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SPATIAL ECOLOGY AND DIEL RHYTHMS OF
NATURAL AND URBAN-DWELLING GULLS

VOLUME 1

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I declare that this thesis was written and organized by me, and I confirm that it has not been previously submitted, in whole or in part, to obtain another academic degree. I confirm that the work described was mostly done by me, and other contributions are clearly acknowledged in the text with appropriate citations/references. Specifically, I acknowledge the contribution of colleagues of my working group ECOTOP and from SPEA - Sociedade Portuguesa para o Estudo das Aves, who collected all tracking data between 2016 and 2019. All data analysis and thesis writing was done by me.

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Abstract

The growth of urbanization employs changes in the structure and function of natural habitats, where resources can be replaced, and adaptations imposed between species and their environment. Therefore, urban areas can develop into novel ecosystems, creating new patterns of ecological relations, where most opportunistic species thrive and take advantage of the new available resources. Gulls, as coastal seabirds, have evolved into highly versatile and generalist species and widely adapted their behaviour to cope with the expansion of urban areas. Urban-dwelling gulls have been a case of study in recent years due to the fast dominance of urban sites and increasing conflicts with humans. The availability and abundance of anthropogenic-associated resources have been the main cause for a growing urban settlement however gulls can display distinct foraging strategies, in space and time, and in response to human activities or natural extrinsic factors, both at a population and individual level. Here we evaluated and compared the spatial ecology of yellow-legged gulls breeding in two distinct locations – Porto, an urban colony, and Berlenga Island, a natural colony – with the use of tracking devices, focusing on patterns of habitat use and foraging behaviour between the gulls' breeding and wintering seasons, also indicating differences in diel rhythms potentially shaped by human activity. GPS tracking data revealed differences in foraging strategies, as gulls from the natural colony had longer foraging trips and travelled farther from the colony than their urban conspecifics, especially during the wintering season. Additionally, gulls from the urban colony showed minimal dispersion between the breeding and wintering seasons, showcasing the impact of urban areas in the foraging behaviour of these birds. Habitat use was distinct between colonies, as gulls from the urban colony preferably selected urban habitats while gulls from the natural colony foraged mainly at sea and nearby fishing harbours. However, individual differences in habitat use were found within the two colonies, predominantly in the wintering season, which may be relevant to establish management measures for this species. Daily activity rhythms did not differ greatly when comparing workdays and weekends. Still, time-series analysis showed different patterns among used habitats and between the two colonies, suggesting that gulls adapted their foraging

activity to match human routines. Our findings indicate that the variation in the foraging ecology and distribution of yellow-legged gulls may relate to their breeding sites and that human activity and consequent environmental changes influence the behaviour of these natural and urban-dwelling birds in different ways.

Resumo

O aumento da urbanização impõe mudanças na estrutura e funcionamento dos habitats naturais, onde os recursos podem ser substituídos, e adaptações são impostas entre as espécies e seu ambiente. Assim, os espaços urbanos podem desenvolver-se em novos ecossistemas, apresentando novos padrões e relações ecológicas, onde as espécies mais oportunistas conseguem prosperar e beneficiar dos novos recursos disponíveis. As gaivotas, como aves marinhas costeiras, evoluíram como espécies altamente versáteis e generalistas e adaptaram amplamente o seu comportamento para lidar com a expansão das áreas urbanas. As gaivotas urbanas têm sido caso de estudo nos últimos anos, devido ao seu rápido domínio dos espaços urbanos e ao aumento de conflitos com os seres humanos. A disponibilidade e a abundância de recursos antropogénicos são das principais causas deste aumento gradual em espaços urbanos, no entanto as gaivotas podem apresentar, no tempo e no espaço, estratégias de alimentação distintas, e em resposta a atividades humanas ou a fatores extrínsecos naturais, tanto a nível populacional como individual. Neste estudo, é avaliada e comparada a ecologia espacial da Gaivota-de-patas-amarelas a reproduzir-se em dois locais distintos – no Porto, uma colónia urbana, e na Ilha da Berlenga, uma colónia natural – através do uso de dispositivos GPS, focando nos padrões de uso de habitat e comportamento de alimentação entre as épocas de reprodução e pós-reprodução, indicando também diferenças nos seus ritmos diários, potencialmente moldados pela atividade humana. Os dados de GPS revelaram diferenças nas estratégias de alimentação, onde as gaivotas da colónia natural demonstraram viagens mais longas e procuraram alimentar-se a maiores distâncias da colónia do que as gaivotas da colónia urbana, sobretudo na época pós-reprodutora. Inclusivamente, gaivotas da colónia urbana mostraram pouca dispersão entre as épocas de reprodução e pós-reprodução, demonstrando o impacto das áreas urbanas no comportamento de alimentação destas aves. O uso de habitat foi distinto entre colónias, ao que as gaivotas da colónia urbana selecionaram preferencialmente habitats urbanos, enquanto as gaivotas da colónia natural procuraram alimentar-se principalmente em zonas marinhas e em portos de pesca. No entanto, diferenças individuais no uso de habitat foram encontradas nas duas colónias, predominantemente

durante a época pós-reprodutora, o que pode ser um parâmetro relevante na criação de medidas de gestão para esta espécie. Os ritmos de atividade diária não demonstraram diferenças significativas quando comparados entre dias da semana e fins-de-semana. No entanto os resultados mostraram diferentes padrões entre os habitats usados e entre as duas colónias, sugerindo que as gaivotas adaptaram de facto o seu comportamento de alimentação de forma a corresponder a rotinas diárias humanas. Estes resultados indicam que a variação na ecologia e distribuição da gaivota-de-patas-amarelas pode estar relacionada com o seu local de reprodução e que a atividade humana e consequentes alterações ambientais influenciam o comportamento nestas aves de ambientes naturais e urbanos.

Palavras-chave: Gaivotas urbanas, estratégia de alimentação, uso de habitat, recursos antropogénicos, ritmos diários

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1. Introduction

1.1   Urban ecosystems and emerging novel habitats

The world's human population has exponentially grown over the last century and seems to continue this tendency, as world regions become more developed and population momentum continues, expecting scenarios such as 9 billion people by the year 2045 (Van Bavel 2013). This ever-growing tendency prompted vast changes in the surrounding environments, as the proportion of world surface modified by human activities continues to grow, both in the ocean and on land (Watson *et al*. 2018). The concentration of the human population in certain areas have converged into a process known as urbanization (Vlahov and Galea 2002). Urbanization, at a global scale, is in constant progress, as more countries increase their cities and urban spaces, to cope with the ongoing growth of the human population, and to sustain and centralize needed resources for such growth (Berry 1990). As such, the sheer concept of urbanization implies a modification, mostly dramatic, of an ecosystem, where anthropogenic pressure forces changes in the structure and function of the composing habitats (Shochat *et al*. 2006). Consequently, urban areas transcend such habitats and substitute resources, creating new dynamics, inferring adaptations between living organisms and their conspicuous abiotic relations (Byrne and Houston 2020). Coastal habitats, for standard, are one of the most studied examples of modified ecosystems. Besides being the areas that concentrate the larger amount of the human population, they are one of the most altered habitats throughout the years (Creel 2003). The modification at a soil level, niche occupation and resource change are the biggest causes of local species extinction within this new imposed urban settings (Byrne and Houston 2020).

The study of urbanization and urban habitats provides a better understanding of biological patterns associated with changes imposed on natural settings (Endlicher *et al*. 2011), focusing on species interactions and processes that may affect their physiology. Research on these newly established environments needs to take into account methods that can explain such biological patterns and the influence of anthropogenic pressures, resulting in a better understanding of a species' response to such pressures (Byrne and Houston 2020). As urban occupation introduces modifications to pre-existing natural processes (Shochat *et al*. 2006), new resources and

environmental status take place, forcing native species to adapt in order to survive. Urban areas become, in this context, novel ecosystems, with specific characteristics and new patterns of relationships. Most studies point to the extinction and extirpation of species in their native settings because of habitat occupation or destruction, as diversity and species richness can be restrained, posing a great threat to wildlife in general (Vitousek *et al*. 1997, Mckinney 2002). However, even though most species are not able to survive such pressures, urban habitats are not always hostile to all. Some can adapt and even thrive in a specific urban setting (Chevin *et al*. 2010). As such, species respond differently to this alterations, as urban areas display a more steadily and continuously accessibility of specific resources in general (Faeth *et al*. 2005).

Species that can survive and thrive in urban areas are normally associated with flexibility in behaviour and generalist adaptations (Ducatez *et al*. 2015). Many studies have put forward that most species adjust their behaviour because of a prone adaptation inherent to the individual, imposed by an evolution in the flexibility to use a diverse range of habitats. Another probability is of a species predisposition as a generalist omnivore, that is 'pre-adapted' to live in human structures (Sih *et al*. 2011). With human activities being able to modify environment dynamics and with the appearance of new urban habitats, opportunistic and generalist species are expected to respond with a change in their distribution and activity patterns, according to the availability of new resources, prompting them to thrive in urban areas as they may not need to spend energy looking for them (Anderies *et al*. 2007). The display of these novel resources in urban areas, that are more readily and continuously available, often means behavioural adaptations in foraging, breeding and niche occupation by some species, and generalist species tend to adopt more to this type of resources (Mennechez and Clergeau 2006).

Seabirds comprise many species known to be very agile and resourceful, and evolved to be experts in exploring ocean environments. Natural environments are known to be greatly heterogeneous in terms of resource availability, as resources are normally irregularly distributed in both spatial and temporal scales (Prins and Langevelde 2008). The ocean or, in general, marine habitats are specific habitats that comprise great spatial and consequently temporal heterogeneity

(Spalding *et al*. 2007), therefore species that evolved in ocean environments are often prepared to take advantage of such resources, depending on their availability (Trevail *et al*. 2019). The effects of this heterogeneity, and the responses to the distribution of resources, are the fundamental aspects to determine a successful predator in a vast ocean area (Fritz *et al*. 2003). Seabirds are, for that reason, top predators. As top predators and experts in tracing resourceful areas, seabirds tend to feed, forage and breed in environments that may have a nearby high density of food, such as upwelling zones, in the ocean, or coastal areas (Xavier *et al*. 2004, Ceia and Ramos 2015). Coastal seabirds represent a particular group of seabirds that tend to feed in coastal areas, where prey is relatively abundant and transition into different habitats is more facilitated (Schreiber and Burger 2001). With intensive urbanization and with most coastal habitats likely to be modified, anthropogenic resources may be available in high quantities in certain areas such as fishery ports and landfills. This novel environment forces altering behaviours and genetic discrepancy among certain populations, and the ability of organisms to behave appropriately under these new conditions is crucial for determining their immediate success or failure in these modified environments (Schlaepfer *et al*. 2002, Sih *et al*. 2011).

A big clade of species known to be a coastal prone species are Gulls (Laridaea). Gulls often feed and forage near coastal habitats and are well adapted to the transition zone between the ocean and land. Most gull species evolved into an omnivorous and generalist behaviour, demonstrating natural plasticity in their foraging and feeding strategies (Isaksson *et al*. 2015). Consequently, gulls, being predominantly coastal species and generalists, were one of the groups of seabirds that most altered their behaviour and distribution to cope with increasing urban settlements (Goumas *et al*. 2020, Pais de Faria *et al*. 2022).

1.2   Urban-dwelling gulls

Urban-dwelling gulls have been a case of study in recent years, as it is noted that populations and distribution are in a steady increase, within urban areas (Belant 1997, Pais de Faria *et al*. 2022). The fast dominance of these areas also led to conflicts with humans and rapid management measures from local government agencies to control populations, often considered

pests (O'Connell 1995, Ramos *et al.* 2009a, Soulsbury and White 2015). Most conflicts are related to damage to structures, aggressive behaviour towards people and feeding behaviours such as snatching food in nearby restaurants (Goumas *et al.* 2019, Pais de Faria *et al.* 2021a), but studies show that gulls can also be vectors of diseases that can be transmitted in recreational beaches and in water (Nelson *et al.* 2008) posing great threats to public health. Also, gulls are responsible for affecting coastal vulnerable species, posing negative impacts in events of predation and distress in their niche areas, even accounting for a larger percentage of mortality to some populations (Hario 1994, Oro *et al.* 2005).

Many reasons have been put forward to explain the main cause of this "invasion" of urban sites, most being coupled with higher reproductive success and reduced mortality (Coulson and Coulson 2009, Kroc 2018). But the main drive of this expansion seems to be resources, as human-derived activities display more readily available food sources than other conspicuous habitats (Auman *et al.* 2008). As gulls are adapted to prey on a highly diverse diet, their versatility enables them to forage in different habitats and alternate their strategy to access such resources. Most gulls prey naturally on small fish, crustaceans and molluscs, however the high display of anthropogenic food sources and more steady availability has led many species to forage garbage dumps, fishery discards, from fishing vessels and fishing harbours, and agricultural sites (Matias and Catry 2010, Cama *et al.* 2012). The modification of the foraging behaviour consequently leads to a change in breeding behaviour and habitat use (Matich *et al.* 2011, Navarro *et al.* 2017).

With urbanization on the rise and with food resources more scattered through cities and urban areas, gulls have also extended their nesting areas to these sites, colonizing rooftops and abandoned houses, to breed and reproduce near feeding sites (Perlut *et al.* 2016, Pais de Faria *et al.* 2022). Many rooftops of city buildings and industrial sites are being colonised by gulls, yet the density of these colonies is still lower that in natural nesting sites (Dolbeer *et al.* 1989). Monaghan (1979) found out that these alternative nesting and breeding sites provide more security and safety to the offspring, often from other gulls, however, the most predominant factor was still

the proximity to food resources. The irregularity of the nesting sites and the low density suggests that gulls can nest and reproduce in urban areas just to take advantage of the resources.

1.3 Feeding and foraging strategies of gulls

Gull species are often considered sedentary, as they form large colonies, especially during the breeding season (Spear 2001, Kralj *et al*. 2014). This seasonal variation is also distinctive in terms of feeding behaviour, as it often tends to be more restrictive during the breeding season, when individuals feed next to the colony (Ramos *et al*. 2009b, Arizaga *et al*. 2010b, Pierotti and Annett 2013, Ceia *et al*. 2014a). Colonies usually aggregate in habitats where food is more abundant, and more importantly, where they can have fewer energetic costs (Masello *et al*. 2010, Ramírez *et al*. 2010). The reasons behind this selection of colony sites often arise from breeding constraints, in which during chick-rearing, gulls are restricted to a limited area, as the energy dispensed during this period is higher (Mawhinney *et al*. 1999, Dies and Dies 2017, Egunez *et al*. 2017), being predictable that gulls try to minimize time away from their chicks and optimize their foraging trips (Isaksson *et al*. 2015). Nonetheless, incubation and chick-rearing are performed by both parents, and their foraging time and behaviour may alternate (Ramírez *et al.* 2010). With these shifts, it is needed a more individual approach to understand the behavioural patterns that may take place, particularly in relation to the breeding season, foraging specialization and habitat choice.

The new anthropogenic food sources can determine the dynamics of some populations, influencing distribution patterns and contributing to population growth (Ramos *et al*. 2009a). In recent years, numerous studies on the feeding ecology of yellow-legged gulls in the Iberian Peninsula (Ramos *et al*. 2009a, Arizaga *et al*. 2010a, 2013, Moreno *et al*. 2010) have been carried out. However, despite most studies indicating the clear presence of anthropogenic based foods in the diet of many gull populations, as a fundamental resource that is continuously obtained, the overall diet of coastal breeding urban gulls is still dominated by fish and marine prey (Pais de Faria *et al*. 2021b). This species' behavioural plasticity in a spatial context can demonstrate a

response in relation with the availability of human derived food resources and contribute to explain dietary differences among populations (Alonso *et al*. 2015). This plasticity is also expected to be present in the specialisation of foraging strategies, with different individuals and subpopulations specializing to feed on different food sources, both in space and time, providing insight into how anthropogenic resources are utilized at a species level (Ceia *et al*. 2014b).

Foraging strategies may vary according to extrinsic factors, such as oceanographic conditions or prey abundance (Mendes *et al*. 2018). Gulls may adopt a marine strategy when marine prey is abundant, especially during their breeding season if restricted to a more natural habitat. This marine foraging strategy is more frequent around productive marine areas, such as coastal areas and shallow waters (Ceia and Ramos 2015) and the abundance of marine resources is normally associated with the phenomenon of upwelling or in areas of oceanic fronts. In Portugal, the tendency for a coastal upwelling is around the summer season and converges with the breeding season of most gull populations along the coast (Paiva *et al*. 2010, Lopes 2012). Climatic variation, depicted by the North Atlantic Oscillation, could be another factor connected to an uprising of warm waters and species abundance (Mendes *et al*. 2018). These oceanic and climate differences could influence the foraging strategies of gulls, depending on the geographical area where the colony or the individuals may be encountered.

