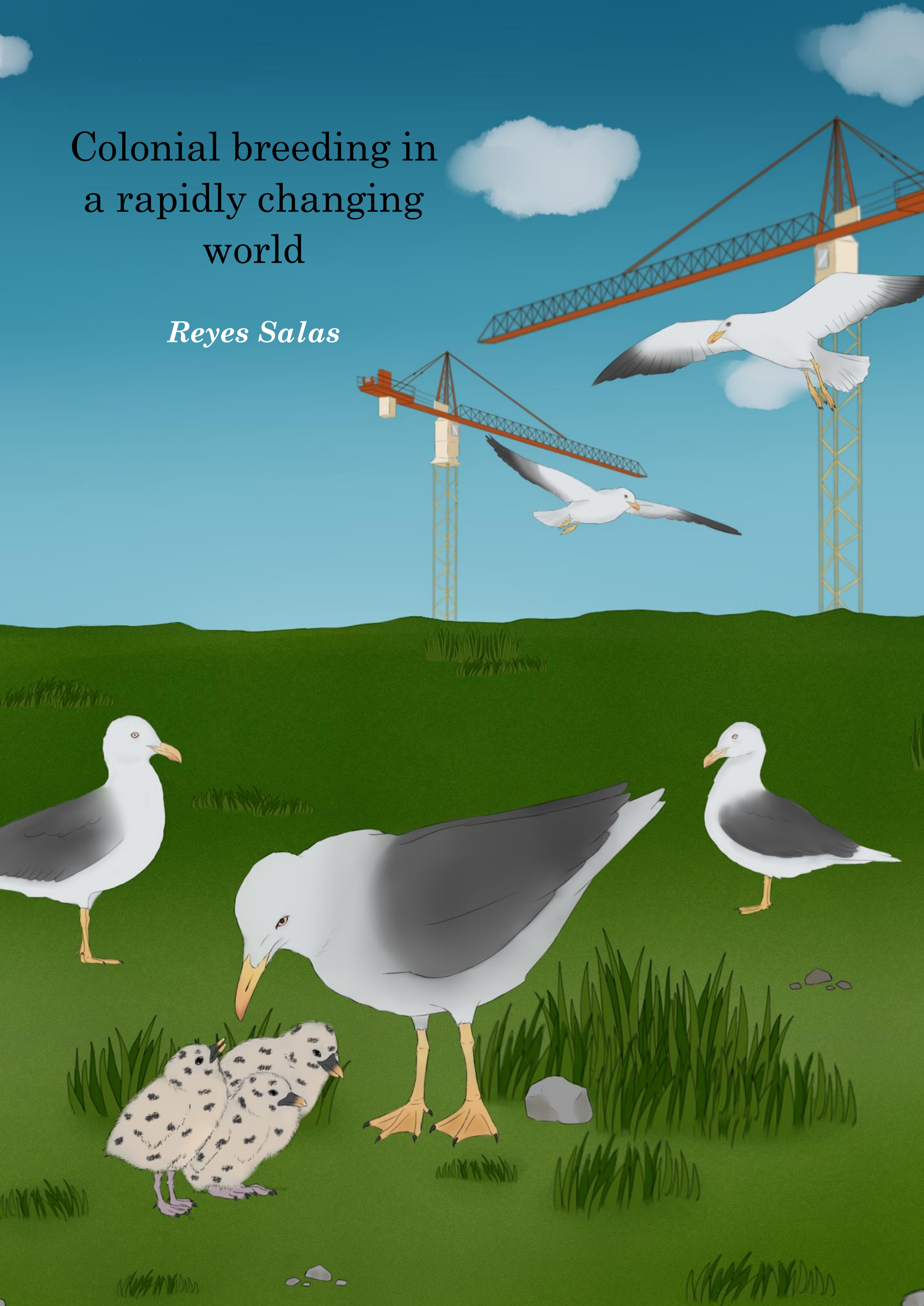
Colonial breeding in a rapidly changing world

Reyes Salas



Faculty of Science

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Colonial breeding in a rapidly changing world

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To be defended by

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Summary

The world is witnessing unprecedented rates of habitat degradation due to anthropogenic activities, especially urbanisation. The amount of urban land cover will possibly double by the end of the century, which has far-reaching consequences for wildlife primarily by habitat loss or habitat degradation. Yet, some species are commonly believed to have successfully adapted to breed in urban areas. However, most of this knowledge is based on abundance data, while we have still a poor understanding of the actual fitness consequences. The fact that animals are attracted to an urban environment might conceal that urban landscapes can act as ecological traps, since even highly opportunistic species might have difficulties to keep up with the high rate of environmental change and habitat loss. This dissertation tackles this question by exploring the reproductive consequences of losing the nesting territory in anthropogenic environments along with in depth studies on the costs of territoriality for the adults, and on the importance of territory choice for the offspring. To this end, a colonial breeding seabird species, the lesser black-backed gull (*Larus fuscus*), which is thought to thrive in highly anthropogenic environments, is used as model species.

First, I explored whether and how nesting site relocations, as frequently occur in rapidly changing urban environments, impact on reproductive success. Based on a long-term dataset of individual lesser black-backed gull nest locations and measures of reproductive investment that were collected during a period that included several episodes of loss of suitable breeding habitat, I could show that individuals that lost their breeding site laid smaller eggs and that the likelihood of skipping a breeding season increased. Thus, estimating the success of the

species based on its presence underestimates the reproductive costs of relocations. The costs I revealed might be related to an increased time and energy investment of holding a nesting spot in a new (social) environment, which might impose carry-over effects on reproductive success at the onset of reproduction. Yet our knowledge on the costs of territoriality was as yet limited. Through the use of GPS tracking devices, I then showed that keeping a territory indeed requires a significant time investment, and investing in territoriality reduced the time that was available for foraging during a period of up to 4 weeks, which resulted in an impaired reproductive investment. While not measured explicitly, it can be assumed that these costs increase after a relocation. These data hence allow to better estimate and interpret the implications of breeding in rapidly changing urban environments.

While the first part focused on the adults, we currently lack a profound understanding of the importance of a territory for the chicks, even though it is known that the social early-life environment can shape an individual's (behavioural) phenotype. This is particularly relevant in lesser black-backed gulls, because here chicks move independently from early ages onwards but experience high levels of aggression when crossing into a neighbouring territory. Mothers may therefore prepare their offspring via pre-natal effects to the social environment they will experience post-hatching. Through a sophisticated full clutch cross-fostering within and between social environments (i.e., high and low breeding densities), I could disentangle the complex interplay between pre- and post-natal environmental effects on the chicks' behavioural phenotypes. I found that the chicks' exploration activity was reduced in plots with high breeding density. Interestingly, both the pre-natal and the post-natal environment contributed to a comparable extent to differences in the offspring's behavioural phenotype. In a final step, I deployed a novel, ultra-wide band tracking technology to study for the first time the movement behaviour of the chicks in the colony. Following the same experimental design, I could show that the post-natal but not the pre-natal environment, affected the movement activity, territory size and associations among chicks from neighbouring nests. The number of contacts with neighbouring chicks was very low which, along with the results of the previous study, fits with the idea that the chicks' behaviour is shaped by a hostile early-life social environment.

