β***	***SE***	***Pr (>|z|)***	***β***	***SE***	***Pr(>|z|)***
Habitat (Riverside)	-0.74	0.60	0.22	-0.82	0.77	0.29
Habitat (Parks)	0.29	0.80	0.72	0.72	0.86	0.41
Habitat (CityGardens)	-0.72	0.61	0.24	**2.13**	**0.63**	**<0.001**
Habitat (CitySquares)	-0.14	0.62	0.82	**2.01**	**0.67**	**<0.001**
Habitat (Rooftops)	-0.15	0.60	0.81	**-2.22**	**0.89**	**0.01**
Month (2)	**-1.30**	**0.39**	**<0.001**			
Month (3)	-0.42	0.43	0.33			
Month (4)	**-1.10**	**0.48**	**0.02**			
Month (5)	-0.55	0.57	0.34			
Month (6)	0.46	0.51	0.36			
Month (7)	0.00	0.39	0.99			
Month (8)	**0.81**	**0.39**	**0.04**			
Month (9)	**1.27**	**0.39**	**<0.001**			
Month (10)	0.36	0.40	0.37			
Month (11)	0.17	0.39	0.65			
Month (12)	**-0.97**	**0.45**	**0.03**			
Age (LMA)	-0.17	0.14	0.21			
Habitat (Riverside)*Month (2)	**1.44**	**0.59**	**0.02**			
Habitat (Parks) *Month (2)	0.86	0.77	0.27			
Habitat (CityGardens)*Month (2)	**1.35**	**0.60**	**0.03**			
Habitat (CitySquares)*Month (2)	**1.42**	**0.68**	**0.04**			
Habitat (Rooftops)*Month (2)	**1.42**	**0.57**	**0.01**			
Habitat (Riverside)*Month (3)	0.61	0.61	0.32			
Habitat (Parks) *Month (3)	0.40	0.79	0.62			
Habitat (CityGardens)*Month (3)	0.02	0.76	0.97			
Habitat (CitySquares)*Month (3)	-0.49	0.73	0.51			
Habitat (Rooftops)*Month (3)	0.68	0.61	0.26			
Habitat (Riverside)*Month (4)	0.57	0.66	0.39			
Habitat (Parks) *Month (4)	0.48	0.82	0.56			
Habitat (CityGardens)*Month (4)	1.09	0.68	0.11			
Habitat (CitySquares)*Month (4)	-0.31	0.72	0.67			
Habitat (Rooftops)*Month (4)	1.04	0.65	0.11			
Habitat (Riverside)*Month (5)	0.53	0.73	0.47			
Habitat (Parks) *Month (5)	0.06	0.88	0.95			
Habitat (CityGardens)*Month (5)	-0.35	0.81	0.66			
Habitat (CitySquares)*Month (5)	-0.05	0.78	0.95			

Table S4.1. *continued*

Parameters	***Conditional Component*** β	***SE***	***Pr (>|z|)***
Habitat (Rooftops)*Month (5)	0.19	0.71	0.79
Habitat (Riverside)*Month (6)	-0.53	0.70	0.45
Habitat (Parks) *Month (6)	-1.34	0.84	0.11
Habitat (CityGardens)*Month (6)	-1.43	0.87	0.10
Habitat (CitySquares)*Month (6)	-0.92	1.17	0.43
Habitat (Rooftops)*Month (6)	-0.70	0.67	0.30
Habitat (Riverside)*Month (7)	-0.03	0.61	0.96
Habitat (Parks) *Month (7)	-1.01	0.77	0.19
Habitat (CityGardens)*Month (7)	**-1.74**	**0.87**	**0.05**
Habitat (CitySquares)*Month (7)	**-2.11**	**0.87**	**0.02**
Habitat (Rooftops)*Month (7)	-0.08	0.57	0.88
Habitat (Riverside)*Month (8)	-0.68	0.61	0.27
Habitat (Parks) *Month (8)	**-2.07**	**0.77**	**0.01**
Habitat (CityGardens)*Month (8)	**-1.52**	**0.73**	**0.04**
Habitat (CitySquares)*Month (8)	**-2.00**	**0.71**	**0.01**
Habitat (Rooftops)*Month (8)	-0.72	0.57	0.21
Habitat (Riverside)*Month (9)	**-1.54**	**0.58**	**0.01**
Habitat (Parks) *Month (9)	-1.73	0.91	0.06
Habitat (CityGardens)*Month (9)	**-2.37**	**1.16**	**0.04**
Habitat (CitySquares)*Month (9)	-1.23	0.78	0.11
Habitat (Rooftops)*Month (9)	**-1.77**	**0.58**	**<0.001**
Habitat (Riverside)*Month (10)	0.03	0.59	0.96
Habitat (Parks) *Month (10)	-0.96	0.78	0.22
Habitat (CityGardens)*Month (10)	-0.67	0.72	0.35
Habitat (CitySquares)*Month (10)	0.14	0.70	0.85
Habitat (Rooftops)*Month (10)	-0.61	0.58	0.30
Habitat (Riverside)*Month (11)	-0.11	0.59	0.86
Habitat (Parks) *Month (11)	-0.14	0.77	0.86
Habitat (CityGardens)*Month (11)	0.21	0.68	0.76
Habitat (CitySquares)*Month (11)	-0.11	0.67	0.87
Habitat (Rooftops)*Month (11)	-0.08	0.58	0.89
Habitat (Riverside)*Month (12)	0.97	0.62	0.12
Habitat (Parks) *Month (12)	0.97	0.80	0.22
Habitat (CityGardens)*Month (12)	0.83	0.68	0.22
Habitat (CitySquares)*Month (12)	0.85	0.64	0.19
Habitat (Rooftops)*Month (12)	0.78	0.61	0.20

Table S4.2. *Summary statistics for the candidates GLM models representing the effects of each parameter on the number of intervention requests. AICc = Akaike's information criterion corrected for small sample size and logLik = loglikelihood ratio statistic.*

Models	***AICc***	***logLik***
City District + Season + Year	369.3	-169.5
City District + Season	370.3	-173.0
Season	419.5	-205.4
Season + Year	423.3	-204.9
City District	441.1	-211.2
City District + Year	443.5	-209.6
Year	463.2	-227.3

***Table S4.3.** Summary statistics for the candidates GLARMA models representing the effects of each parameter on the number of Yellow-legged gulls* Larus michahellis *attracted to city squares. AIC = Akaike's information criterion and logLik = loglikelihood ratio statistic.*

Models	***AIC***	***logLik***
Season + Time + Weekend + Humans + FG + SP + LS + FT	1238.9	-607.46
Season + Time + Weekend + FG + SP + LS + FT	1236.6	-607.29
Season + Time + FG + SP + LS + FT	1235.3	-607.65
Time + FG + SP + LS + FT	1250.9	-616.45
Season + FG + SP + LS + FT	1233.1	-607.70
Season + FG + LS + FT	1231.4	-607.70
Season + FG + FT	1231.1	-608.54
Season + FG + SP + FT	1232.7	-608.33