With the growing of anthropogenic pressures, natural resources will be less abundant in certain areas, and other food sources like garbage dumps, industrial and agricultural areas, and fisheries discards will become the easy choice to feed (Hebert *et al*. 2008, Matias and Catry 2010). These new food sources, like garbage dumps, can lead to a higher survival rate, as they are often rich in protein and other highly energetic components (Ramos *et al*. 2009b, Spelt *et al*. 2019). With more readily available food sources, more easily can gulls provide food for their offspring and guarantee a successful reproductive season. The use of human food sources has been documented extensively for decades. For example, Sol et al. (1994) indicated that *Larus michahelli*s in Barcelona exploited with great intensity various garbage dumps in the city and that it is a common site of consumption for these gulls. Outside of the breeding season, many studies

appointed that many gull species tend to use this human food sources extensively, as they present a more available resource and are easily encountered, saving energy in foraging time. Arizaga (2014) found out that, in the winter, gulls that frequently used garbage dumps as a resource were forced to move greater distances from their feeding site when these dumps closed. This high plasticity can also be visible in the use of fishing vessels and fishing ports as a food source. For example, it has been reported that yellow-legged gulls that vastly exploited marine resources seemed to forage extensively on fishery discards (Duhem *et al*. 2003, Ramos *et al*. 2009a). Most gulls' niche is known to be shaped by fishery activities and the intensity of fisheries, or their presence and absence, can be a factor of variation in the foraging strategies of gulls (González-Solís 2003, Yorio and Caille 2004).

The increasing evidence that many species of urban-dwelling gulls are more adapted to urban environments and foraging in urban areas is higher than predicted before. The foraging habitats used by species of gulls in urban settlements are dictated by nearby human food sources like fish harbours and landfills (Bosch *et al*. 1994, Sol *et al*. 1995, Duhem *et al*. 2003). The predisposal opportunistic behaviour developed in this species a tendency to show foraging site fidelity, especially in urban colonies, as the predictable food resources drive individuals to decrease their foraging effort (Grémillet *et al*. 2004, Arizaga *et al*. 2014). These changes in a timescale are also due to anthropogenic activity patterns (Yoda *et al*. 2012). The example of *Larus michahellis* and their diurnal behaviour towards fishing vessels represents a dietary rhythm that varies normally with time (Oro *et al*. 1995). Yellow-legged gulls, although presenting a diurnal foraging behaviour, are known to forage at dawn, taking advantage of fish discards from fishing vessels. The number of individuals foraging around such vessels is correlated with the number of fishing vessels during the day and at dawn. It is also known that these fish discards constitute an important food source for this species, as the prey species that were obtained by the fishing vessels corresponded with the prey acquired by the gulls (Matos *et al*. 2018). The variation in the density of individuals towards fishing vessels throughout the day demonstrates a foraging rhythm, and an important food source that is learned and optimized, due to the versatility and opportunistic

behaviour of gulls. Gulls have been shown to adjust their foraging strategies to match daily and weekly rhythms in various urban food sources. Gulls in urban environments have the behavioural flexibility to adapt to human time schedules by making use of different anthropogenic resources depending on the timings of their availability (Cama *et al*. 2012, Tyson *et al*. 2015). Spelt *et al*. 2019 showed that these time schedules differ from natural circadian or seasonal rhythms, however, gulls adapted to such irregular patterns, even differentiating weekday and weekend type activities. In a particular feeding ground observation, in a waste centre, the temporal pattern of the number of gulls present in the area differed between the weekdays and weekends. During the weekend, the waste centre had no waste, and the number of gulls diminish. Furthermore, the foraging strategy implemented by most individuals consisted in waiting for waste to arrive on weekdays to feed, instead of foraging actively for food, enforcing the idea of adaptability and diel rhythms.

Differing from foraging natural patterns at sea, the spatial use of terrestrial areas or the adaptability of human activities may indicate that urban food resources are also more predictable when compared to natural resources and that gulls have some knowledge of food resources in space and time (Yoda *et al*. 2012). Numerous animals are able to adapt to temporal patterns in natural food availability, but whether species living in relatively novel environments such as cities can adapt to anthropogenic activity cycles is an important case of study. Gulls that visit natural and urban feeding grounds at specific times of the day, corresponding to their temporal pattern of availability, could show new patterns that may better elucidate the terming of urban ecology and understand new foraging strategies by this species and species alike.

There is increasing evidence that memory effects help individual seabirds to optimise their foraging strategies, most probably in conjunction with local enhancement via feeding groups. It has also been speculated that seabird colonies function as information centres and that individuals within breeding assemblages tend to share specific foraging patterns and foraging distributions (Camphuysen and Van Der Meer 2005). In this context, Grémillet *et al*. (2004a) indicated that neighbouring seabird colonies foraging in a similar marine environment may

develop different behavioural types due to strong local 'cultural identities' tailored by group and memory effects. As seabird populations are subdivided at different spatial scales and are made of breeding groups that can exchange individuals and become extinct, they may function as metapopulations. A key process requiring specific efforts is thus to understand which factors affect the dispersal of individuals and their consequences.

1.3   Spatial ecology and biologging approach

Spatial ecology is the most used approach to study processes of spatial distribution of organisms in a specific environment, and tackles concepts that may predict behavioural changes in species and populations, in relation to changes in resources and ecological events, that often lead to the disruption of environments (Fletcher and Fortin 2018). Seabirds are known to be good ecological indicators of such changes in ocean and marine environments, as most species show to be versatile, abundant and can be monitored and observed with more ease than underwater species (Durant *et al*. 2009, Gregory and Strien 2010). Seabirds are also top predators, meaning that they can demonstrate not only changes in their trophic level but also changes in inferior trophic levels. In spatial ecology, this species are crucial in demonstrating environmental changes, as their mobility allows them to respond to such changes on different spatial and temporal scales (Furness and Camphuysen 1997, Cury *et al*. 2001).

Most studies indicate that human activities, such as overfishing, have major consequences on gulls' behaviour, especially in the breeding season. Because these consequences lead to a shift in foraging behaviours, promoting the expansion of some species to urban areas and influencing their population density and stability, knowing the spatial movements of urban-dwelling gulls is essential to further understand how these species have adapted to urban environments and to design effective management measures to mitigate potential conflicts with humans (Navarro *et al*. 2017a, Fuirst *et al*. 2018, Spelt *et al*. 2019).

Global Positioning System loggers (GPS-loggers) are high-resolution devices and nowadays one of the most efficient techniques used to track free-ranging movements of animals,

and thus study their spatial ecology, making it possible to collect data in more than one individual, reduce sampling biases and volume of data collection, in comparison to more traditional methods (Shamoun-Baranes *et al*. 2012, Allan *et al*. 2013). With GPS devices, it is possible to obtain 24-hour coverage of the movement of an animal, with rapid tracking successions (Tomkiewicz *et al*. 2010), providing vital information on their behaviour. For gulls, it is possible to assess their foraging behaviour and foraging locations and explore their use of habitats (Rock *et al*. 2016). As these devices are lightweight, they pose no interference to the general movement of the bird (Recio *et al*. 2011). By assessing several parameters such as trip duration, trip distance and geographical positioning, it is possible to identify individual variations in foraging behaviours of gulls.

The main aim of this study is to evaluate and compare the year-round spatial ecology between natural and urban-dwelling yellow-legged gulls, in two distinct locations varying in habitat composition, with special focus on diel rhythms and foraging strategies. The yellow-legged gull is a widely distributed species, with great plasticity and adaptability, making a fit model to compare the impacts of anthropogenic pressure in the overall behaviour of this generalist species. Results aim to provide a better understanding of this species' distribution and individual differences, comparing, in particular, patterns of spatial ecology and habitat use, between the breeding and wintering seasons. Overall, this raises the possibility that bird species and populations which might be considered as urban living may make use of resources from outside urban areas and that their behaviour and habitat use may change throughout the breeding stages. This potentially needs to be considered when designing management actions for any urban species.

It is hypothesized that habitats and foraging behaviours used should differ between urban and natural breeding gulls, mostly during the breeding season. Urban breeding gull populations are expected to use more anthropogenic food sources than natural breeding populations and are expected to spend less time foraging as these resources are more predictable. Diel rhythms of natural and urban breeding gull populations are expected to differ when managing resources due

to habitat choice and food availability, predicting that gulls can adjust their foraging strategies in conformity to human daily routines, at different habitats, contrasting in temporal patterns. Evaluating the role of human activities in shaping this species' behaviour is important for a better understanding of the adaptations of this generalist species to such activities, in order to manage the growth of urban gull populations, their conflicts with humans (Pais de Faria *et al.* 2021a) and comprehend the species patterns, predicting conservation efforts.

2. Material and Methods

2.1. Study sites

To understand foraging and spatial differences between established urban colonies and natural colonies of *Larus michahellis*, the study was conducted in two different locations in Portugal. Data collection was carried out in one urban colony – Porto – and one natural colony – Berlenga Island (**Fig. 1**). Data collection was conducted from 2016 to 2019, lasting through the species breeding and wintering seasons.

Porto (41°08'N, 8°36'W) is the second-largest city in Portugal and the most industrial and commercial developed area in the northern part of the country (Encyclopaedia Britannica 2021). With ca. 231 828 inhabitants (INE 2021), it is located along the Douro River estuary and has a major fishing harbour and many coastal areas nearby. Although the exact gull population in the city is still unknown, it is estimated that around 593 to 813 breeding pairs exist within the urban centre alone. In Portugal, around 1.250 to 1.727 breeding pairs are expected to nest on rooftops, tall buildings and urban surfaces, representing about 34% of the total breeding population in the country (Oliveira and Alonso 2022).

Berlenga Island belongs to the Berlengas archipelago (39°23'N, 9°36'W), a small archipelago located in the Northeast Atlantic at about 12 km from Cape Carvoeiro, next to the city of Peniche. The island had long been a site of interest due to the vast biodiversity of wildlife and unique biological value, and was integrated in 1997 into the Natura 2000 network and, in 2011, it was recognized by UNESCO as a World Biosphere Reserve (Santos *et al*. 2012). It is one of the most important breeding sites for seabirds in continental Portugal, among which some colonies of Cory´s shearwater (*Calonectris borealis*), Band-rumped Storm-petrel (*Hydrobates castro*) and the European shag (*Phalacrocorax aristotelis*) (Ramírez *et al*. 2008). Berlenga has one of the largest breeding colonies of yellow-legged gulls in Europe and the biggest colony in Portugal. It had reached 45000 individuals in the 1990s, but presently the number of breeding pairs is about 8500 (Morais *et al*. 1998, Vidal *et al*. 1998, Calado *et al*. 2018).
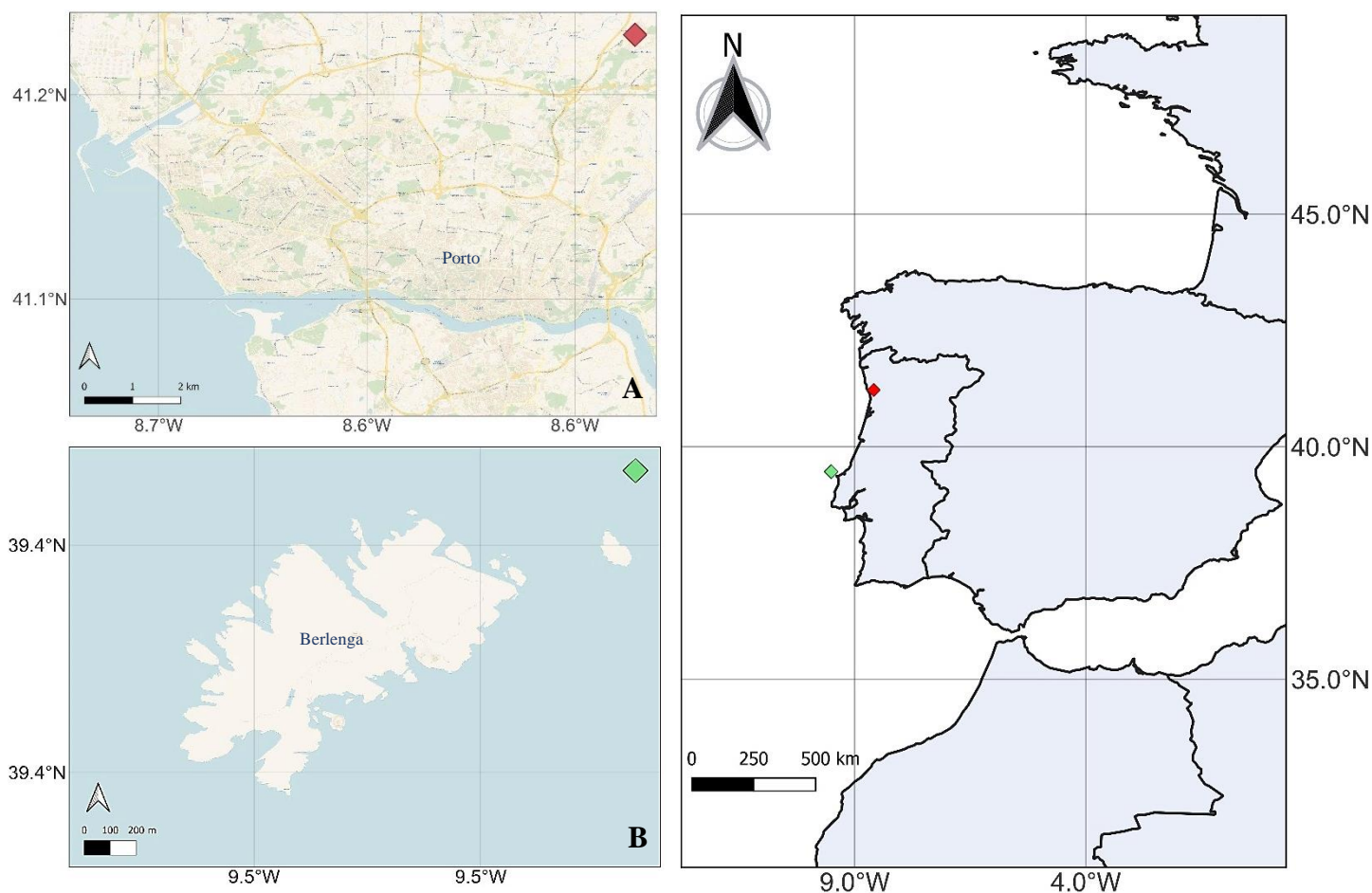
Figure 1. Study area depicting the location of the urban colony (city of Porto – A) and the natural colony (Berlenga Island – B).

2.2. Study species

The Yellow-legged gull, *Larus michahellis* (Naumann, 1840), is a coastal seabird belonging to the order Charadriiformes, family Laridae. It is among the largest species of gulls (*Larus* spp.), with the males often being slightly larger and heavier than females (Arizaga *et al*. 2008, Aguirre *et al*. 2009). Like most gull species it has a high adaptability and often colonises a wide arrange of habitats, where it can form large colonies, especially in the breeding season, only dispersing mainly if the habitat has no conditions or if food availability is scarce (Arizaga *et al*. 2010b, Van Toor *et al*. 2017). With *Larus michahellis*, the breeding season begins around April and extends until June. Females can produce two to three eggs and both parents take part in the incubation stage and the feeding of the chicks (Ramírez *et al*. 2010). The breeding population of this species in recent years has had an exponential growth, occupying different areas, notably coastal habitats. Individuals are often encountered in coastal lines, along with fishing ports, agricultural fields, urban sites, saltpans, and garbage dumps. In some places, this species may

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predate heavily on small birds (Ceia *et al.* 2014a, Isaksson *et al.* 2015, Martín-Vélez *et al.* 2022). In southern Europe, the yellow-legged gull can be found across the Iberian Peninsula, around the Mediterranean Sea and Macaronesia Islands. In Portugal it is found from the coastal line into the mainland, nesting in beaches, rocky shores, islands, islets and recently, in rooftops and isolated buildings. Like most gulls, it is known to be largely sedentary, as individuals often do not disperse over long distances or forage in the sea, but mostly in coastal and inland areas. In the Berlengas archipelago, the growing number of nesting pairs became a problem to other seabird colonies, preying on young chicks and destroying their nesting and breeding sites (Morais *et al.* 1998, Atlas 2008).

Yellow-legged gulls, like most gulls, are well adapted to pursue and predate marine prey, choosing between crustaceans, molluscs, and fish. But as generalists, they can capture a wide arrange of different food sources. New anthropogenic food sources determine the dynamics of some populations, influencing distribution patterns, and contributing to population growth (Ramos *et al.* 2009a). Yet even when human resources are more available, during the breeding season, birds in colonies near the coast still use marine resources (Sotillo *et al.* 2019, Spelt *et al.* 2019, Pais de Faria *et al.* 2021b). Gulls that are far away from the coast and are more dependent on the urban resources, use more landfills and other areas to feed during the breeding season (Duhem *et al.* 2005). The availability to different food sources and the adaptability to different foraging strategies makes the yellow-legged gull a good model species to analyse aspects of urban impact and the responses given at a population and individual level, helping with better management and conservation measures.