Taken together, the time and possibly energy costs for establishing and maintaining a (novel) territory, as well as subtle fitness implications will ultimately determine whether a supposedly generalist seabird species can keep up with the current rate of anthropogenic change. This could also depend on how well the phenotypes of the future gull generations, which are shaped by pre-natal maternal effects as well as by post-natal environmental effects that facilitate living in a (sub)urban colony, prepare them for the forthcoming, altered adult environment - if these effects are long-lasting.

Samenvatting

De wereld ervaart een ongekende achteruitgang van habitat als gevolg van antropogene activiteiten, met name verstedelijking. Tegen het einde van de eeuw zal de hoeveelheid verstedelijkt gebied mogelijk verdubbeld zijn, wat verstrekkende gevolgen heeft voor dieren, voornamelijk door het verlies of de achteruitgang van habitat. Toch wordt van sommige soorten algemeen aangenomen dat ze zich met succes hebben aangepast aan het broeden in verstedelijkte gebieden. Deze kennis is echter grotendeels gebaseerd op gegevens over aantallen, terwijl we nog weinig inzicht hebben in de werkelijke fitnessgevolgen. Het feit dat dieren aangetrokken worden door een stedelijke omgeving zou kunnen verhullen dat stedelijke landschappen kunnen fungeren als ecologische vallen, aangezien zelfs zeer opportunistische soorten moeite kunnen hebben om de hoge snelheid van milieuverandering bij te houden. Dit proefschrift behandelt deze vraag door de gevolgen van het verlies van het broedterritorium voor de reproductie te onderzoeken in antropogene omgevingen, samen met diepgaande studies naar de kosten van territorialiteit voor de volwassenen, en naar het belang van territoriumkeuze voor de nakomelingen. Om dit te onderzoeken is een in kolonie broedende zeevogelsoort, de kleine mantelmeeuw (*Larus fuscus*), als modelsoort gebruikt, waarvan wordt aangenomen dat hij goed gedijt in sterk antropogene omgevingen.

Eerst heb ik onderzocht of en hoe nestverplaatsingen, die vaak voorkomen in snel veranderende stedelijke omgevingen, van invloed zijn op het voortplantingssucces. Op basis van een langetermijndataset van individuele nestlocaties van mantelmeeuwen en metingen van investeringen in de

voortplanting die werden verzameld gedurende een periode die verschillende episodes van verlies van geschikt broedhabitat omvatte, kon ik aantonen dat individuen die hun broedplaats verloren kleinere eieren legden en dat de kans op het overslaan van een broedseizoen toenam. Een schatting van het succes van de soort op basis van haar aanwezigheid onderschat dus de voortplantingskosten van verplaatsingen. De kosten die ik aan het licht bracht, zouden verband kunnen houden met een verhoogde tijds- en energie-investering voor het behouden van een nestplaats in een nieuwe (sociale) omgeving, wat mogelijk nawerkingen heeft voor het voortplantingssucces bij het begin van de voortplanting. Onze kennis van de kosten van territorialiteit was echter nog beperkt. Met behulp van GPS-tracking apparatuur toonde ik vervolgens aan dat het behouden van een territorium inderdaad een aanzienlijke tijdsinvestering vereist, en dat investeren in territorialiteit de tijd die beschikbaar was om te foerageren verminderde voor een periode tot 4 weken, wat resulteerde in een kleinere investering in de voortplanting. Hoewel dit niet expliciet is gemeten, kan worden aangenomen dat deze kosten na een verplaatsing toenemen. Deze gegevens maken het dus mogelijk de gevolgen van het broeden in een snel veranderende stedelijke omgeving beter in te schatten en te interpreteren.

Terwijl het eerste deel gericht was op de volwassen dieren, ontbreekt het ons momenteel aan een diepgaand inzicht in het belang van een territorium voor de kuikens, ook al is bekend dat de sociale omgeving in het vroege leven het (gedrags)fenotype van een individu sterk kan beïnvloeden. Dit is bijzonder relevant bij kleine mantelmeeuwen, omdat de kuikens zich hier vanaf jonge leeftijd zelfstandig verplaatsen, maar veel agressie ondervinden bij het doorkruisen van een naburig territorium. Moeders kunnen hun nakomelingen daarom via prenatale effecten voorbereiden op de sociale omgeving die zij na het uitkomen van het ei zullen ervaren. Door het uitwisselen van legsels binnen en tussen sociale omgevingen (hoge en lage broeddichtheden) kon ik de complexe wisselwerking tussen pre- en postnatale omgevingseffecten op de gedragsfenotypes van de kuikens ontrafelen. Ik vond dat de exploratieactiviteit van de kuikens verminderde bij een hoge sociale broeddichtheid. Zowel de prenatale als de postnatale omgeving droegen in vergelijkbare mate bij tot verschillen in het gedragsfenotype van de nakomelingen. Als laatste stap gebruikte ik een nieuwe, ultra-wide band tracking technologie om voor het eerst de verplaatsingen van de kuikens door de kolonie te bestuderen. Met dezelfde proefopzet kon ik aantonen dat de postnatale omgeving, maar niet de prenatale, de bewegingsactiviteit, territoriumgrootte en associaties tussen kuikens van naburige nesten beïnvloedde. Het aantal contacten met naburige kuikens was zeer laag, wat, samen met de resultaten van de vorige studie, past bij het idee dat het gedrag van de kuikens wordt gevormd door een vijandige sociale omgeving tijdens het vroege leven.

Al met al zullen de kosten van tijd- en mogelijk van energie-investering voor het verkrijgen en onderhouden van een (nieuw) territorium, alsmede de subtiele fitnessimplicaties uiteindelijk bepalen of een verondersteld generalistische zeevogelsoort het huidige tempo van antropogene veranderingen kan bijbenen. Dit zou ook kunnen afhangen van hoe goed de fenotypes van de toekomstige meeuwengeneraties, die gevormd zijn door prenatale maternale effecten en door postnatale milieueffecten die het leven in een (voor)stedelijke kolonie vergemakkelijken, hen voorbereiden op de komende, veranderde omgeving als volwassene - als deze effecten langdurig zijn.

Lesser black-backed gull (colour-ringed and GPS tracked) with its offspring.

CHAPTER 1

General introduction

Colonial breeding

Colonial breeding describes the dense aggregation of individuals during reproduction, where the breeding site itself does not contain any resources other than nesting sites (Wittenberg and Hunt 1985; Danchin and Wagner 1997). It occurs in various taxa such as spiders (Uetz et al. 2002), reptiles (Trillmich and Trillmich 1984) and mammals (Campagna et al. 1992), but it is especially remarkable in seabirds, with about 95% of the species breeding in colonies (Wittenberger and Hunt 1985).

Breeding in close proximity can confer several advantages. For instance, it has been shown that colonial breeding can enhance the defence against predators through dilution effects (i.e., the risk of predation per capita is lower as colony size increases, see Krebs and Davies 1978; Hötker 2000) or by allowing an earlier detection of predators (Brown and Brown 2001), and an increased efficiency of social mobbing (Hoogland and Sherman 1976; Siegel-Causey and Kharitonov 1990, Coulson 2002). Moreover, colonies can act as 'information centres', where individuals at the colony can acquire information about food patches from the behaviour of others that have foraged successfully (Ward and Zahavi 1973; Emlen and Demong 1975; Weimerskirch et al. 2010). An aggregation of birds in space can also facilitate mate finding and retention (McCarthy 1997; Dubois et al. 1998).

However, colonial breeding also involves a considerable number of disadvantages. The likelihood of depleted food resources within the vicinity of the colony increases (Furness and Birkhead 1984; Lewis et al. 2001; Ballance et al. 2009; Lamb et al. 2017). In crowded conditions competition for nest sites and mates becomes more severe (Møller 1987; Hötker 2000; Kokko et al.

2004). Coloniality also increases the number of intra-specific aggressive interactions in general due to the close proximity of a high number of conspecifics (Danchin and Wagner 1997; Hötker 2000; Ashbrook et al. 2008), which can also lead to cannibalism and infanticide (Davis and Dunn 1976; Wittenberg and Hunt 1985, Møller 1987). Colonial breeding can moreover facilitate disease and parasites transmission (Olsen et al. 2006). Colonial breeders are at a higher risk of disease and parasite transmissions because of the dense aggregation of birds in the same area for a prolonged period of time (Brown and Brown 1986; Møller 1987; Uhart et al. 2018; Dias et al. 2019). Recently, the highly pathogenic avian influenza has illustrated this again, since the beginning of 2022, avian influenza outbreaks have caused the death of hundreds of thousands of seabirds in or close by to their colonies.

While colonial breeding entails costs and benefits that may among others determine the size of a given colony, or the location where an individual settles, it is from an evolutionary point of view still a puzzle how this form of group living evolved. Some more recent hypotheses purport that coloniality could have evolved from group foraging, since it is easier to form a group when returning to a colony instead of finding conspecifics at the foraging areas (Richner and Heeb 1995; Richner and Heeb 1996). Danchin and Wagner (1997) proposed that high quality individuals tend to congregate in good quality sites, or that competition for breeding partners can promote sexual selection and thus coloniality. The ‘commodity selection’ hypothesis (Danchin and Wagner 1997) is a more integrative concept that states that animals may evaluate a suite of ecological factors, like potential mates, habitat quality, and reproductive success by using the presence in the breeding area of successful conspecifics as cue. Yet not only the origins of colonial breeding are unknown, but also whether the evolution of colonial breeding populations may change given the current rate of anthropogenic change.

Colonial breeding in a changing world

Anthropogenic change and the resulting levels of habitat loss and degradation both directly and indirectly affect various ecosystem processes, cause steep biodiversity loss, and impact on wildlife (Grimm et al. 2008; Sih et al. 2011). Seabirds are one of the most threatened taxa worldwide with many species facing population declines and several being in risk of extinction (Croxall et al. 2012; Dias et al. 2019). Climate change for instance has advanced the timing of prey availability on marine ecosystems, while many seabird species have been shown to be unable to adjust their breeding phenology to those shifts. These mismatches reduce chick survival and has hence direct fitness and thus consequences at the population level (Keogan et al. 2018; Sauve et al. 2023). In addition, many seabird species die directly from anthropogenic activities - as by-catch during fishing activities (Hall et al. 2000, Grémillet et al. 2018). Moreover, pollution of the oceans is of outmost concern, where it is predicted that 99% of the species will ingest plastics by 2050 if no management measures are taken (Wilcox et al. 2015).

The above-mentioned challenges are all related to their foraging at sea, but all seabirds have to go on land to reproduce, where they are exposed to further anthropogenic effects. Here, the main current threats for seabirds are related to anthropogenic habitat loss or degradation (Croxall et al. 2012), where environmental change due to human-related activities is particularly strong in urban environments (i.e., cities and sub-urban areas such as coastal, rural and industrial areas), since they represent a hotspot for anthropogenic activities.

Although this has negative consequences for many species, including seabirds, and even causes steep biodiversity loss (Marzluff 2001; Grimm et al. 2008; Sih et al. 2011), some species adapted to exploit these novel anthropogenic environments. Urban environments, for example, can provide predictable, constant and abundant foraging opportunities (Greig et al. 1986; Rock 2005; Oro et al. 2013). Seabirds, and particularly gulls, are a prime example of species that successfully make use of anthropogenic food sources, typically fishing discards in ports and at sea (Furness et al. 1992; Camphuysen 1995), earth worms and small vertebrates on agricultural fields, i.e., after ploughing (Isaksson et al. 2016; Spelt et al. 2019), or human waste on open-air landfills, in cities or on beaches (Belant et al. 1998; Duhem et al. 2003, Spelt et al. 2021).

In addition, gulls also opportunistically use human-made environments as breeding grounds. Yet, while urban habitats provide foraging opportunities, seabird species breeding in urban areas could be susceptible to anthropogenic activities, particularly urbanization, and to the resulting changes to their breeding habitat, which range from short-term disturbances to the sealing of suitable habitat. Seabirds are particularly vulnerable to these rapid changes, since they typically exhibit a high degree of nest-site fidelity, meaning that they tend to preserve their nesting site over consecutive breeding seasons (Birkhead 1977; Aebischer et al. 1995; Seyer et al. 2022). If breeders have to move to a different colony, which is generally infrequent in natural colonies, this is normally associated with disturbances in the breeding area, partner loss (Shields 1984; Forero et al. 1999; Robert et al. 2014), or poor breeding success over successive seasons (Switzer 1997; Forero et al. 1999; Schaub and Von Hirschheydt 2009).

Therefore, forced relocations due to anthropogenic activities presumably entail fitness costs due to the trade-offs between exploring and exploiting a new habitat, the difficulties of finding a new territory in a new (sub)colony, or the problems when finding a new partner, since nesting sites can function as meeting points for pairs (Morse and Kress 1984; Cézilly et al. 2000). Such costs could force individuals to skip the following breeding season (Roff 1992; Harris and Wanless 1995), and remain prospecting for new nesting sites and mates. Furthermore, competing in order to establish a new territory may be very costly, because nest site fidelity increases the degree of familiarity with neighbouring breeding individuals, and it may hence reduce the number of costly aggressive interactions ('dear-enemy phenomenon', Fisher 1954; Temeles 1994). Taken together, forced anthropogenic-derived relocations may have a substantial impact on the population dynamics of colonial breeding species by affecting individual reproductive success via various pathways. To understand the consequences of relocations, it is also absolutely necessary to have a better knowledge of the processes of how to establish a territory as well as of the role of the territory for chick development and survival, yet both are highly understudied.