2.3. GPS tracking

To collect spatial movement data of yellow-legged gull individuals, 21 breeding adults were captured (13 from Porto; 8 from Berlenga) with a walking trap placed over the nest and equipped with a GPS transmitter (GPS-GSM Flyway-18 from Movetech Telemetry). Two individuals were discarded from further analysis (BER9 from Berlenga and 873 from Porto) as

they hold insufficient data (**Table 1**). The devices are high-precision GPS with inbuilt accelerometer and temperature sensors, which transmits the information through the 3G mobile network. Devices were attached to the birds' back with four Teflon strings tied with dental floss, so that it breaks several months later, and the birds do not stay with the device attached for life. The total mass of the devices weighed less than 3% of the adult mass of the individuals.

Table 1. Details of the GPS devices deployed on yellow-legged gulls in Berlenga and Porto (Mann-Whitney U test; p-value = 0.07, no significant differences are found in total duration of tracking period between colonies). Individuals marked as "BER" are from the colony in Berlenga Island and individuals with a number series are from the colony in Porto.

Individuals	Date of first GPS fix	Date of last GPS fix	Total Duration (days)
BER2	13 August 2016	12 October 2017	425
BER3	13 August 2016	23 November 2016	102
BER4	13 August 2016	30 May 2017	290
BER5	16 August 2016	23 May 2019	1010
BER6	13 August 2016	27 January 2019	897
BER7	13 August 2016	30 September 2017	413
BER8	13 August 2016	17 October 2016	65
848	20 May 2019	18 August 2019	90
871	20 May 2018	25 July 2018	66
874	20 May 2018	4 June 2019	380
875	20 May 2018	23 April 2019	338
877	20 May 2018	21 June 2018	32
1085	20 May 2019	9 September 2019	112
1089	20 May 2019	3 August 2019	75
1095	20 May 2019	10 October 2019	143
1097	20 May 2019	24 August 2019	96
1098	20 May 2019	11 July 2020	418
1101	20 May 2019	31 October 2019	164
1104	20 May 2019	22 June 2019	33

2.4. Data analysis

To correctly identify the gulls' habitat use, in both breeding and wintering season, and considering the gulls' resting and foraging behaviours, all GPS locations were accounted for in the study. The location of each nest/colony was obtained at the moment of capture for each individual, creating one sampling point during breeding, at the colony, and used to measure the distance to the sampling point by each GPS device. The proportion of habitat use was calculated, for each yellow-legged gull, as the number of GPS position points for a specific habitat divided by the total GPS points recorded during the entire tracking period. The GPS locations were overlapped with land cover information (CORINE Land Cover 2018; Copernicus Land

Monitoring Services 2022; <10m resolution) to assess habitat use. Habitat classification was determined by grouping CORINE Land Cover habitat classification into 9 categories: urban area, industrial sites, sea environment, natural habitat, water courses, beach, agricultural fields, fishing ports and garbage dumps (**Table 2**). The spatial analysis was performed with excel and QGIS 3.24.3.

The nonparametric fixed kernel density (FKD) estimator was used to visualise density of position points in the area of habitats where core foraging locations may occur. Kernel densities were examined under the *adehabitatHR* R package (Calenge 2006) by generating Kernel Utilization Distribution (Kernel UD) estimates within the R environment (R 4.1.1). Kernel UD contour areas of 50%, defined as core areas, and 95%, defined as foraging areas, were considered to represent the home range (HR) of each individual, using functions "kernelUD", "getverticeshr" and "getvolumeUD" of the package. The percentage of within-colony overlap in core areas (50% kernel UDs) and foraging areas (95% kernel UDs) between different breeding stages was computed to identify spatial segregation among individuals with the "kerneloverlap" function and HR method of the *adehabitatHR* package. A kernel UD overlap index (UDOI) was then estimated and compared between breeding and wintering seasons within each colony using a Welch's two sample t-test to test the null hypothesis that there were differences in space use and distribution among individuals. If the null hypothesis is true, overlap between seasons 50% and 95% kernel UDs should differ significantly (p-value < 0.05).

To investigate habitat specialisation of individual gulls, the proportional similarity index (PSi) was used, which is a measure to quantify the average pairwise overlap of the niche distribution of individuals and the population in relation with resources utilization (Schoener 1968, Bolnick *et al*. 2002). PSi measures of individual specialization are given a value ranging from 0, which indicates an absolute specialist individual in habitat use, and 1, indicating an absolute generalist. Average PSi among individuals was calculated to determine the prevalence of individual specialization in habitat use within the population (IS). PSi was calculated for each individual, differing in colony type – urban and natural – and in reproductive seasons – breeding and wintering. All analysis were performed with the *RInSp* R package (Zaccarelli *et al*. 2013).

Table 2. Corine land cover (CLC) corresponding to habitat types/categories analysed.

Habitat categories	Correspondent CLC categories
Urban area	Continuous/Discontinuous urban fabric Road network Green urban area Sports and Leisure facilities
Industrial sites	Industrial or commercial units Mineral extraction sites Construction sites
Sea	Sea and Ocean
Natural Habitat	Broad-leaved forest Coniferous forest Mixed forest Natural grassland Heathland Transitional woodland shrub
Watercourses	Inland marshes Salines Intertidal flats Watercourses Water bodies Estuaries
Beach	Beaches, dunes and sand plains Bare rocks
Agricultural fields	Land principally occupied by agriculture Non-irrigated arable land Permanently irrigated land Fruit trees and berry plantations Pastures Annual crops associated with permanent crops Complex cultivation patterns Agro-forestry areas
Fishing Port	Port areas
Garbage dump	Dump sites

To further understand individual habitat selection, *phuassess* R package and means of permutation-based combination of sign tests (Fattorini *et al.* 2017) were used under R 4.1.1. The calculation of the overall p-value determined the proportional habitat use within all habitat classifications. The tests were performed separated for each colony and, within each colony, separated between breeding and wintering seasons. The proportion of each habitat classification used was calculated to specify if the individuals were using each habitat in proportion to its availability, if it was preferred or avoided.

All tracking data were analysed according to each GPS position and distance to colony allowing the separation of each data set into individual foraging trips, defined from the time the birds departed from the colony until they returned. The filtered data were used to characterise foraging behaviour for individual gulls, classifying each GPS position point as a behavioural state, applying the Expectation-Maximization binary Clustering (EMbC), implemented in the *EMbC* R package (Garriga *et al*. 2016). *EMbC* algorithms use velocity and turning angle to differentiate tracking data into four behavioural states: foraging behaviour (low velocity, high tortuosity), resting behaviour (low velocity, low tortuosity), travelling (high velocity, low tortuosity) and relocating (high velocity, high tortuosity). High velocity and high tortuosity behaviour, when comprised between foraging and travelling states, were considered travelling behaviour to better separate true foraging activities and to facilitate statistical analysis.

Variables of foraging activity for individual trips were defined, for each gull, and were composed by trip duration (days), time spent foraging (%), time spent resting (%), time spent travelling (%), geographic position at maximum distance from the colony (latitude and longitude) and maximum distance to colony (km). Variables were calculated for each individual gull and separated between breeding and wintering seasons. To compare foraging trip measurements between colonies and between breeding and wintering seasons, generalised linear mixed models (GLMMs) were built using the *glmmADMB* package (Skaug *et al*. 2018) and *lme4* package (Bates *et al*. 2014). Variables of foraging activity were log-transformed to obtain normality and homoscedasticity and set as response variables. Colony type, seasons (breeding vs wintering) and the interaction between colony type and seasons were set as the explanatory variables and bird identity as a random effect to control for pseudo-replication and account for multiple trips per individual. Results are presented as mean ± standard deviation and were considered statistically significant when $p < 0.05$. All statistical analyses were conducted within the R environment v. 4.1.1.

To illustrate the gull's daily activity patterns in each habitat considered, a 24-hour time-series waveform analysis was performed for every tracked individual, calculated with the total amount of GPS positions in each habitat per hour, in relation with the entire tracking period.

Time-series analysis was performed at an hourly basis for each habitat and separated between colonies. Temporal use over a 24-h period corresponds to average of time frequencies accounted in each hour. To distinguish diel rhythms and the effect of weekdays based on human activity in each habitat, the analysis was performed with data assembled from workdays (Monday to Friday) and weekends (Saturday and Sunday) separately. Waveforms from the two variables were plotted simultaneously in order to observe differences in the activity patterns among habitats and between colonies. All statistical analyses were conducted within the R environment v. 4.1.1.

3. Results

3.1. Habitat selection, specialization and home range of gulls from urban and natural colonies

Based on the filtered GPS positions, yellow-legged gull individuals from both the urban and the natural colony selected a broad range of habitats and used them in different proportions throughout their breeding and wintering seasons (**Figs. 2** and **3**). Tracked gulls from the urban colony used naturally urban areas as the main habitat (81% for the breeding season and 68% for the wintering season; average percentage of locations), only followed to a lesser extent by industrial sites (4% in both seasons) and sea and ocean environment (4% at breeding seasons and 8% at wintering seasons; **Fig. 2**). Although some variation in habitat use occurred between seasons, all other habitats accounted showed <5% total proportion used, the lowest being Beach and Dump, accounting for <1% of the overall locations. Individuals 877, 1097 and 1104 were only tracked during their breeding season.

Figure 2. Proportion of habitat use by yellow-legged gulls from Porto, tracked during the breeding and wintering seasons. Each individual is represented by a vertical bar, and different colours represent different habitats. Also shown is the average proportion of habitat use for all individuals (far left bar) and the Individual Specialization Index (PSi; black line with dots).

Tracked gulls from the natural colony differed in their habitat use, displaying a more predominant use of natural environments, exhibiting an average of 65% of GPS locations in natural habitats during the breeding season and 21% in the wintering season. Relative to the urban colony, birds from the natural colony also displayed a more predominant use of port areas, with 17% of locations during the breeding season and 26% during the wintering season. Urban areas were selected to a greater extent during the wintering season, with an average of 35% of total locations in comparison to 9% during the breeding season. The lowest accounted habitats selected were Dump and Watercourses, accounting for <1% of the overall locations (**Fig. 3**). Individuals BER3 and BER8 were only tracked during the wintering season.
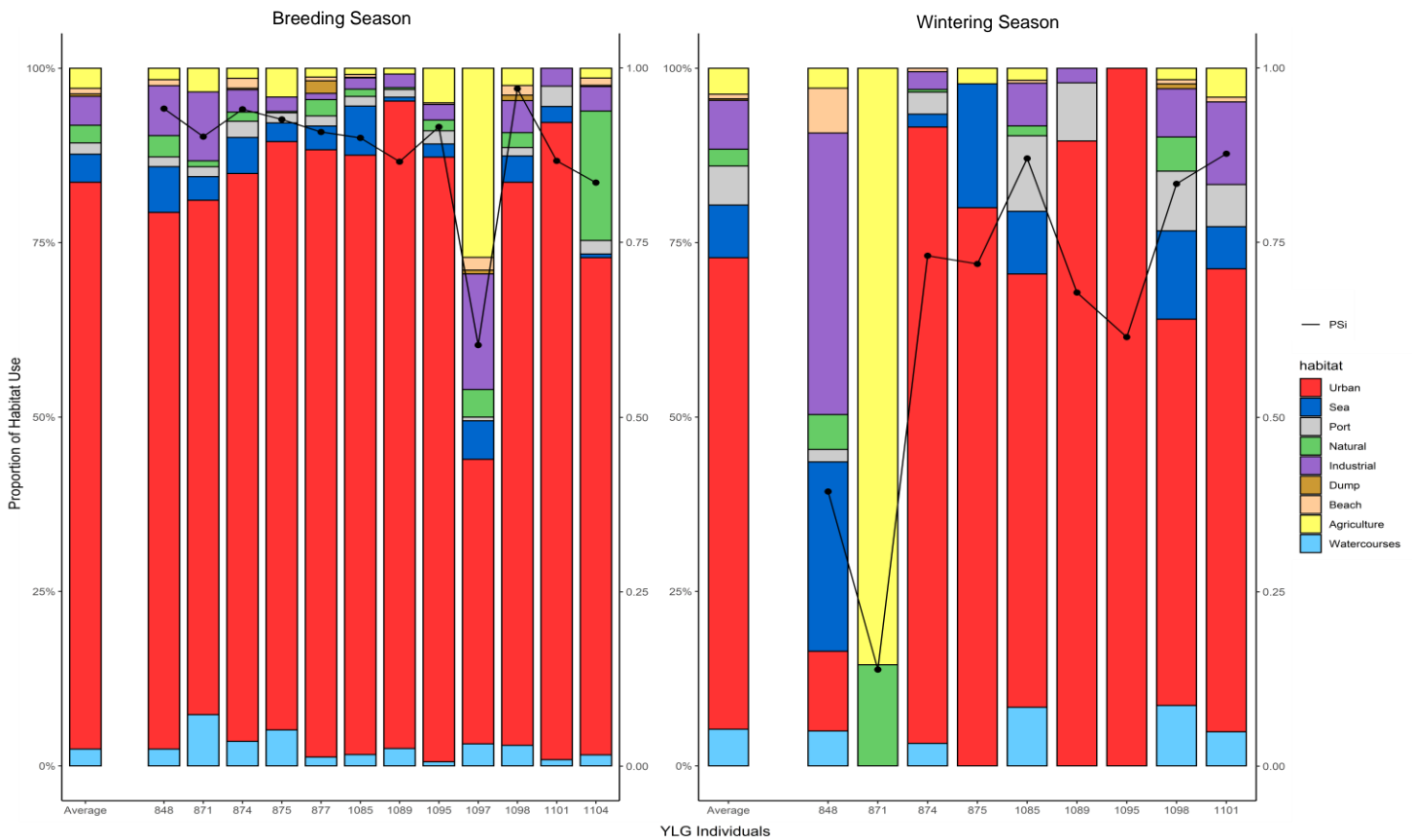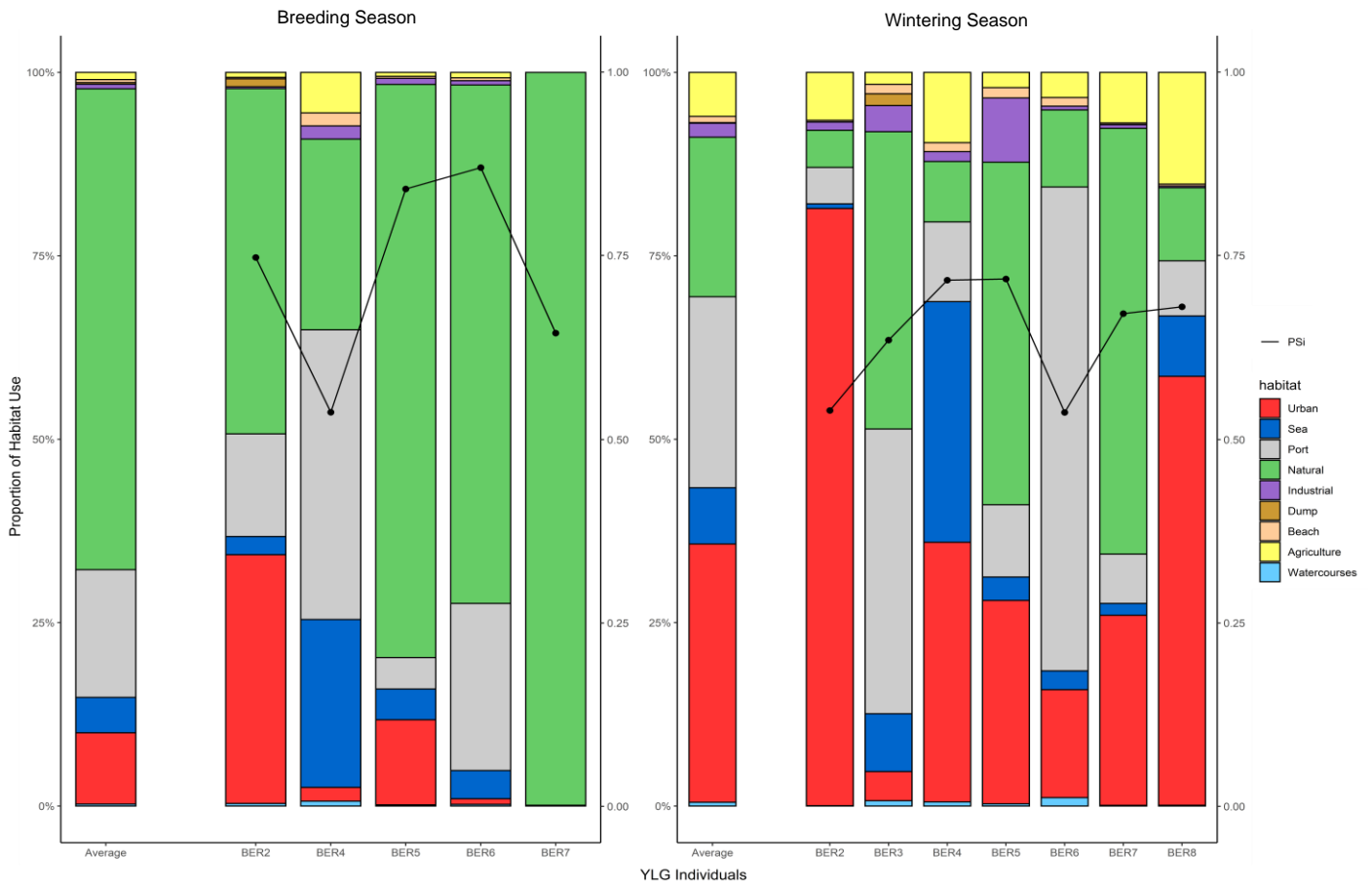

Figure 3. Proportion of habitat use by yellow-legged gulls from Berlenga Island, tracked during the breeding and wintering seasons. Each individual is represented by a vertical bar and different colours represent different habitats. Also shown is the average proportion of habitat use for all individuals (far left bar) and the Individual Specialization Index (PSi; black line with dots).