The adult's perspective: the importance of the territorial establishment period

While breeding in close proximity can provide substantial benefits, this thesis focuses on the potential costs of colonial breeding, in particular those related to territoriality. The period of territorial establishment entails high levels of competition, especially in crowded conditions, when intra-specific competition for nest sites and mates becomes extremely severe (Møller 1987; Hötker 2000;

Kokko et al. 2004). Inside a territory, individuals court, mate and raise their offspring, so having chosen a nesting site, individuals (typically males), defend an area around it (i.e., the territory) to keep other conspecifics out. Therefore, individuals unable to establish a territory in the colony can miss breeding opportunities (Danchin and Cam, 2002), which again emphasizes that acquiring and maintaining a territory is essential for reproduction. Coloniality hence increases the number of intra-specific aggressive interactions because of the close proximity of a high number of individuals (Danchin and Wagner 1997; Hötker 2000; Ashbrook et al. 2008), and it is therefore likely energy and time demanding to successfully establish and defend nesting territories against other potential competitors. However, the energy and time investment in territorial defence may co-vary with breeding density or physical attributes of the nesting site. Commonly, central parts of the colony show both the highest breeding densities and highest per capita breeding success (Savoca et al. 2011), since the risk of predation (notably by ground predators such as foxes) on offspring is lower in dense areas due to dilution effects (Hötker 2000; Pratte et al. 2016). Moreover, vegetation cover of the nesting site can also provide protection for the offspring from weather conditions and predation and positively affect breeding success in ground nesting species (Pierotti 1982; Kim and Monaghan 2005). Intraspecific competition for the most productive nesting areas within a colony thus likely increases the energy and time that adults have to invest in territoriality.

It is against this background that many colonial breeding seabird species have evolved a broad signalling repertoire, including postures and calls, to reduce overt conflict between neighbours by indicating the opponent their competitive ability if a territorial contest was to happen (Tinbergen 1960; Figure 1).

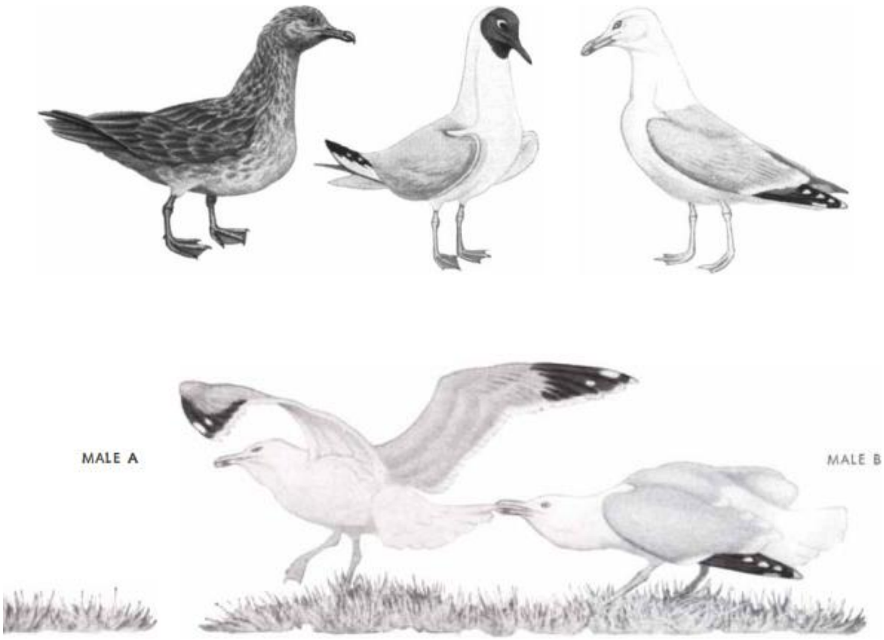

Figure 1. The upright position is a threat display meant to signalling the readiness to attack (top; Tinbergen 1960). An actual attack occurs when an individual invades the territory of another individual (down; Tinbergen 1960).

Territorial establishment and defence often start immediately upon arrival at the breeding colony, typically long before the onset of breeding (Del Hoyo et al. 1996). But the period when birds establish their territories is also key for accumulation of resources, both for self-maintenance and for clutch production before the onset of reproduction (Wendeln 1997; Reynolds et al. 2003), especially for migratory species that need to re-gain energy reserves after coming back from their wintering grounds. However, territoriality requires that birds are present in their chosen territory for a considerable amount of time, even if the actual number of overt territorial interactions is limited. The time that individuals invest inside their chosen territories is therefore an aspect that has to be considered in order to fully understand the costs of territoriality. Individuals are likely facing trade-offs between acquiring and holding a site for nesting and the necessity to accumulate resources for self-maintenance and reproduction. Such trade-offs could be further emphasized when birds relocate into new colonies (see above). However, little is known about possible time costs and constraints or how individuals balance foraging for self-maintenance and reproductive investment, and territorial activity. Even though this knowledge will be crucial to understand or predict how that will render them sensitive to anthropogenic change when breeding in urban colonies.

The offspring's perspective: the importance of the early-life period

The early-life period is of fundamental importance and an extremely challenging period for the offspring. In *Larus* gulls, parents play a key role by provisioning their chicks with food and by protecting them against predators and conspecifics. Moreover, by choosing and establishing a territory, parents set the environment that their offspring experiences during their development. This has significant consequences as it might lead to phenotypic differences among individuals (Bateson and Martin 1999), because the early life environment plays a fundamental role during development by triggering the expression of specific phenotypes by a particular genotype. For instance, wood frog tadpoles (*Rana sylvatica*) develop bigger tails for faster swimming when growing in water that has hosted predatory dragonfly larvae (Buskirk and Relyea 1998). In the European map butterfly, the expression of the summer and spring colour morphs depends on the temperature experienced during the larval period (Weismann 1875). Adverse (nutritional) conditions during early-life then again have been shown to induce detrimental effects on growth and hence size at adulthood, with long-term consequences for behaviour and fitness (Lindström, 1999; Arnold et al. 2007; Monaghan, 2008; Van Oers et al. 2015). Finally, social isolation or adverse social interactions early in life has been proven to cause long-lasting disturbances in exploratory, foraging and sociability behaviours (Broom and Leaver 1978; Ferdman et al. 2007; Lihoreau et al. 2009, Hunt et al. 2018).

For colonial breeding species it is the social component of the early-life environment that might be particularly relevant, among others because of the large aggregation of individuals in close proximity. The social environment and therewith the environmental effects resulting from it are a very special case in evolutionary terms, as an individual’s behaviour or phenotype can be directly influenced by the actions of other conspecifics (so-called “interacting phenotypes”, Moore et al. 1997). This implies among others that individuals are both agents and targets of selection, and that the resulting indirect genetic effects can influence evolutionary trajectories of phenotypic traits. Studying early environmental effects in colonial breeding species can hence provide fundamental insights into the causes of individual phenotypic variation.

Another indirect genetic effect that could play a significant role is the so-called parental effect, as parents may prenatally prepare their offspring for the (social) environment they likely will encounter (Bernardo, 1996; Mousseau and Fox, 1998, Badyaev and Uller, 2009). Given the predominant role of the females, in birds this is usually referred to as maternal effects. As Mousseau and Fox (1998) stated: "*Maternal effects often provide a mechanism for adaptive transgenerational phenotypic plasticity, in which the environment experienced by the mother is translated into phenotypic variation in the offspring*". Mothers may allocate a range of resources prenatally to their embryos, such as nutrients, hormones or antibodies. As mentioned above, from a Behavioural Ecologists perspective, maternal effects are thought to better prepare individuals for particular situations they will most likely encounter in their post-hatching environment, and that can have lasting effects on the offspring's behavioural phenotype (Ward and Weisz, 1980; Schwabl 1996; Schwabl et al. 1997; Ketterson and Nolan, 1999; von Engelhardt and Groothuis, 2011). For instance, maternal yolk androgens are correlated with an increased exploratory behaviour (Ruuskanen and Laaksonen 2010), higher activity (Daisley et al. 2005) and greater territorial behaviour (Müller et al. 2009) of their offspring.

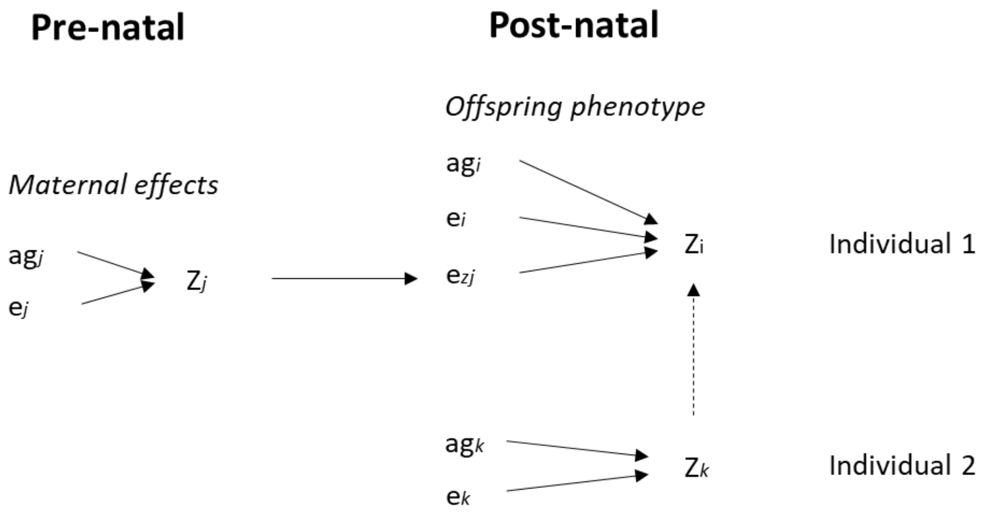

Figure 2. Genetic and environmental contributions to the phenotype in colonial breeders (modified from Wolf et al. 1998). Ag=additive genetic effect; e = environmental effect; Z= phenotype. In the example, the maternal phenotype (Z_j) and the phenotype of Individual 2 (Z_k) are influenced by environmental (e_j and e_k respectively) and additive genetic components (ag_j and ag_k respectively). The offspring phenotype (Z_i) will be shaped by its genes (ag_i), and both the environment it experiences (e_i) and the one experienced by its mother and transmitted via maternal effects (e_{zj}). The social environment is also a key component shaping the developing individuals' phenotype through social interactions (expression of Z_i is influenced by the social interaction with z_k, represented by the dashed line).

Maternal effects hence might play a significant role in colonial breeding species by pre-adjusting their progeny to the social environment (i.e., breeding densities, proximity to neighbours) in which the offspring will be raised. Variation in the social early life environment is hence supposed to translate into variation in offspring behaviour, and if these effects are lasting, it might also have consequences for the behavioral phenotype at adulthood.

Study system: the Lesser black-backed gull

The lesser black-backed gull (*Larus fuscus intermedius*) is a migratory and colonial seabird. As many other seabird species, lesser black-backed gulls are a long-lived (generally longer than 10 years old, the maximum longevity recorded was of almost 35 years old; Robinson et al. 2022), monogamous species, where pair-bonding plays a key role and takes a considerable amount of time. They are sexually dimorphic, with males being bigger than females (Snow et al. 1998). Conventionally, breeding colonies were found along the coasts of northern and western Europe. Over the past century, the species expanded its breeding range inland and colonized new habitats, such as urban areas (Cramp and Simmons 1983; Olsen and Larsson 2004; Ross-Smith et al; 2014. Spelt et al. 2019). For instance, breeding colonies of Lesser black-backed gulls in Belgium and south of the Netherlands are now often found in industrial ports and city rooftops. Lesser black-backed gulls migrate to a broad range of wintering grounds, the Dutch and Belgian populations typically to Africa or Southern Spain, but also to France or even the UK (Baert et al. 2018). Lesser black-backed gulls return to the breeding colony long before the start of the breeding (del Hoyo et al. 1996). In our study populations, first birds are seen in the colony at the beginning of March with males and females arriving at the colony at the same time (Bosman et al. 2012). First, birds establish and defend their (previous) nesting sites, and re-unite with their breeding partners. It then takes more than two months after the first arrivals in the colony before egg laying starts, (i.e., first eggs in our study colonies are generally found during the last week of April, see Baert et al. 2021). Females typically lay a single clutch consisting of three eggs. After egg-laying, both parents are involved in incubation, which lasts about three weeks. During the chick-rearing phase, both parents contribute to offspring provisioning and share duties regarding offspring defence from predation or cannibalism. Chicks fledge at around a month after hatching, but parents and offspring initially stay close to the colony and parents keep feeding their chicks until they are independent.

Lesser black-backed gulls not only expanded their geographical range to inland and urban areas in the past century (Cramp and Simmons 1983; Olsen and Larsson 2004; Ross-Smith et al. 2014, Spelt et al. 2019), but also extended their ecological niche nowadays by exploiting highly predictable, anthropogenic-derived resources such as landfills or rubbish dumps (Hunt and Hunt 1973; Bond 2016). The lesser black-backed gull is considered a generalist species (Coulson and Coulson 2009, Camphuysen et al. 2010), but individuals often specialize on particular food sources (Juvaste et al. 2017; Van den Bosch et al. 2019).