At the individual level, PSi values varied among different colony types. Gulls at the urban colony had PSi values ranging from 0.60 to 0.94 for the breeding season, with the most specialized individuals (low PSi values) exploiting more natural, agricultural and industrial sites when compared to other individuals. During the wintering season, values of PSi had a broader range, between 0.13 and 0.87, with individuals exploiting some habitats almost exclusively (individual 871 with positions only in Natural and Agricultural habitats and individual 1095 with positions only for Urban habitats) and other gulls with greater tendency to use Industrial and Sea areas (e.g. individual 848). More generalist individuals (higher PSi values) used a higher diversity of habitats (**Fig. 2**). Monte-Carlo analysis of population niche variation indicated that the overall Individual Specialization was low (0.88 for the breeding season and 0.65 for the wintering season) but that the prevalence of more specialized individuals (with lower PSi values) in the population was significant, within both seasons (p < 0.001). The prevalence to Individual Specialization in the urban colony was higher for the wintering season, showing the lower PSi values.

Individuals from the natural colony had PSi values ranging from 0.53 to 0.87 for the breeding season, with the most specialized individuals (low PSi values) mostly using Port areas and Sea environments (e.g. individual BER4) and almost exclusively Natural sites (e.g. individual BER7). For the wintering season, the PSi values ranged between 0.53 and 0.71, with more specialized individuals exhibiting a greater use of Urban and Port areas, in contrast with the overall habitat use of the population (**Fig. 3**). Individual Specialization was low overall (0.73 for the breeding season and 0.64 for the wintering season), as shown through Monte-Carlo analysis of population niche variation, but the prevalence of more specialized individuals (lower PSi value) was significant throughout both seasons (p < 0.001). The prevalence to Individual Specialization in the natural colony was higher for the wintering season, showing the lower registered PSi values.

Home range of individual gulls from the urban and natural colonies varied among seasons, mostly at foraging areas (95% kernel UDs). For the urban colony, core areas (50% kernel UDs) did not differ significantly between the breeding and wintering seasons (**Table 3**), with the selection of core foraging habitat being focused on the city of Porto, confirming the overall

predisposition to the use of habitat in urban areas and around the colony. Foraging areas (95% kernel UDs) contrasted in the use of certain locations around the city (**Fig. 4**). In the breeding season, gulls foraged mainly around the city, spreading to Matosinhos and making use of the nearby fishing harbour (Porto de Leixões), also dispersing to the south, making use of coastal areas, and north, using a great industrial site with a refuse dump area accolated (RIMA – Resíduos Industriais e Meio Ambiente; **Fig. 4A**). During the wintering season, foraging areas were similar, however gulls used more refused dumps (Aterro Sanitário de Canedo and Aterro de Inertes da Louseira da Boneca) south of the colony and extended further out, reaching an industrial site and accolated refuse area (Resulima), all the way to Spain, in a small coastal town (Carnota, Galiza), north of the colony (**Fig. 4B**).
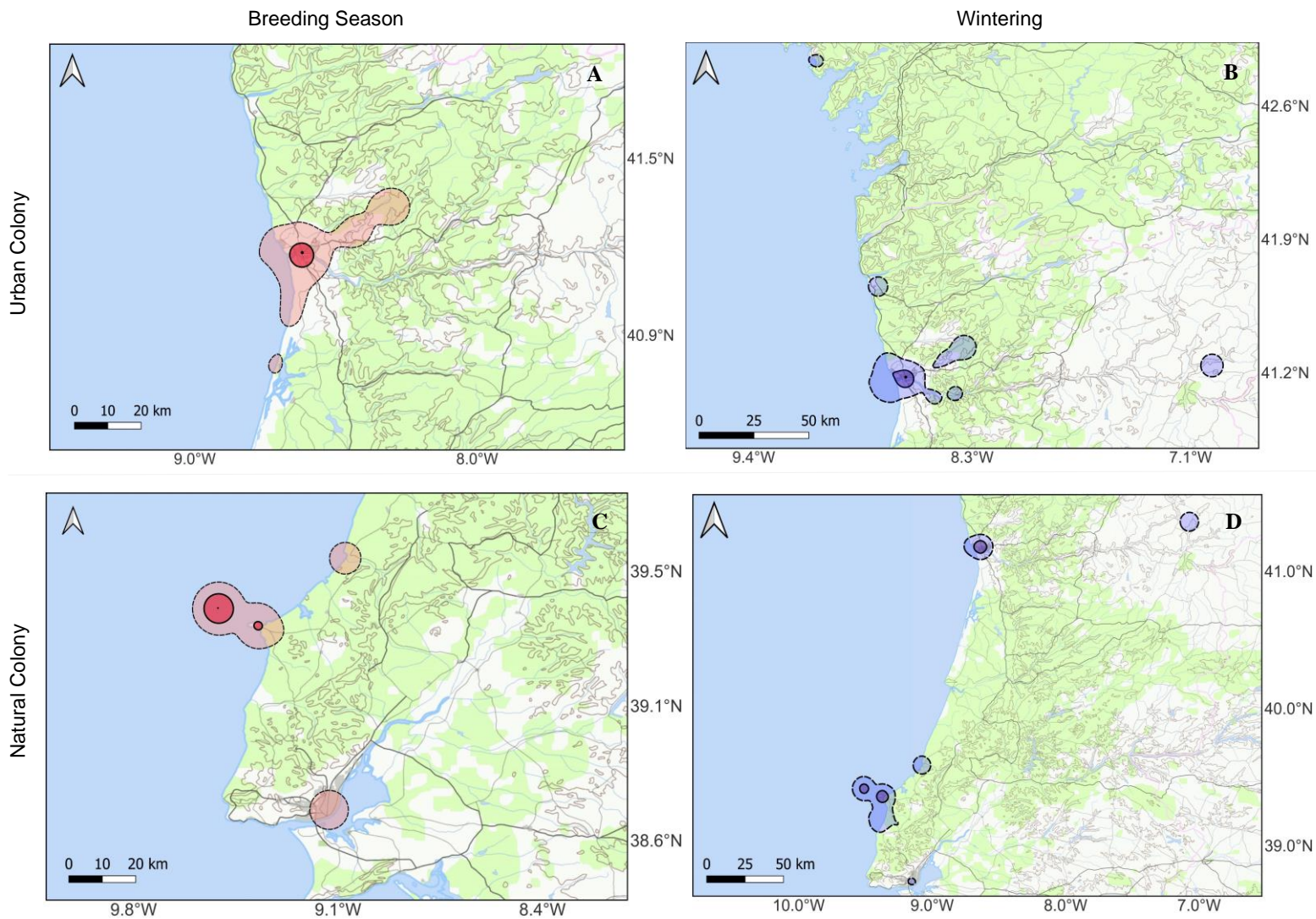
Figure 4. 95% (dashed lines and lighter polygons) and 50% (filled lines and darker polygons) Kernel Utilization Distributions (UD) of yellow-legged gulls from Porto (urban colony – A and B) and Berlenga Island (natural colony – C and D) during the breeding and wintering seasons. Single dot indicates the colony's location.

Core areas (50% kernel UDs) within the natural colony changed significantly between the breeding and wintering seasons (**Table 3**), with gulls displaying a greater use of habitats around the colony, in Berlenga, and in the nearby city of Peniche, but dispersing in the wintering season to the city of Porto. The core area was also larger around Berlenga in the breeding season than in Peniche, and the opposite (Peniche having the larger core area) occurred during the wintering season (**Figs. 4C** and **4D**). Foraging areas were not similar, in terms of overall range, between seasons, but were mostly located around the core areas. In the breeding season, gulls from Berlenga used the habitat surrounding the island and the city of Peniche, extending to a fishing village north of the colony (Nazaré) and south to Lisbon, in the urban centre (**Fig. 4C**). In the wintering season, foraging areas around Peniche were larger, with gulls exploring and using more the surrounding sea and nearby coastal areas, contrasting with the areas used in the Porto metropolitan area and further east on agricultural fields (**Fig. 4D**).

Table 3. Percentage of within-colony overlap between seasons for core areas (50% kernel UDs) and foraging areas (95% kernel UDs). "Colony" represents the comparison between seasons (breeding and wintering) within the same colony, for all individuals. P-value represents results of Welsh's two sample t-test to identify significant differences on kernel UD overlaps between seasons. Significant differences shown in bold.

Kernel UD	Colony	Overlap (%)	p-value
50%	Berlenga	33.8	**0.04**
	Porto	83.2	0.32
95%	Berlenga	53.3	0.13
	Porto	63.2	0.33

According to the availability of habitats (phuassess analysis) along the foraging range of gulls from the two colonies, individuals from the urban colony did not use habitats in proportion to its availability (p-value overall < 0.05), for both breeding and wintering seasons, whilst for the natural colony, individuals used the surrounding habitats according to their availability (p-value overall > 0.05), for both seasons (**Table 4**).

Table 4. Phuassess (p-value overall < 0.05) simplified ranking matrix for yellow-legged gull individuals (n=19) comparing proportions of habitats used within the available habitat (home-range total extent). Values represent proportion of habitat used for foraging overall (phu.F), variable between 0 and 1, paired with the habitat preference acquired. Significant values are in bold. Prop=Proportionally Used.

Colony Type/ Season	Habitat Classes									*p-value* (<0,05)
	Urban	Sea	Port	Natural	Industrial	Dump	Agriculture	Beach	Watercourse	
Urban / Wintering	Preferred (0.889)	Avoided (0.000)	Prop (0.667)	Avoided (0.003)	Prop (0.556)	Avoided (0.111)	Avoided (0.111)	Prop (0.556)	Prop (0.556)	**0.023**
Urban / Breeding	Preferred (1.000)	Avoided (0.000)	Preferred (1.000)	Avoided (0.083)	Preferred (1.000)	Prop (0.500)	Avoided (0.083)	Prop (0.667)	Preferred (0.833)	**0.002**
Natural / Wintering	Preferred (1.000)	Avoided (0.000)	Preferred (1.000)	Prop (0.428)	Prop (0.571)	Prop (0.428)	Avoided (0.000)	Preferred (1.000)	Avoided (0.000)	0.062
Natural / Breeding	Prop (0.667)	Avoided (0.000)	Prop (0.833)	Preferred (1.000)	Prop (0.500)	Prop (0.167)	Avoided (0.000)	Prop (0.667)	Prop (0.667)	0.218

Gulls from the urban colony had Urban habitats significantly preferred in both seasons and Sea habitats significantly avoided. In the wintering season, almost all habitats were used in proportion to their availability, changing when gulls reached their breeding season, where Port, Industrial and Watercourse habitats were significantly preferred. The disproportional use of different habitats in relation to its availability demonstrates an overall preference for certain habitats within the home range of all individuals tracked in the urban colony.

Individual gulls from the natural colony had Natural, Beach and Port habitats with a higher preference in habitat use, in comparison with gulls from the urban colony. During the breeding season, almost all habitats were used in proportion to their availability, with Natural habitats significantly preferred. Port and Urban habitats were preferred in the wintering season, alongside coastal areas (Beach). Both seasons had Sea habitats significantly avoided.

3.2. Foraging strategies of gulls from urban and natural colonies

Gulls from both colonies, urban and natural, had distinct foraging strategies most evident during the wintering season, when the dispersal of individuals exhibited a large discrepancy between the two colonies (**Fig. 5**). Gulls from the urban colony limited most of their foraging

trips to the colony surroundings and the city of Porto in both seasons, with only one individual (848) dispersing farther out into Spain, in the wintering season, where it spent most time foraging at sea and neighbouring islets (**Figs. 5A** and **5B**). Gulls from the Berlenga colony showed the most distinct foraging behaviour between seasons: when breeding, the foraging trips were mostly in the area around the colony (the longest trips were from two individuals foraging in the city of Lisbon) but during the wintering season, all individuals dispersed along the coast of Portugal, from Viana do Castelo in the north to Portimão in the south (**Fig. 5D**), with the most predominant route of foraging trips occurring between Berlenga Island and the city of Porto.
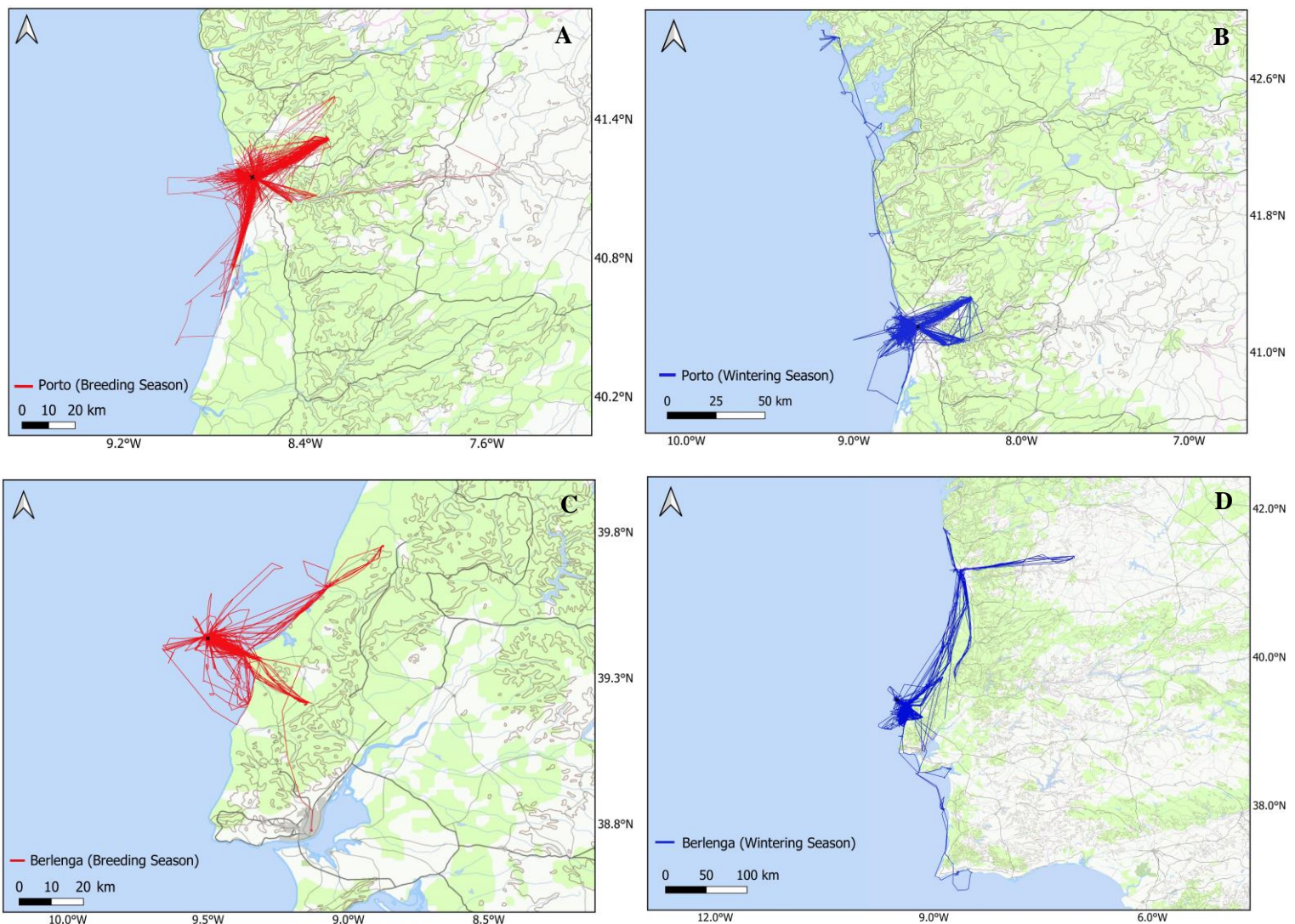
Figure 5. Foraging trips derived from GPS locations of yellow-legged gulls from Porto (urban colony, n=12, A and B) and Berlenga Island (natural colony, n=7, C and D) differenciated between breeding (red tracks) and wintering (blue tracks) seasons. Colors represent all foraging trips from every indidivudal tracked in each colony. Breeding colonies are marked with a dot.

Foraging activity parameters obtained from the 12 individuals of the Porto' urban colony showed a mean foraging trip duration of 1.4 days and a maximum distance to colony of 17.1 km, with some variation among tracked individuals (**Table 5**). The most analogous foraging parameters were maximum latitude and longitude, were the average results show that gulls did not extend their trips further out from the city centre and around the colony. Individuals also spent most of their time foraging - during each trip - and less time resting and travelling (**Table 5**).