Figure 3. The study species of this thesis, the Lesser black backed gull (*Larus fuscus intermedius*), equipped with a GPS logger.

Study area

I focused on two breeding colonies situated at the North Sea, one at the coast of Belgium and the other at the coast of the Netherlands (Figure 3). Both study populations are situated in industrial ports, where adults and chicks were colour-ringed allowing individual identification and monitoring of reproductive success. Initially, the Belgian colony at the port of Zeebrugge had different sub-colonies and reached over 4500 pairs between 2004 and 2011. The population has experienced a steep decline in the last decade, where minimum numbers were found in 2020, when only 401 pairs were found in the port (Stienen et al. 2021). Moreover, in the early 2000s, several human-made building activities were carried out within the port of Zeebrugge. Several birds relocated then to the port of Vlissingen (the Netherlands), where an intensive colour-ringing and monitoring program was ongoing (Roland-Jan Buijs, Buijs Eco-Consult). This colony had four different sub-colonies and also around 4500 breeding birds, but in 2020, again building activities in the industrial area of the port of Vlissingen erased suitable areas in two of the four sub-colonies, triggering the departure of individuals to other colonies.

Figure 4. Map of the two study colonies in Zeebrugge (Belgium, in orange) and Vlissingen (The Netherlands, in green). Plotted with package leaflet in R.

As other typical seabird colonies, my study colonies exhibited a large variation in nesting densities, where central parts were associated with the highest breeding densities. The vegetation cover was highly homogenous in both colonies. The colony in the port of Zeebrugge was fenced to avoid fox predation, and we also divided it in 8 plots of similar size using fences in order to facilitate the recapture, testing and tracking of chicks. We always provided shelters for the chicks after hatching in both colonies.

Thesis outline

In this thesis, I investigated the consequences of territory choice for both adults and offspring in a colonial breeding, migratory seabird, the lesser black-backed gull. I hypothesized that forcedly relocating, i.e., due to anthropogenic activities and nest site loss, to a new breeding site presumably entails costs, as individuals have to invest time and energy into finding and settling in new (sub)colonies, and in acquiring and maintaining a territory. Thus, in **Chapter 2** I first investigated the fitness consequences of anthropogenic change for the lesser black-backed gull, by quantifying the effect of forced nest-site relocation on reproductive investment.

In **Chapter 3**, I focused on the possible drivers underlying the costs of relocation. I hypothesized that defending a territory might pose a trade-off for birds, who have to weigh up their time between nest defence and other relevant activities like foraging. Moreover, these costs may vary among individuals and between nest locations, because competition is supposed to vary with breeding densities, with more central breeding spots being more attractive. Therefore, I studied how much time birds invest in territoriality, and whether this in turn has effects on their reproductive investment.

The choice of territory not only has consequences for the adults, as they may face a number of trade-offs when defending a territory, but likely also for the offspring. Chicks crossing into a neighbouring territory experience high rates of aggression from neighbouring adult breeding pairs, which will happen more often in dense areas of the colonies, where territories are closer together. In **Chapter 4** I therefore investigated whether high breeding densities decrease the exploration activity of the chicks. Here, I specifically took into account that the behavioural phenotype may also depend on maternal effects, which are thought to pre-adjust offspring behaviour to match the conditions experienced post-hatching.

Given the exposure to aggression**,** I also hypothesised that high breeding densities would reduce their movement activity given also the smaller territory size in high breeding densities. Chicks would still likely be more socially connected to other chicks in such high density areas because of a higher spatial proximity. I therefore investigated in **Chapter 5** the effects of the early-life environment on the movement behaviour of the chicks. As in chapter 4, I designed experiments as such that I could quantify the impact of both pre-natal maternal effects and post-hatching environment.

Finally, in **Chapter 6**, I integrate the findings of this dissertation over a comprehensive general discussion, and point out the limitations of my study.

Subcolony of Zeebrugge in the early 2000s.

CHAPTER 2

Forced nest site relocations negatively affect reproductive investment in a colonial seabird species

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Abstract

Species breeding in urban environments are highly prone to a wide variety of non-natural, human activities, which range from short-term disturbances to the degradation or loss of suitable habitat. The latter in turn may force individuals to relocate to new sites for foraging or breeding, both of which presumably entails fitness costs due the trade-offs of finding and exploring new habitat. Species showing a high level of spatial foraging specialisation or nest site fidelity are expected to be most vulnerable. In this study, we explored the consequences of nest site loss on the reproductive investment of lesser black-backed gulls (*Larus fuscus*), a site faithful seabird species breeding in an urban environment. We monitored a population of 1.173 colour-ringed gulls across 13 years, that involved several episodes of spatially restricted loss of breeding habitat. We found that birds which lost their breeding territories reduced their investment into the eggs as reflected in a decrease of the clutch volume. They relocated over larger distances compared to birds that relocated voluntarily. Moreover, the likelihood of skipping the subsequent breeding season increased after a forced relocation. These negative effects of forced relocation likely contribute to the decline in the number of breeding pairs in our urban population as observed during the last ten years, and highlights the importance of maintaining a stable breeding environment in urban areas for the conservation of this and potentially other colonial breeding seabird species.

Introduction

Colonial breeding is defined as a dense aggregation of individuals during the breeding period, where the breeding area does not contain any other resources other than nesting sites (Wittenberg and Hunt 1985; Danchin and Wagner 1997). It is believed to entail a number of benefits, such as enhanced anti-predator efficacy (Götmark and Andersson 1984; Arroyo et al. 2001; Hernández-Matías et al. 2003), easier access to potential partners (McCarthy 1997; Dubois et al. 1998), or improved foraging efficiency when colonies act as 'information centres' (Ward and Zahavi 1973; Emlen and Demong 1975; Weimerskirch et al. 2010). Colonial breeding occurs in a variety of species including reptiles (Trillmich and Trillmich 1984), mammals (Campagna et al. 1992), spiders (Uetz et al. 2002) and fishes (Gross and MacMillan 1981), and has intensively been studied in birds, where about 13% of the species breed colonially (Lack 1968).

In long-lived colonial breeding birds, pairs typically tend to keep the same nesting territory for an extended period (Spendelow et al. 1995; Vergara 2006; Robert et al. 2014), which may entail several advantages. Within-colonies, there are likely differences in nest site quality (Minias 2014) or in predation risk, with central breeders achieving higher breeding success as a result from lower predation rates on eggs and offspring (Coulson 1968; Savoca et al. 2011; Minias et al. 2012; Pratte et al. 2016). Pairs should hence aim to retain their territory once they obtained a high-quality nesting site. Keeping the territory may also facilitate mate retention (Morse and Kress 1984; Cézilly et al. 2000), which in turn benefits reproductive success, since pair bond duration is positively associated with breeding success (Coulson 1966; Sanchez-Macouzet et al. 2014). Finally, nest site fidelity can promote a stable social environment within colonies, a particularly relevant aspect since colonial breeding also involves high levels of intra-specific competition for nesting sites (Danchin and Wagner 1997). According to the ‘dear-enemy phenomenon’ (Fisher 1954; Temeles 1994), territorial animals are thought to respond less aggressively towards neighbours than to strangers. As nest site fidelity increases the degree of familiarity with neighbouring breeding individuals, it may reduce the number of costly aggressive interactions.

If nest site relocations occur, this is hence often in conditions when individuals gain a benefit from dispersing to better-quality spots in the colony (Kokko et al. 2004; Acker et al. 2017). Such a switch to other nesting sites is especially common when previous breeding events appeared unsuccessful (Switzer 1997; Forero et al. 1999; Schaub and Von Hirschheydt 2009). Relocations to a new nesting site can also be observed when individuals have lost their partner due to mortality or divorce (Shields 1984; Forero et al. 1999; Robert et al. 2014). Lastly, presence of predators in the colony (Oro et al. 1999; Barros et al. 2016) or habitat loss (Burger and Gochfeld 1994; Cadiou et al. 2010) can make parts of a colony unsuitable for breeding, often forcing individuals to relocate over longer distances, potentially among (sub)colonies, and may in some cases lead to a desertion of their original breeding sites (Fairweather and Coulson 1995; Coulson and Coulson 2009). Nowadays, habitat loss and degradation due to building or other human-related activities, and its consequences on wildlife, constitute a major issue of concern (Grimm et al. 2008; Sih et al. 2011). Human-made environments, which are opportunistically used as breeding grounds, therefore render those individuals especially vulnerable to habitat changes, since such areas represent a hotspot for anthropogenic activities.

Besides the loss of some of the above-cited advantages of social cohesion, forced relocations likely entail a cost for reproduction. Individuals might for example have to skip the following breeding season (Harris and Wanless 1995), and remain prospecting for new nesting sites. This has been observed in the context of artificial nest and egg removal that was implemented to prevent individuals e.g., from nesting on rooftops, which often lead to forced relocations, followed by a disruption of breeding that could be prolonged over the following breeding season (Fairweather and Coulson 1995; Coulson and Coulson 2009). Thus, forced large scale anthropogenic-derived relocations may have a substantial impact on the population dynamics of colonial breeding species, which may threaten the coexistence of humans and colonial breeders in urban environments. However, to our knowledge, there are no long-term studies addressing the effects that forced nest site relocations, mainly driven by anthropogenic activities, may have on individual fitness, or in other aspects of the breeding biology of species, like for instance, partner change.

In this study, we used a long-term dataset to investigate whether forcedly relocating to a new nesting site influences reproductive investment in a lesser black-backed gull (*Larus fuscus*) population breeding in an industrial area in Belgium (Zeebrugge, 51°20′N, 3°10′E). Lesser black-backed gulls are site faithful colonial seabirds (Greenwood and Harvey 1982) that successfully adapted to breeding in anthropogenic environments (Camphuysen 2013; Stienen et al. 2016). Yet, during this study, our focal population was subjected to a series spatially restricted habitat degradation events within the different sub-colonies that each time made a portion of nesting sites unavailable. Using a dataset containing individual-based information on the location of each nest, the availability of breeding sites, partner identity and reproductive investment (clutch volume) of colour-ringed birds across 13 years (2001—2014) we were able to test our prediction that forced relocations will have a negative impact on reproduction in contrast to voluntary changes of nesting sites (=individuals changing their nesting location while their previous nest site is still available), which may rather represent upgrading strategies. Specifically, we hypothesized that individuals that are forced to change their nesting sites are more likely to skip the subsequent breeding season, to relocate across greater distances than when voluntarily relocating and that they are more likely to switch partner. The latter two aspects may contribute to a lower reproductive investment because of a mounting unfamiliarity with increasing relocation distance, and the loss of the benefits of long-lasting pair bonds.

Materials and Methods

General monitoring of the colony

From 2001 to 2014 (except 2003), a population of 1.173 colour-ringed lesser black-backed gulls breeding in an industrial port in Zeebrugge (Belgium) was monitored. The colonies were systematically visited three days a week to identify nests of marked adults. Once a clutch was completed, egg length and breadth were measured to the nearest 0.1 mm using a digital calliper. The egg volume was calculated as 0.476*height*width^2/1000 (Harris 1964). Only 3-egg clutches were measured, and the egg volumes of all three eggs were added to obtain an integrated measure, the total clutch volume. Subsequently, the coordinates of each nest were annotated using a handheld GPS device. Sexing of individuals was determined through direct size comparison of paired individuals, complemented by observations of copulation and courtship behaviour at the breeding colony (294 females, 307 males). Reliability of sex during successive breeding seasons was 100%.

Type of relocation and distance moved

To determine if and over which distances birds relocated between breeding seasons, great circle distances were calculated with the distHarvestine function in Geosphere package (Hijsman, 2016) using the GPS coordinates of the successive nesting sites. Whether individuals relocated voluntarily or forcedly was annotated in Quantumgis. Taking the accuracy of the GPS into account we considered birds that moved less than 15 meters (n = 772) as sedentary. To further distinguish between forced and non-forced relocation, polygons with all recorded nesting sites were created for each year and compared with historical data. Forced relocations are defined as changes in nesting sites because of (a) building activities such as the construction of warehouses or asphalting for parking that made the nest site unsuitable and (b) the presence of foxes that always leads to abandonment of the nest site. Whereas voluntary relocations are movements to new sites while the previous breeding location was still available and suitable ($N_{\text{forced}} = 114$; $N_{\text{voluntary}} = 366$).

Pair bond duration and partner change

When both partners were colour-ringed (n = 382), we could assess whether the pair was still composed of the same individuals as in the previous breeding event. We were not always able to distinguish divorce from mate loss, since information on mortality of our ringed birds was incomplete. The term partner change is hence used for the remainder of this manuscript. In our dataset, there were 38 cases of partner change. Pair bond durations within the time frame of our study ranged from one to nine years.

Data selection

We only used data from individuals with at least two breeding events to be able to calculate a relocation distance. Because carry over effects of a relocation likely diminish over time, only data where the gap between two breeding events was at maximum two breeding seasons were taken into account (1.252 recordings from 601 individuals). We therefore incorporated egg laying gaps of one year, as individuals might not succeed to breed the year immediately following a relocation or partner change. To facilitate the comparison of clutch volumes across years, Z-scores were calculated by subtracting the year-based average clutch volume from each clutch of that year, divided by the corresponding standard deviation.