Table 5. Trip characteristic (mean ± SD) derived from GPS transmitters tracking yellow-legged gulls breeding in Porto, urban colony.

	Larus michahellis (Porto)												
	848	871	874	875	877	1085	1089	1095	1097	1098	1101	1104	**Total**
Trip duration (days)	0.6 ± 0.3	1.2 ± 0.6	3.9 ± 3.4	3.5 ± 3.0	1.1 ± 0.8	0.9 ± 0.7	0.7 ± 0.6	0.5 ± 0.4	1.2 ± 0.9	1.4 ± 1.3	1.3 ± 1.1	0.8 ± 0.6	1.4 ± 1.1
Max. distance (km)	17.1 ± 12.6	4.6 ± 4.9	22.9 ± 15.1	48.4 ± 17.3	15.1 ± 11.6	16.1 ± 10.8	8.1 ± 10.3	11.7 ± 7.7	19.9 ± 10.1	19.2 ± 11.7	8.9 ± 4.5	12.8 ± 11.9	17.1 ± 11.2
Max. Latitude	41.2 ± 0.2	41.2 ± 0.1	41.2 ± 0.1	41.2 ± 0.1	41.1 ± 0.1	41.2 ± 0.1	41.1 ± 0.05	41.2 ± 0.05	41.2 ± 0.1	41.2 ± 0.1	41.1 ± 0.01	41.2 ± 0.1	41.2 ± 0.1
Max. Longitude	-8.4 ± 0.1	-7.9 ± 0.7	-8.4 ± 0.1	-8.4 ± 0.2	-8.5 ± 0.1	-8.6 ± 0.1	-8.5 ± 0.1	-8.5 ± 0.1	-8.4 ± 0.1	-8.48 ± 0.1	-8.6 ± 0.01	-8.5 ± 0.1	-8.4 ± 0.2
Prop. time foraging	0.5 ± 0.1	0.6 ± 0.3	0.3 ± 0.1	0.3 ± 0.2	0.7 ± 0.1	0.6 ± 0.2	0.7 ± 0.2	0.4 ± 0.2	0.4 ± 0.1	0.7 ± 0.2	0.7 ± 0.2	0.5 ± 0.1	0.5 ± 0.2
Prop. time resting	0.5 ± 0.2	0.3 ± 0.2	0.5 ± 0.1	0.7 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	0.4 ± 0.2	0.4 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.2	0.3 ± 0.1
Prop. time travelling	0.1 ± 0.1	0.1 ± 0.2	0.2 ± 0.1	0.03 ± 0.05	0.04 ± 0.05	0.2 ± 0.1	0.03 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1

In Berlenga Island, foraging parameters from the 7 tracked yellow-legged gulls showed, on average, longer trip durations (2.4 days) and a larger distance travelled from the colony, in comparison with individuals from Porto (**Table 6**). However, individuals from Berlenga spent less time foraging in comparison with the urban colony and more time resting. Maximum latitude and maximum longitude did not vary greatly in average among individuals from the natural colony, showing a higher concentration of foraging trips around the colony.

Table 6. Trip characteristic (mean ± SD) derived from GPS transmitters tracking yellow-legged gulls breeding in Berlenga Island, natural colony.

	Larus michahellis (Berlenga)							
	BER2	BER3	BER4	BER5	BER6	BER7	BER8	**Total**
Trip duration (days)	2.4 ± 5.1	1.9 ± 2.3	1.4 ± 1.2	2,8 ± 1.5	2.0 ± 2.5	4.4 ± 5.1	1.7 ± 1.6	2.4 ± 2.8
Max. distance (km)	32.3 ± 49.1	24.2 ± 32.6	23.3 ± 35.4	12.4 ± 21.4	20.6 ± 28.8	32.7 ± 52.2	56.1 ± 73.1	28.8 ± 41.8
Max. Latitude	39.6 ± 0.6	39.4 ± 0.4	39.4 ± 0.3	39.4 ± 0.2	39.5 ± 0.4	39.5 ± 0.5	39.9 ± 0.8	39.5 ± 0.5
Max. Longitude	-9.2 ± 0.4	-9.3 ± 0.2	-9.3 ± 0.2	-9.3 ± 0.2	-9.3 ± 0.2	-9.2 ± 0.4	-9.1 ± 0.6	-9.2 ± 0.3
Prop. time foraging	0.3 ± 0.1	0.8 ± 0.1	0.5 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.1
Prop. time resting	0.6 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.2	0.6 ± 0.1	0.5 ± 0.1
Prop. time travelling	0.1 ± 0.1	0.03 ± 0.1	0.02 ± 0.1	0.03 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1

In general, yellow-legged gulls from the natural colony performed significantly longer trips, in both space and time, but spend less time foraging when compared with yellow-legged gulls from the urban colony (**Table 7**). When comparing seasons, individuals from both colonies had longer trips (in distance and duration) during the wintering season (**Table 7**). In terms of foraging behaviour, yellow-legged gulls from Porto also spent more time travelling than individuals from Berlenga, with larger differences for the wintering season. The percentage of foraging time and resting time were significantly different among colonies, with individuals from Porto spending more time foraging within their excursions and individuals from Berlenga resting more (**Tables 6** and **7**).

Maximum latitude and longitude were significantly different between colonies and between seasons, with gulls from the urban colony having higher values in geographical positioning, demonstrating the prevalence of foraging trips within foraging range (**Tables 5**, **6** and **7**).

Table 7. Generalized Linear Mixed Models (GLMMs) testing the effect of the interaction between colony type (Urban and Natural) and season (Breeding and Wintering) on foraging trip characteristics. Individuals were used as a random effect to avoid pseudo-replication. Significant values are in bold. The main effect was verified with a Post-Hoc multiple comparison Tukey´s test.

Foraging trip characteristics	*Variables*	$\beta \pm SE$	*p*	*Main effect*
Trip duration (days)	Intercept	0.73 ± 0.02	**< 0.001**	-
	Colony type	-0.02 ± 0.03	0.418	-
	Season	0.09 ± 0.01	**< 0.001**	Wintering > Breeding
	Colony type*Season	-0.08 ± 0.02	**< 0.001**	Natural*Wintering > others
Maximum distance to colony	Intercept	1.63 ± 0.03	**< 0.001**	-
	Colony type	-0.03 ± 0.04	0.394	-
	Season	0.03 ± 0.01	**0.018**	Wintering > Breeding
	Colony type*Season	-0.04 ± 0.01	**0.022**	Natural*Wintering > others
Maximum Latitude	Intercept	39.3 ± 0.04	**< 0.001**	-
	Colony type	1.82 ± 0.05	**< 0.001**	Urban > Natural
	Season	0.23 ± 0.02	**< 0.001**	Wintering > Breeding
	Colony type*Season	-0.20 ± 0.03	**< 0.001**	Urban*Wintering > others
Maximum Longitude	Intercept	$-0,19 \pm 0.01$	**< 0.001**	-
	Colony type	$0,37 \pm 0.01$	**< 0.001**	Urban > Natural
	Season	$0,07 \pm 0.01$	**< 0.001**	Wintering > Breeding
	Colony type*Season	$-0,05 \pm 0.01$	**0.018**	Urban*Wintering > others
Time foraging (%)	Intercept	-1.92 ± 0.14	**< 0.001**	-
	Colony type	0.36 ± 0.17	**0.035**	Urban > Natural
	Season	0.18 ± 0.18	0.311	-
	Colony type*Season	0.01 ± 0.24	0.964	-
Time resting (%)	Intercept	-1.56 ± 0.12	**< 0.001**	-
	Colony type	-0.63 ± 0.18	**< 0.001**	Natural > Urban
	Season	-0.11 ± 0.16	0.507	-
	Colony type*Season	-0.57 ± 0.33	0.087	-
Time travelling (%)	Intercept	-2.65 ± 0.24	**< 0.001**	-
	Colony type	0.63 ± 0.29	**0.035**	Urban > Natural
	Season	-0.64 ± 0.32	0.052	-
	Colony type*Season	0.77 ± 0.39	**0.046**	Urban*Wintering > others

3.3. Diel rhythms and feeding behaviour of gulls from urban and natural colonies

Time-series analysis showed an overall diurnal activity pattern, mainly around 4:00h and 18:00h in most habitats, with some exceptions being most noticeable when comparing both colonies (**Figs. 6** and **7**). For the majority of habitats, where waveforms have a major diurnal activity, most peaks of proportional foraging locations occurred in the morning and evening hours, with drops in activity around noon and night-time. However, peaks varied between habitats and between colonies, displaying a different activity pattern and use of habitats between individuals from Porto and Berlenga (**Figs. 6** and **7**). Activity rhythms from workdays and weekends did not differ greatly in most habitats for the two colonies, varying slightly in the peaks of foraging locations. However some habitats displayed, compared between seasons (breeding and wintering), a more distinct daily activity patterns in both weekends and workdays and among colonies (**Figs. A1** to **A4**, **Appendix**).

3.3.1 Daily activity patterns of gulls from Porto

Individuals from Porto did not present a great overall discrepancy between periods (workdays and weekends), as indicated by the different habitats evaluated, based on the specific activity patterns of all tracked gulls from the colony, with the exception of Port areas and Agriculture sites, where peaks of activity were distinct (**Fig. 6**). Night-time activity was greater in weekends in Port habitats, with more activity shown in early hours (around 2:00h to 4:00h) in contrast to workdays where most activity occurred in the morning. Agriculture sites had a distinct peak of daily activity in the afternoon, on weekends, in comparison with workdays. Night-time activity was also more distinct in Sea and Watercourse habitats, where peak activity patterns occurred in early hours (2:00h to 4:00h) and at noon/night (20:00h to 22:00h). Both Sea and Watercourse habitats show a similar activity pattern between them, among all individuals (**Fig. 6**).

Figure 6. Time-series analysis of diel activity patterns in each habitat, used by yellow-legged gulls tracked during both breeding and wintering seasons in the urban colony (Porto), in relation to the type of day – workdays and weekends. Dark grey shading indicates night-time. The average number of GPS locations is shown.

In contrast, morning/evening activity was more predominant in Beach, Industrial and Natural habitats, with almost no activity at night and only slight differences between periods, where Industrial and Beach activity pattern peaks were higher in weekends than workdays, but at the same hours, within each habitat (around 12:00h in Industrial habitats and 6:00h to 8:00h in Beach habitats). The most unique patterns of daily activity occurred in Urban areas and Dump sites. In comparison with the other habitats, Urban habitats had almost no differences in daily activity between weekends and workdays, presenting a very uniform pattern, shown to be similar throughout the 24h daily cycle (**Fig. 6**). With Dump sites, almost all activity was presented in the afternoon, between 18:00h and 20:00h, mainly displayed in workdays (not all individuals presented weekend activity in Dump sites – see **Figs. A1** and **A2**, **Appendix**).

3.3.2 Daily activity patterns of gulls from Berlenga

Daily activity of yellow-legged gulls from Berlenga were similar when comparing periods (weekend and workday) in each habitat, but were distinct in activity patterns among them, with greater differences found for Industrial sites and Beach habitats. Overall daily activity patterns were essentially diurnal, where morning activity was most prevalent for habitats such as Urban, Agriculture, Sea, Watercourses and Port (**Fig. 7**). Sea and Watercourse were the most similar habitats, where activity patterns where almost identical between them, for both weekends and workdays. Port areas also follow a similar pattern with both Sea and Watercourse habitats, with peaks activity matching the same hours, being only more uniform towards afternoon/night hours (**Fig. 7**).
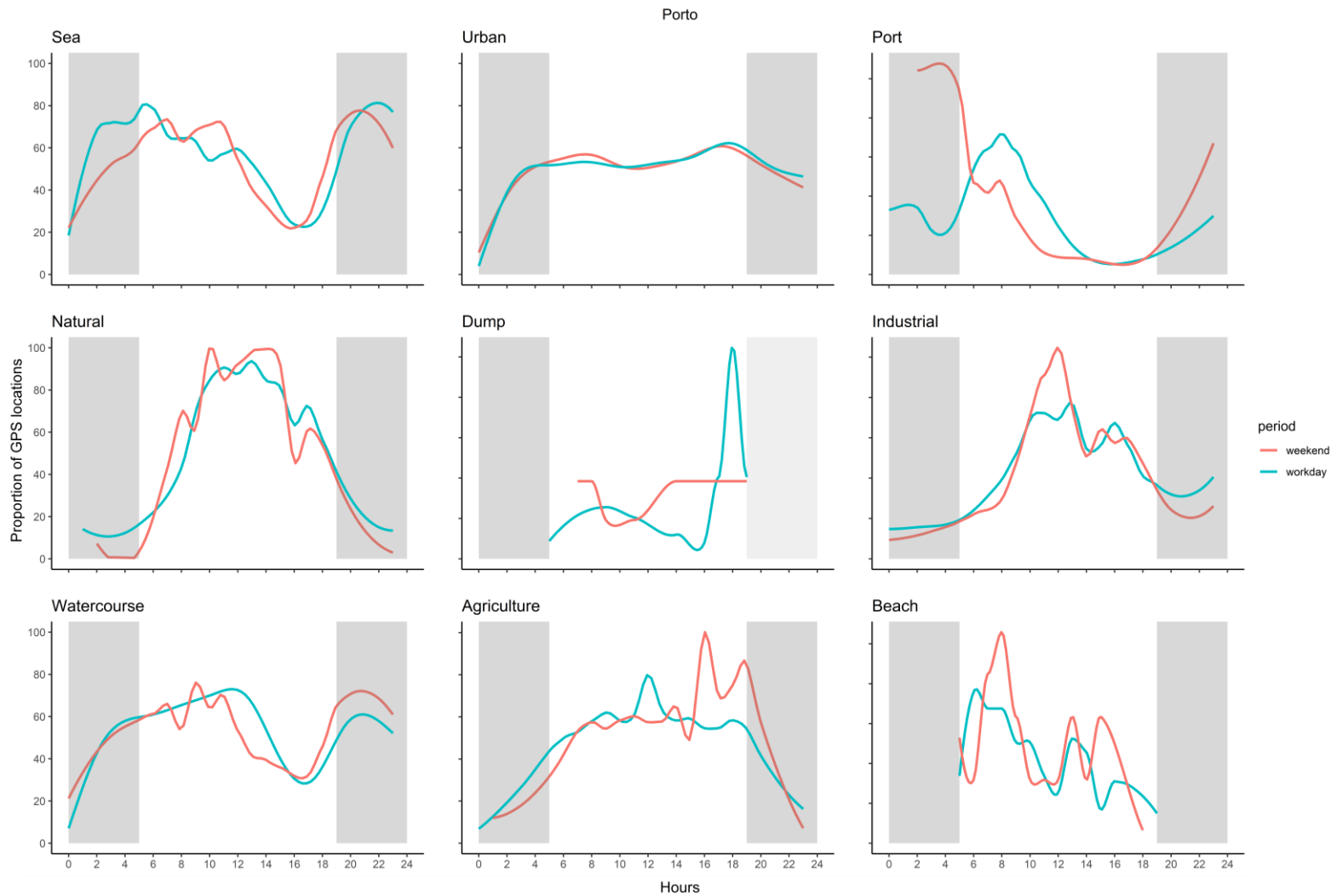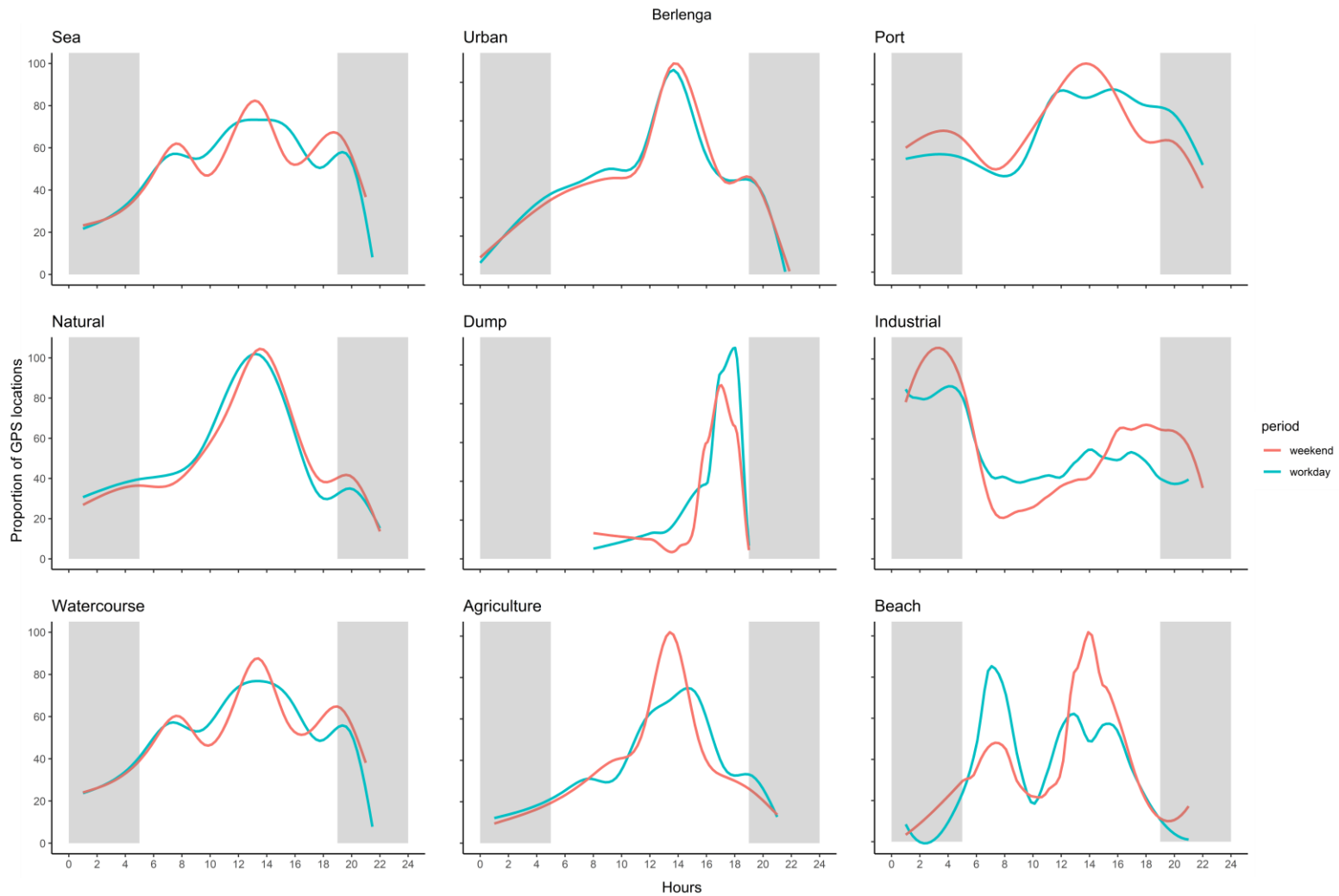

Figure 7. Time-series analysis of diel activity patterns in each habitat, used by yellow-legged gulls tracked during both breeding and wintering seasons in the natural colony (Berlenga Island), in relation to the type of day – workdays and weekends. Dark grey shading indicates night-time. The average number of GPS locations is shown.

The most contrasting habitats, in terms of activity patterns, were Industrial, Beach and Dump habitats. Gulls visited industrial sites at every hour of the day but had their activity peak at night and early morning hours, around 2:00h and 4:00h, in both weekends and workdays, then strongly decreased the use of this habitat during morning, followed by a slight increase in the afternoon (**Fig. 7**). Dump sites presented activity patterns almost exclusively in the afternoon, peaking between 18:00h and 20:00h, with only some GPS locations being accounted earlier in the morning. Beach habitats had the most divergent patterns between workdays and weekends, where peak activity, in workdays, happened in the morning (6:00h to 10:00h) and in weekends, in the afternoon (12:00h to 18:00h; **Fig. 7**).

4. Discussion

Our study examined the spatial ecology of yellow-legged gulls to compare possible differences in habitat use and foraging behaviours between individuals from two distinct colonies, urban and natural, by tracking 19 gulls with GPS-GSM transmitters over the course of their breeding and wintering seasons. It was also examined how their feeding behaviour is affected by periods of contrasting human activity – workdays and weekend – demonstrating specific daily rhythms that may be correlated with foraging distribution and seasonal-related constraints. Overall, the foraging behaviour of yellow-legged gulls differed markedly between colonies, especially during the wintering season, when natural breeding gulls travelled further from the colony and performed longer trips than urban breeding gulls. Urban gulls selected more urban and industrial foraging habitats while gulls from the natural colony used more natural habitats and fishing ports. This study confirms the more generalist behaviour of the yellow-legged gull and reports on the tendency of urban-dwelling gulls to forage in urban areas, not dispersing substantially between seasons presumably because anthropogenic based resources in their immediate foraging range are always available and abundant.

4.1 Comparing foraging strategies and distribution between colonies

Although foraging trip durations were significantly different between seasons for both colonies, being longer in the wintering season, gulls from Berlenga travelled farther from the breeding colony and had longer trips than the individuals from the urban colony, dispersing throughout the country, also presenting larger home ranges. This difference in foraging strategy could be highly associated with urban breeding gulls selecting nearby urban foraging habitats and suggests a high food availability close to the colony. Gulls from urban populations are known to adapt and exploit resources within urban environments, even when other habitats are available, decreasing trip distances due to the close proximity to these highly frequented foraging habitats (Fuirst *et al*. 2018, Méndez *et al*. 2020). As gulls from Berlenga performed longer trips and had greater distances from their colony, this could indicate that these individuals experience lower foraging efficiency when compared to urban gulls. However the percentage of time spent actively

foraging, within individual foraging trips, was also significantly higher for gulls from the urban colony. Since these birds had shorter foraging trips in both distance and duration, but a higher proportion of time foraging and travelling, this may indicate that, while foraging areas in urban sites might be closer to the colony, foraging in these places might take longer and the trade-off between travel cost and foraging efficiency is still more rewarding than foraging in other habitats. Travel time accounted in this study also includes some relocation behaviour, where gulls could be moving within the same foraging area and not dispersing to other sites, and this might be higher in urban areas. Other bird species are known to relocate and exhibit short-term flight movements when trying to avoid human disturbance (Fitzpatrick and Bouchez 1998). Also, gulls can present higher agonistic behaviours in more urbanized places, due to greater competition for shared resources that are more available (Pavlova and Wronski 2020). This can result in a higher proportion of relocating behaviours if gulls try to avoid such type of competition and aggression, thus explaining the greater travel time in these birds. Furthermore, when comparing with the higher foraging trip durations and distances travelled by gulls from Berlenga, the discrepancy between the proportion of foraging time among the two colonies may also indicate that natural breeding gulls might spend more time commuting, which implies a reduction in foraging time and food intake. Longer foraging times are usually associated with less proficient foragers (Limmer and Becker 2009), however anthropogenic resources are more predictable in space and time, when compared with natural prey, indicating that urban gulls could have less commuting time and shorter but more frequent trips, where they are able to dispend more time foraging when nearby foraging areas and resources are more accessible and available, especially while breeding (Spelt et al. 2019). Data resolution was also different between the two colonies (15-minute fixtures for Berlenga and 1-hour fixtures for Porto) which may lead to some slight differences in foraging trip parameters between colonies, that might not have been detected by the statistical analysis. Nevertheless visualization of tracking data demonstrates that in fact natural breeding gulls had much longer trips than their urban conspecifics, mostly during the wintering season.

Differences in foraging distribution found between the natural and urban colonies can also be influenced by the size and density of the colony (Duhem et al. 2007). Larger foraging

ranges of the natural colony 'gulls may indicate that density-dependent competition may be forcing individuals to use more distant foraging locations, exploiting more resources far from the colony. Intraspecific competition in growing seabird colonies have reported that larger colonies have broader foraging ranges due to overlapping foraging locations, related also with the reduction of resources in the outskirts of the colony (Lewis *et al*. 2001, Corman *et al*. 2016, Estévanez and Aparicio 2019). Gulls from the natural colony of Berlenga had in fact the largest foraging range, which is consistent with the density-dependent theory. Additionally, even with the city of Peniche at a short distance and various other foraging habitat types occurring in the surroundings of the colony, such as fishing harbours and industrial sites, gulls from Berlenga actively selected specific habitats depending on their availability, both during the breeding and wintering season. This somewhat confirms that the foraging strategies observed might be triggered by a density-dependent foraging range. Berlenga is the largest colony of yellow-legged gulls in Portugal, with around 8500 breeding pairs, considerably higher than the 593 to 813 breeding pairs estimated in Porto (Calado *et al*. 2018, Oliveira and Alonso 2022). To further understand if density-dependent factors could also influence foraging distributions in different colonies, competitive inter and intra-specific studies may be implemented to assess dominance relations between individuals within these populations.

Home ranges of gulls from the two colonies were distinct between seasons, with gulls from Berlenga covering more area within overall foraging range, mostly in the wintering season, compared with urban gulls. Although core areas and foraging areas (50% and 95% kernel UDs, respectively) of the gulls from the natural colony reached the city of Porto, maximum latitude and longitude were significantly higher for gulls from the urban colony. This reveals that, while having a larger foraging range, gulls from Berlenga had their average foraging trips mostly within the colony surroundings (since Porto's colony is geographically positioned at a higher latitude and longitude). Interestingly enough, our study reveals also that core areas and foraging areas (50% and 95% kernel UDs) for gulls in the urban colony did not differ significantly between seasons, where core areas reached 83.2% and foraging areas 63.2% of kernel density overlap. Post-hoc tests for maximum latitude, longitude and trip duration also revealed that foraging

characteristics did not differ significantly between the breeding and wintering season, confirming minimal dispersion all year round for gulls of the urban colony. Hence, we can confirm a low seasonal dispersion for gulls breeding in an urban colony, providing evidence that issues regarding the impact of urban breeding gulls in cities and urban areas may be greater than anticipated, and that management measures should consider the foraging behaviour of gulls in different stages of their annual cycle.

4.2 Habitat selection at a population and individual level

Yellow-legged gulls exploited nine main habitats, from terrestrial to marine areas, including several locations predominantly anthropogenic. The high plasticity of the individuals from both colonies is reflected on the behavioural flexibility of the yellow-legged gull to exploit a wide arrange of resources, including natural and anthropogenic, and use them when available and needed.

4.2.1 Population-level habitat use of gulls from urban and natural colonies

At a population level, habitat selection unveiled differences between colonies and seasons. Gulls from the urban colony selected, to a greater extent, more urban habitats than others, mainly Urban and Industrial areas, and used these habitats disproportionately in relation to their availability. The usage of these areas was larger in the breeding season; however it still remained the most preferred habitats during the wintering season. On the contrary, gulls from Berlenga selected more Natural, Sea and Port habitats (overall more coastal habitats) but increased their use of Urban habitats during the wintering season.

The greater use of Urban habitats among the urban colony individuals, relative to the remaining habitats, suggests a general habitat use likely to be a function of colony-specific foraging preference, especially due to the high degree of home range overlap between the breeding and the wintering season. A recent study employing GPS loggers on Lesser blacked-back gulls from an urban and natural colony also found a great habitat segregation of urban areas connected with high degree of foraging overlap (Langley *et al*. 2022). However this study only

included habitat use during the gulls breeding season. Our long-term tracking enables us to explore greater seasonal changes, if present, in overall foraging behaviour and habitat use of the population. Gulls in urban areas are known to scavenge for food present in human waste materials, predate other urban-dwelling species such as pigeons and use public parks and green urban areas to rest or to drink and bathe in public fountains (Huig *et al*. 2016, Méndez *et al*. 2020, Pais de Faria *et al*. 2021a). Hence, the greater use of urban areas, in both seasons, implies that the selection of this sites appear to be more rewarding, and that the energy intake gained in these habitats is higher than in marine or natural environments, reflecting the state of resource availability and foraging benefits for urban-nesting gulls (Anderies *et al*. 2007, Patenaude-Monette *et al*. 2014). But despite the habitat use of urban gulls displaying a compelling number of locations in urban sites, in both seasons, demonstrating a clear preference for these habitats, Port and Watercourse were also preferred habitats. Comparing with terrestrial and urban foraging sites, marine environments and fishing harbours are also an important part of most gulls foraging strategies (Alonso *et al.* 2015, Calado *et al*. 2021b) and gulls in urban colonies are known to rely on marine resources acquired in these areas, as they can be fundamental in these birds diets, particularly during chick rearing (Pais de Faria *et al*. 2021b). The preference for Watercourse habitats by gulls from the urban colony during the breeding season is most likely related with the use of the fishing port, as most GPS locations of these individuals were accounted in estuaries and riverbanks, which are the main watercourse associated areas near Port habitats, at the city of Porto. Nonetheless, these sites may also be used to rest, socialize with other conspecifics or scavenge for other marine prey, such as crustaceans and molluscs (Navarro *et al*. 2017a, Calado *et al*. 2021b).

In contrast with the urban colony, gulls from Berlenga used more Sea and Port habitats, with the average use of these sites increasing in the wintering season. Pais de Faria (2021) reported that gulls from Berlenga and Peniche mainly consumed marine prey and that these resources are likely more consumed due to their proximity to the coast or to some dependency on fishing discards from the nearby fishing harbour. The greater use of port areas demonstrates once more that fishing activity has a strong effect in the foraging behaviour of gulls, though gulls from

natural colonies seem to feed at a higher trophic level than urban gulls and mainly on marine resources. Langley (2022) also demonstrated a tendency on coastal breeding lesser black-backed gulls to use more coastal foraging habitats than urban breeding gulls, however these birds also avoided urban areas. Gulls from Berlenga increased their use of Urban habitats during the wintering season, being specifically preferred over the remaining habitats, which might indicate that the reduced use of this sites during the breeding season is more likely associated with breeding constraints. Even so, Natural and Port habitats were also preferred and highly used habitats in the wintering season, confirming that these natural breeding gulls search more coastal habitats to forage.

Remarkedly, Sea habitats were significantly avoided, for both colonies and within both seasons. Sea environments for each season had larger areas available in comparison to the area that most GPS locations were accumulated, explaining the overall extremely low proportion of habitat use. Even so, it still validates that in all habitat availability, yellow-legged gulls from Porto and Berlenga did not make great use of these areas and avoided the open sea most of the time during the tracking period, despite the close proximity to the coast. This further demonstrates the tendency of gulls to prey on more predictable food sources in fishing harbours, terrestrial areas and anthropogenic sites than in the ocean. As the dispersion ability of these gulls were not a limiting factor, with the maximum distance away from the colony reaching roughly 300km in Berlenga (individual BER4) and 200km in Porto (individual 848) we can predict that the degree to which the different colonies used the marine environment is likely to reflect different foraging strategies among individuals, considering habitat availability. Spelt (2019) demonstrated that the close proximity to marine areas did not influence the habitat use of lesser black-backed gulls in Bristol, where individuals chose to use more terrestrial habitats and spend two-thirds of their time in urban areas. Garthe (2016) also showed that gulls in the Wadden Sea varied their foraging strategies between marine and terrestrial habitats, having longer or shorter trips most likely depending on food availability between habitats, while also demonstrating that most tracked trips in the sea overlapped with patterns of fish trawlers in the area.

Most published studies also indicate the high importance of resources present in garbage dumps for yellow-legged gulls (Duhem *et al*. 2003, 2005, Ramos *et al*. 2009b). Surprisingly, in our study, the importance of this habitat was low, as it did not present a great percentage of GPS locations, nor did it seem to be a preferred habitat. However it is important to note that, in both breeding stages, gulls from Porto recurrently used two industrial sites north of the city, being a part of the extent of foraging range within the colony surroundings. These industrial sites were identified as RIMA (Resíduos Industriais e Meio Ambiente) and Resulima, which are also large open refuse dump areas for industrial and agricultural residues. It is likely that gulls used more this refuse sites but the close proximity with industrial areas (within CORINE Land Cover 2018) had GPS locations accounted for Industrial habitat. As so, it is expected that a proportion of locations represented in Industrial habitats are in fact accolated to refuse dump sites, and that these areas truly represent an important foraging site for these urban gulls (Industrial habitat was one of the most used habitats by gulls from the urban colony, particularly in the wintering season). This foraging habitat preference has important implications for gull population management (Carmona *et al*. 2021). Refuse reduction measures or structural solutions, sanitation procedures and waste management can decrease food availability for gulls in urban areas and industrial sites (Belant 1997, Kilpi and Öst 1998, Weiser and Powell 2011). These measures can help mitigate human-gull conflict but might also have on impact urban gull populations (Pons 1992). Breeding performance studies should be implemented in multiple colonies, for both natural and urban breeders, in order to understand the influence of urban habitats in the foraging strategies of urban gulls. As gull populations from natural colonies present a greater use of marine and fishing port areas, they are more unlikely to be impacted by such measures.

4.2.2 Individual-level habitat use of gulls from urban and natural colonies

The overall habitat use at an individual level was similar within each colony, as specialization was low among populations, indicating that most individuals displayed a mix of foraging strategies, expressing a generalist behaviour and consequently using different habitats in a similar way (Navarro *et al*. 2017b). However specialization within the population of both urban

and natural colonies was higher in the wintering season. Some studies have already presented some individual range of specialization in the habitat use of gulls when in different breeding stages, where despite a most generalist behaviour is prevalent, various levels of specialization are identified within the population (see Navarro *et al*. 2017a, O'Hanlon *et al*. 2022). Still, no studies explored the comparisons between individual specialization over the year-round habitat use, where possible shifts may occur. Higher individual specialization in the wintering season could be a result of reproductive constraints of gulls during the breeding season, as these birds are more restricted to forage in areas around the colony, to frequently return to incubate the egg or feed the chick. Thus a higher opportunity of specialization within available habitats can arise in the wintering season. Reproductive conditions can influence gulls foraging behaviour and habitat use, with studies showing variation during pre-laying, incubation and chick-rearing periods and even a reduction in searching efforts, with individuals revisiting several previous foraging locations during the breeding season (Pierotti and Annett 1989, Isaksson *et al*. 2015, Enners *et al*. 2018, Baert *et al*. 2021). If limited to use the surrounding habitat in the breeding season, even when resources are always available, gulls could be expected to have higher extent of individual specialization when they are able to extend their foraging range.

The urban colony had individuals with the lower score of specialization index, meaning that they generally presented a more specialist behaviour. The most specialized individual, gull 871, had a PSi value of 0.13, and had their use of habitat restricted to agricultural fields and low shrub forest. Although this may suggest that the individual is extremely specialized, tracking data was also shorter than the majority of the remaining gulls, suggesting that the individual could have used other habitats that simply weren't accounted in the tracking period. Another individual with a low PSi value (0.39) was gull 848, which had a great use of marine and industrial habitats in the wintering season. This individual had the farthest distance to the colony, as it travelled to Spain and remained in the coastal areas of Galicia most of his wintering season.

The natural colony displayed more similar PSi values across the population, with the more specialized individuals having a great use of port areas and urban sites than the other individuals. In the breeding season, the individual BER7 was one of the most specialized in the population

(PSi value of 0.64), using Natural habitat almost exclusively, within the Berlenga Island. A possible explanation for this unique behaviour could be that this individual foraged mainly on swimming crabs and marine prey very close to the colony, consequently with GPS locations not accounting for sea environment because of the resolution error within the data. Gulls from Berlenga are known to rely on Henslow's swimming crab *Polybius henslowii,* a key marine prey for yellow-legged gulls in the Atlantic coast (Calado *et al*. 2020, 2021b), and the presence or absence of this species can influence niche width and foraging behaviour of the yellow-legged gull population in the island, thus changing feeding choices (Ceia *et al*. 2014a).

Even though all individuals of yellow-legged gulls from the two colonies could exploit all available habitats and even the same areas, based in the specialization index and PSi values of the population, there are some differences in habitat use amongst individuals, within the population and within each colony itself. Generalist species are usually composed by distinct individuals that may well differ in behavioural traits (Bolnick *et al*. 2002). Individual specialization is known to exist in several seabird species, including gulls, and can be crucial as it affects ecological processes and population dynamics, where it can facilitate the adaptability to environmental conditions, reduce competition and improve foraging efficiency and breeding success (Ceia and Ramos 2015, Tyson *et al*. 2015, Navarro *et al*. 2017a). As so, measuring individual foraging specialization in gull populations can help predict colony-level responses to environmental pressures and the existence of more specialized individuals in the population of this generalist species could explain their innate adaptation success, serving to understand how gulls can exploit different habitats and explore wide arrange of resources, both anthropogenic and natural (Ceia and Ramos 2015, Navarro *et al*. 2017a, Van Toor *et al*. 2017, Lopezosa *et al*. 2019).

4.3 Diel rhythms of two distinct colonies

Daily activity patterns between workdays and weekends were overall similar within most habitats, with a few exceptions amongst the two colonies. However diel rhythms of foraging activity were present in all habitats and differed from each other, correlating with the habitat use of our tracked individuals and demonstrating that gulls, as an opportunistic species, can adapt

their behavioural schedule depending on human mediated activities, while also indicating that day-specific routines might differ when comparing individuals from a natural and urban colony.

Activity patterns in the more marine-related habitats – Sea, Watercourse and Port – were different when compared between natural and urban colonies but were identical to each other, when within the same colony. These similarities can be explained by the close proximity of marine and freshwater habitats to fishing harbours, as GPS locations accounted for Sea and Watercourse amongst most individuals are in the immediate surroundings of Port habitats. Diel rhythms for the urban colony in these marine areas encompassed most of the activity in early to mid-morning, dropping in the afternoon and then peaking again at night. As marine resources for yellow-legged gulls are highly associated with fishing activity and fishing ports (Alonso *et al.* 2015, Calado *et al.* 2021b, Pais de Faria *et al.* 2021b), the availability of such resources are mostly dependent on anthropogenic rhythms (Tyson *et al.* 2015, Parra-Torres *et al.* 2020). The morning peak of activity within these habitats, for the urban colony, is most likely associated with the arrival of most fishing vessels and trawlers to the harbour and coincides with the moment fisherman move commercial fish (Docapesca 2022). Activity in the end of the diurnal period might also be correlated with the departure of purse-seiners, which operate mostly at night and early morning, and are known to discard higher amount of fish than most trawlers (Matos *et al.* 2018, Calado *et al.* 2021a). Also, foraging activity in Port areas was higher but more limited in time during weekends, with the maximum activity peaking early in the morning at more specific hours and during shorter time periods. One explanation might be that, because of the usual reduction in the number of fishing vessels operating on weekends, gulls tend to exploit high predictable food source such as fishing discards when and where they're available, revealing possible patterns of a somehow nocturnal foraging activity on yellow-legged gulls. As purse-seiners operate during the night (Matos *et al.* 2018), arrival to fishing harbours happens in the morning and gulls might adjust their diel rhythms in order to obtain the most of the resources. For the same reason, activity was more extensive in time in workdays and more over when analysed in Sea environments, where weekends peaked more at night, especially in the wintering season, demonstrating also that gulls might be compensating with lower intake rates if predictable food

sources are not available. For the natural colony, usage of the marine habitat was more unimodal, but activity also peaked mid-morning, being correlated with the arrival of fishing vessels. Differences of activity were distinguishable between seasons, for the natural colony, where patterns of activity increased in the wintering season but remain mostly equal to the breeding season, showcasing the importance of the habitats to these gull's foraging behaviour. It is important to note that the greater use of Industrial habitats for gulls from the natural colony was around the city of Peniche, where large fishery-associated industrial sites and food managing companies are located. The specific daily patterns encountered in these areas, where peak activity happens early in the morning for both workdays and weekends (2:00h to 6:00h) may be correlated with fish delivery to the industries, thus reinforcing the importance of marine prey for individuals from this colony and further demonstrating the flexibility of foraging rhythms that these birds are capable of (Calado *et al*. 2021b).

Although fishing ports and marine environments are known to be an important source of food (Ramos *et al*. 2009b, Alonso *et al*. 2015, Calado *et al*. 2021b), gulls' patterns in these habitats can also be the result of avoidance to other preferred habitats present in their foraging range. Activity in fishing ports can be considered as an alternative choice when the usage of other frequently visited habitats are at peak of human activity, such as garbage dumps, urban areas and agricultural sites, thus influencing foraging choice by evasion to human disturbance (Yoda *et al*. 2012, Parra-Torres *et al*. 2020). An example of this avoidance can be seen in the Dump habitats in our study, where for both colonies, garbage dumps were visited and had their peak activity in the afternoon, which most likely coincides with the end of the human working schedule in these areas (Spelt *et al*. 2021). Also, the frequent usage of these garbage dumps at these specific hours (18:00h to 20:00h) might explain the low activity in fishing ports and marine environments at the same hours. During the wintering season, more activity is seen throughout the day in workdays, which might indicate a greater dependence on refuse subsidies for urban gulls. However, due to low number of GPS locations (especially in weekends), it is difficult to reach conclusions on this matter. On a dissimilar pattern, Urban habitat had a very unimodal daily activity for both colonies, and even between breeding stages. In fact, activity patterns for Urban habitats within the urban

colony were essentially equal for workdays and weekends, and throughout the day. These diel patterns ensure once more the adaptation of these gulls to urban areas and correlate with their year-round presence and foraging behaviour in an urban context. Peak activity in this habitat for natural colony gulls seem to correlate with their arrival at the city of Peniche, as daily activity patterns were similar with the marine habitats and Natural habitat, which are also prevalent in the city.

Other patterns of habitat use tending from avoidance (or preference) to human presence are seen in Agriculture and Beach habitats. In agricultural areas, the gull's activity was mainly equally observed throughout the day, decreasing at night. In the natural colony, peak activity was around early-afternoon for both workdays and weekends, however for the urban colony, an increase of activity was detected daily at around 16:00h to 20:00h. Agricultural fields can be important areas of alternative resources and studies show that gulls can take advantage of human presence, when encountering recently cultivated land to feed on insects or in human absence to roost (Rock *et al.* 2016, Spelt *et al.* 2019, Parra-Torres *et al*. 2020). Beaches, one of the most selected main habitats in this study (and highly preferred by gulls from the natural colony during the wintering season), are known to be considerably used by gulls when human activity is lower or absent (Lafferty *et al*. 2013, Parra-Torres *et al*. 2020). Indeed, daily activity patterns display differences in week periods, more precisely in the natural colony, where peak of activity completely change between workdays, where it happened in the morning, and weekends, where it happened in the afternoon. Berlenga Island and Peniche have a great beach-centred tourism, so it is highly expected that the presence of humans influences the activity of gulls in these areas.

4.4 Final remarks

In the present study we found that gulls from different colony types, natural and urban, differed in terms of habitat use and foraging behaviour. Furthermore, we also report distinct foraging distributions between breeding stages, showing that urban colony gulls have a low year-round dispersion, when specific foraging preferences exist within the population. Gulls are also

quite adapted to their patterns of habitat use and foraging distribution, in function of human mediated activities, as shown by the distinct diel rhythms of the two colonies.

Variations in the year-round foraging behaviour of different colonies are important concepts to take in consideration when applying management measures, as differences in these populations suggest different outcomes. Of particular concern interest is the influx of birds from natural areas into urban habitats during the wintering (non-breeding) season. This should contribute to the overall increase of urban gull populations during winter, potentially leading to an increasing number of conflicts with humans during this season (Pais de Faria *et al*. 2021a). Nevertheless, individual differences within the population, especially between seasons, can lead to different results in such procedures. The study of the spatial ecology for the yellow-legged gull can provide valuable data and help further understand ecological and evolutionary processes that may shape natural and urban populations of this species, highly influenced by human-related activities and resources.

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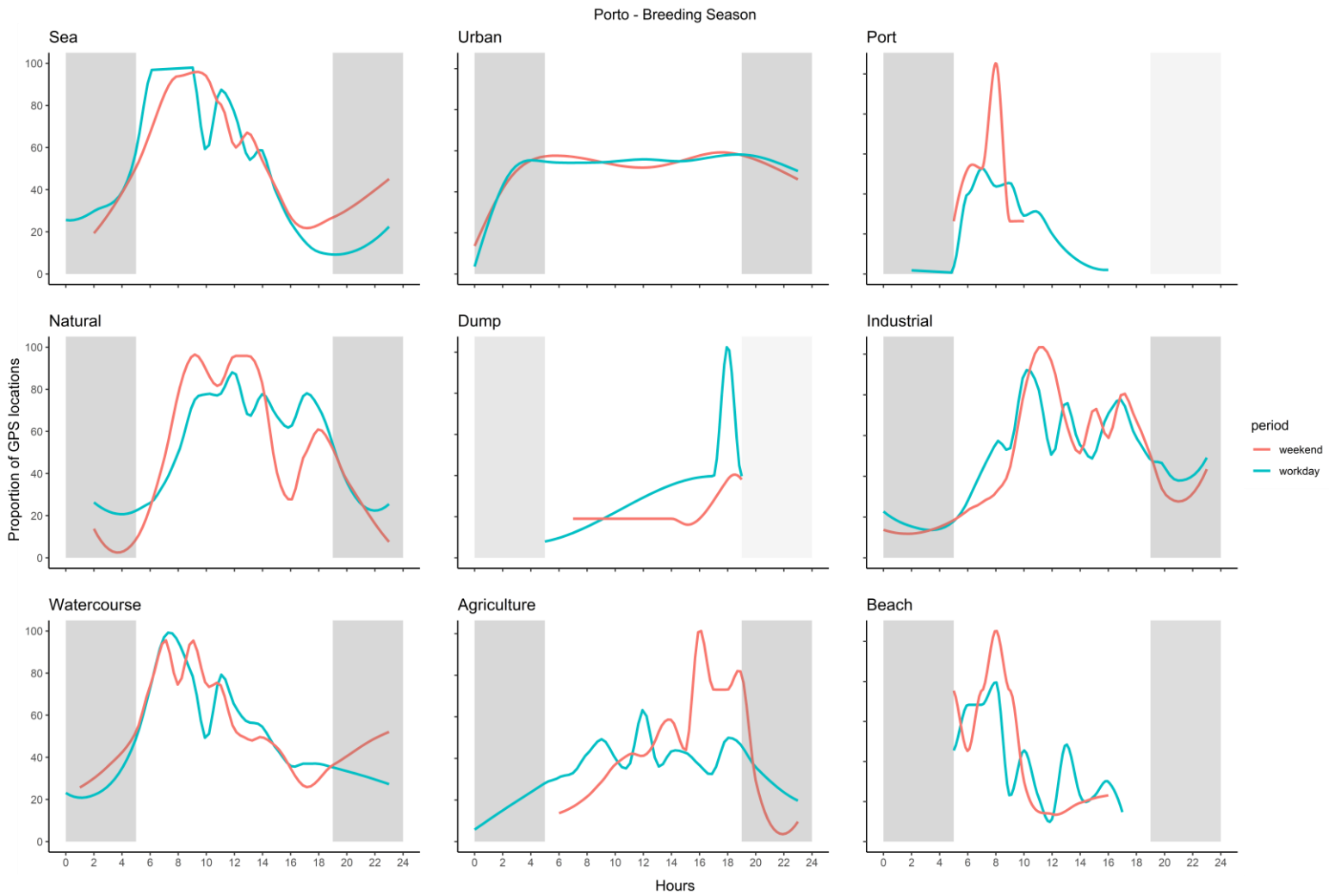
Appendix

Figure A1. Time-series analysis of diel activity patterns in each habitat, used by yellow-legged gulls tracked during the breeding season in the urban colony (Porto), in relation to time period – workdays and weekends. Dark grey shading indicates night-time. The average number of GPS locations is shown.
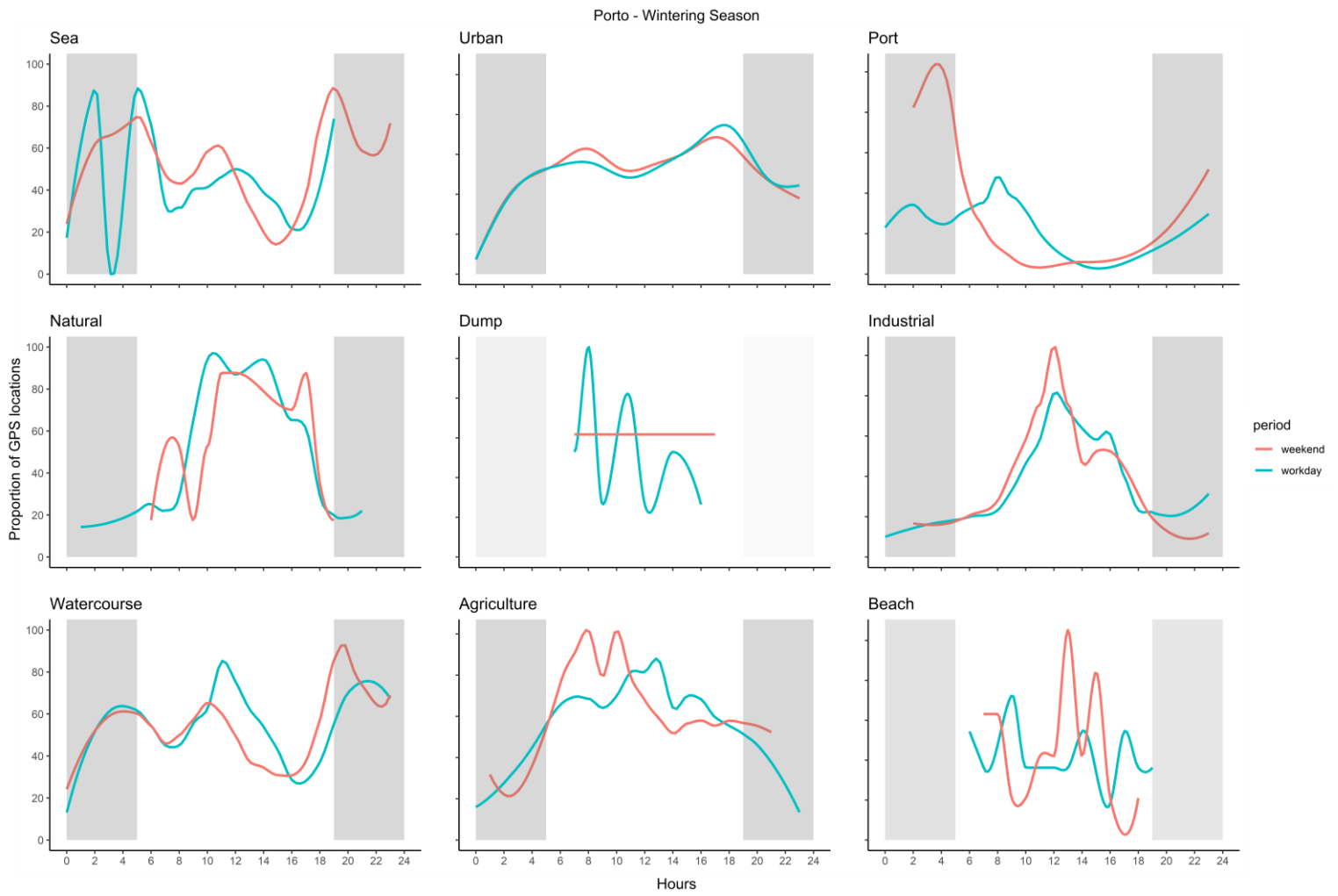
Figure A2. Time-series analysis of diel activity patterns in each habitat, used by yellow-legged gulls tracked during the wintering season in the urban colony (Porto), in relation to the type of day – workdays and weekends. Dark grey shading indicates night-time. The average number of GPS locations is shown.
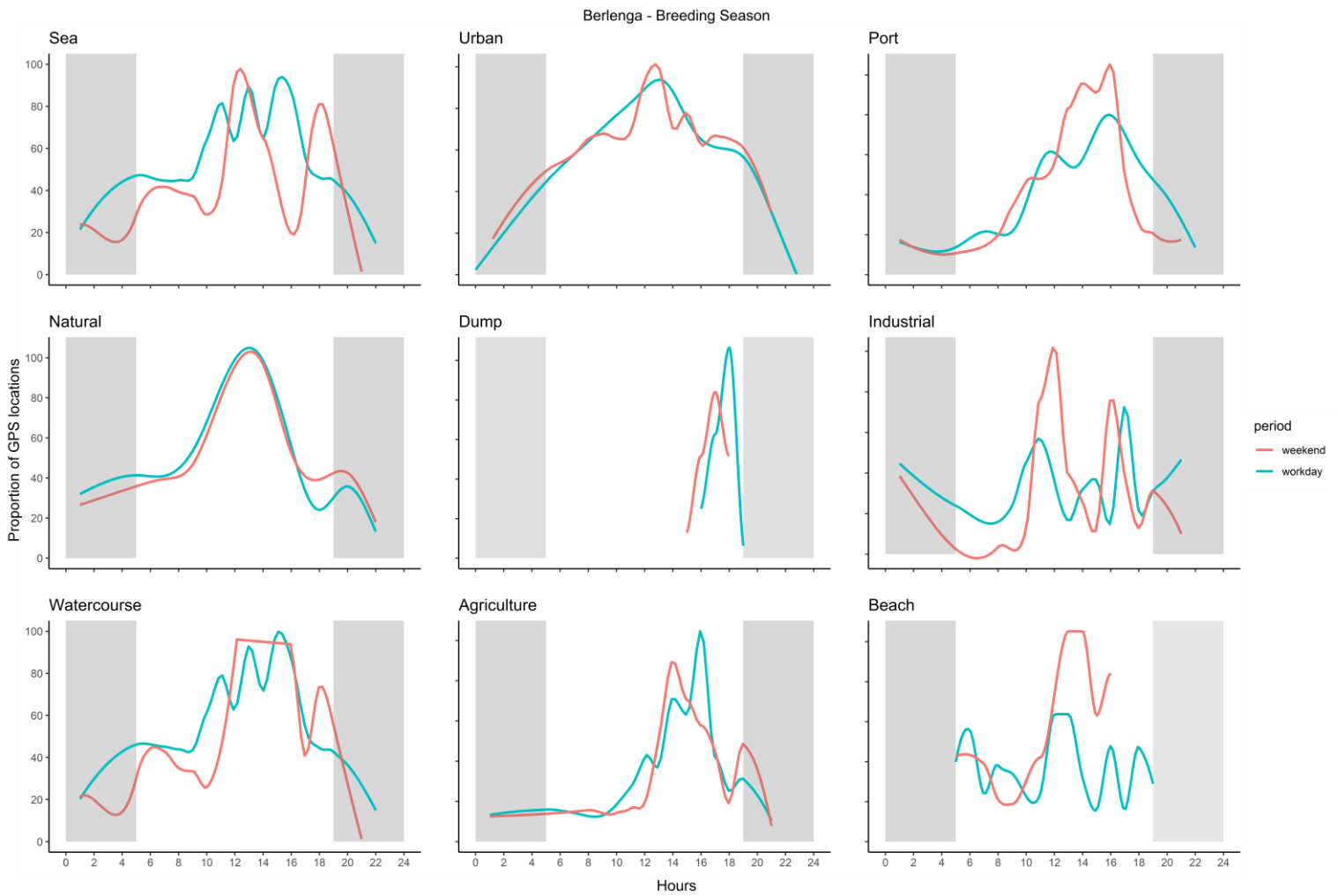
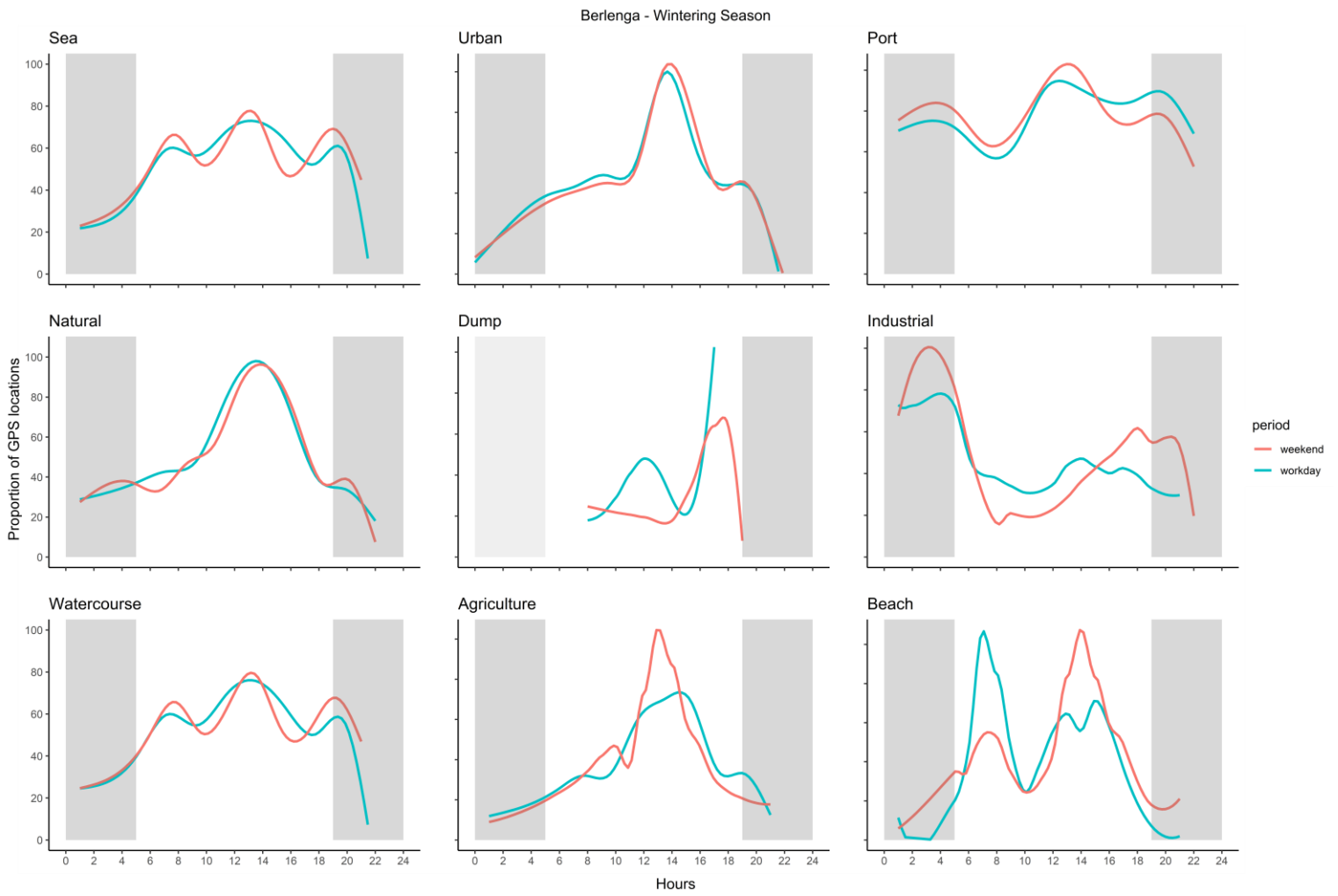**Figure A3.** Time-series analysis of diel activity patterns in each habitat, used by yellow-legged gulls tracked during the breeding season in the natural colony (Berlenga Island), in relation to the type of day – workdays and weekends. Dark grey shading indicates night-time. The average number of GPS locations is shown.

Figure A4. Time-series analysis of diel activity patterns in each habitat, used by yellow-legged gulls tracked during the wintering season in the natural colony (Berlenga Island), in relation to the type of day – workdays and weekends. Dark grey shading indicates night-time. The average number of GPS locations is shown.
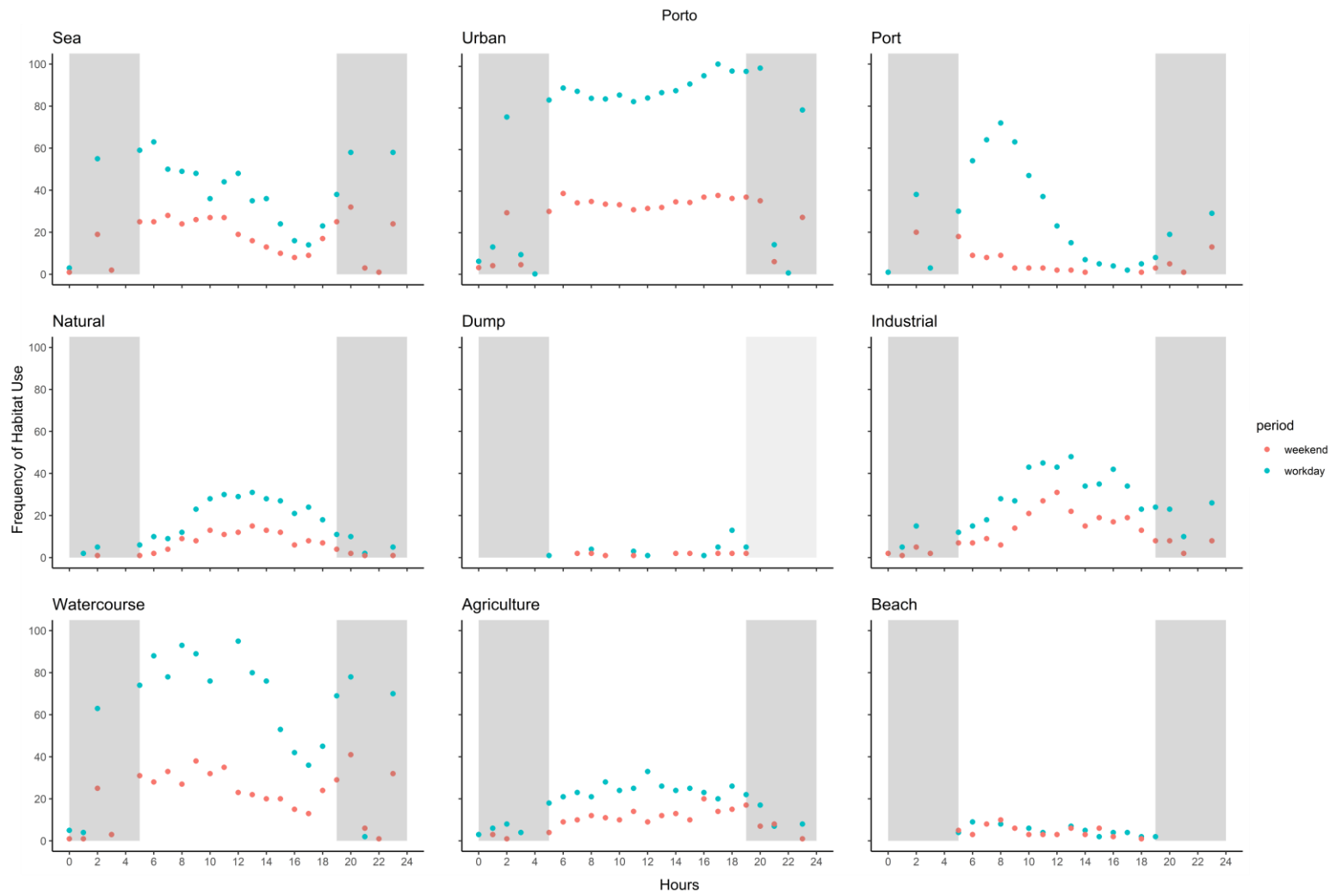
Figure A5. Time-series analysis of diel activity of each habitat, used by yellow-legged gulls tracked during the breeding and wintering seasons in the urban colony (Porto), in relation to the type of day – workdays and weekends. The frequency of habitat use of the population is displayed for each habitat. Dark grey shading indicates night-time.
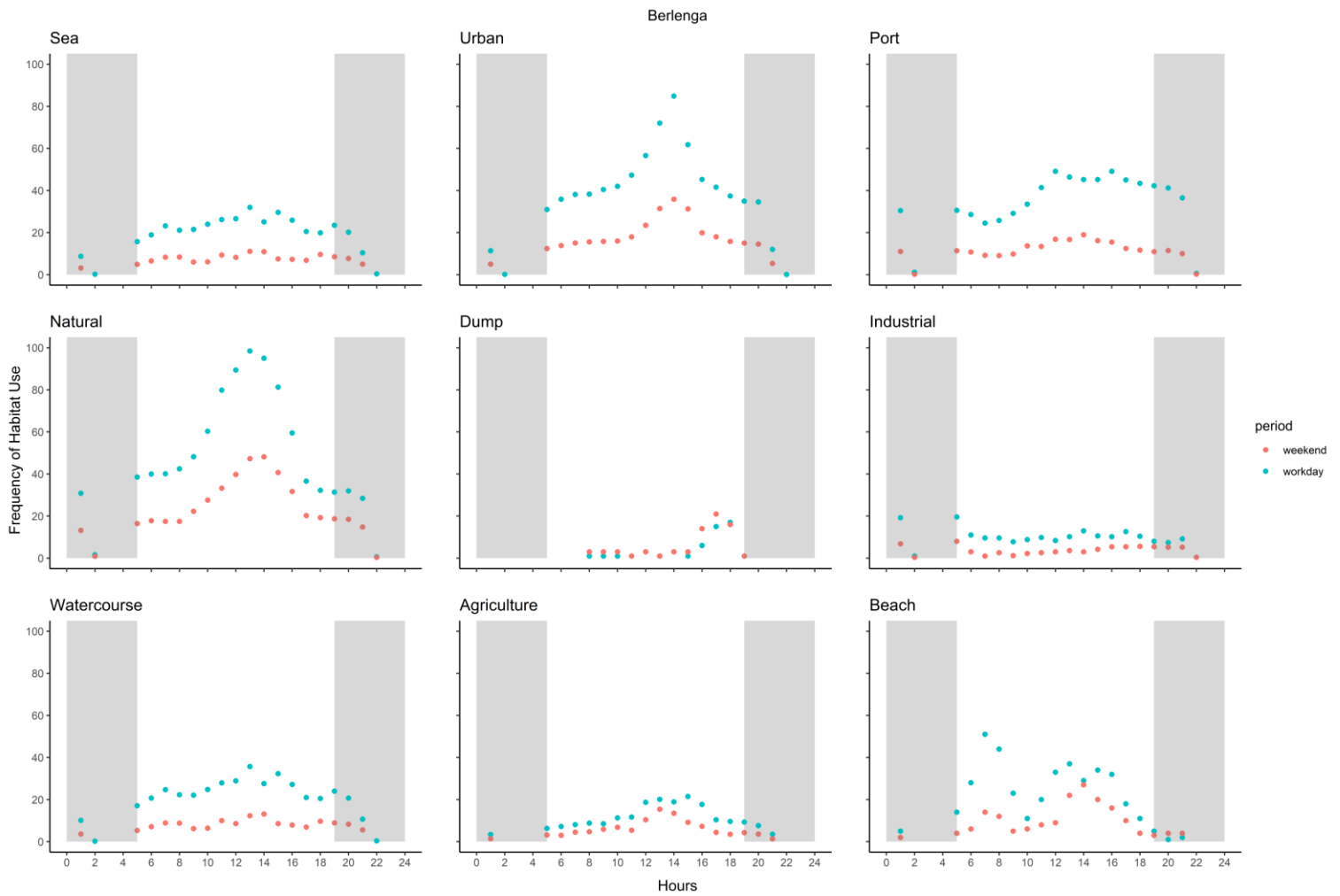
Figure A6. Time-series analysis of diel activity of each habitat, used by yellow-legged gulls tracked during the breeding and wintering seasons in the natural colony (Berlenga Island), in relation to the type of day – workdays and weekends. The frequency of habitat use of the population is displayed for each habitat. Dark grey shading indicates night-time.