Statistical analyses

First, we fitted a linear mixed model with reproductive investment (year-corrected Z-score of clutch volume) as dependent variable (n = 382) and the type of nest site relocations (forced, voluntary, sedentary), partner change (yes = 1 / no = 2), the time elapsed between two breeding events (1 year vs. 2 years) and sex as fixed factors. All paired interactions between the fixed effects were included. Individual ID (thus controlling for pseudoreplication associated with repeated measures from the same individuals) and pair ID (each individual is not independent from its partner) were selected as random effects. After a change of partner, individuals were assigned a new pair ID.

Second, we fitted a linear mixed model testing whether clutch volume (year-corrected Z-score) was affected by the relocation distance (excluding the sedentary category and thus avoiding zero inflated distributions), sex, time elapsed between breeding events and/or nature of relocation, including pairwise interactions (n = 480). In this way, we also maximized the sample size by taking into account cases for which information regarding partner change were not available (colour-ringed birds with an unringed partner), and took into account only birds that changed their nesting sites. This linear mixed model was performed using individual ID and pair ID as random factors.

Third, we run a GLMM with a gamma distribution to explore whether relocation distance (square root transformed) varied according to type of relocation (forced or voluntary), partner change (yes = 0 / no = 1), sex (female = 0, male = 1), and all paired interactions. Individual and pair ID were included as random effects.

Fourth, we fitted a binomial GLMM to investigate whether the likelihood of skipping a breeding season was affected by the same explanatory variables as stated above (i.e. type of relocation, partner change, sex, and their interactions). Again, individual and pair ID were the random effects.

Finally, we fitted a binomial GLMM to assess if partner change was sex-dependent, and/or influenced by the type of relocation (including pairwise interaction between fixed effects), with individual and pair ID as random effects.

For statistical analysis, we fitted linear mixed models and generalized linear mixed models to our data using the ‘lme4’ package (Bates et al. 2015) in R (R Core Development Team 2016). Normality, independence and homoscedasticity were explored by analysing model residuals. Post hoc tests were conducted using the ‘emmeans’ (Lenth et al. 2018) and ‘phia’ (De Rosario-Martínez 2015) R packages. For visualization of results, package ‘ggplot2’ was used (Wickham 2016). A backwards elimination procedure was used to obtain the most parsimonious models. Statistical significance was set at a critical α level of 0.05.

Results

Changes in reproductive investment in function of partner change and nest site relocation

Both, the effect of partner change and the effect of type of relocation on clutch volume were different when birds laid a clutch in the subsequent year compared to breeding after a one-season gap (Table 1). Voluntarily moved birds had bigger clutch volumes after relocation than sedentary birds, independently of the time elapsed between breeding events ($t = -2.17$, $p = 0.03$; $t = -2.41$, $p = 0.02$), whereas forced relocated birds had smaller clutch volumes in the season immediately following such relocation ($t = 5.60$, $p < 0.001$). However, in the second year following forced relocation (2-year difference in between measurements), the Z-scores increased significantly and were closer to values of sedentary individuals ($t = 0.11$, $p = 0.91$; Fig. 1-A). When birds stayed with the same partner and skipped one breeding season, they also laid bigger clutch volumes ($t = -5.15$, $p < 0.001$). But this positive effect vanished if partner change occurred (Fig. 1-B).

Table 1. Full linear mixed models (1.) testing the effects of type of relocation, partner change, sex and likelihood of intermittent breeding on reproductive investment (clutch volume, year corrected Z-scores). A similar mixed model (2.) was fitted to test the effect of relocation distance on clutch volume, excluding the effect of partner change to increase sample size. Models included all pairwise interactions. * = statistically significant.

	Chisq	d.f.	*p*
1. Reproductive investment (Z-score)			
Movement type	31.54	2	< 0.001*
Partner change	0.503	1	0.48
Likelihood of intermittent breeding	1.03	1	0.31
Sex	0.03	1	0.85
Movement type * partner change	3.88	2	0.14
Movement type * likelihood of intermittent breeding	12.51	2	0.002*
Partner change * likelihood of intermittent breeding	4.2	1	0.04*
Movement type * Sex	0.05	2	0.98
Partner change * Sex	0.67	1	0.41
Sex * likelihood of intermittent breeding	0.02	1	0.87
2. Reproductive investment (Z-score)			
Movement type	0.03	1	0.87
Distance	1.48	1	0.22
Sex	2.71	1	0.09
Likelihood of intermittent breeding	0.004	1	0.95
Movement type * distance	4.22	1	0.04*
Movement type * likelihood of intermittent breeding	1.14	1	0.29
Movement type * Sex	1.32	1	0.25
Distance * Sex	0.85	1	0.36
Distance * likelihood of intermittent breeding	0.04	1	0.85
Sex * likelihood of intermittent breeding	0.03	1	0.85

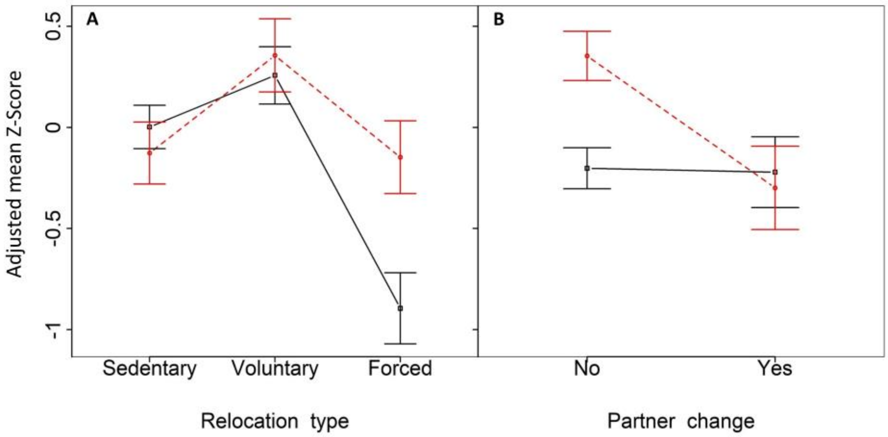

Fig. 1. Reproductive investment (adjusted mean values of egg investment, Z-scores) and standard error in function of (A) the type of relocation, distinguishing sedentary birds, birds that voluntarily moved to new nest sites, and birds that were forced to relocate. Data are separated for birds that laid in the subsequent breeding season (black) or that skipped one breeding season (red). (B) Reproductive investment in function of partner change, again separated for birds that laid in the subsequent breeding season (black) or that skipped one breeding season (red).

The effect of the type of relocation (forced versus voluntary) on clutch volume varied with the distance that birds moved (relocation * distance, $\chi2 = 3.98$, $p = 0.05$). For birds that were forced to relocate, the negative effects on reproductive investment became amplified with increasing relocation distance compared to birds that voluntarily moved (Figure 2).

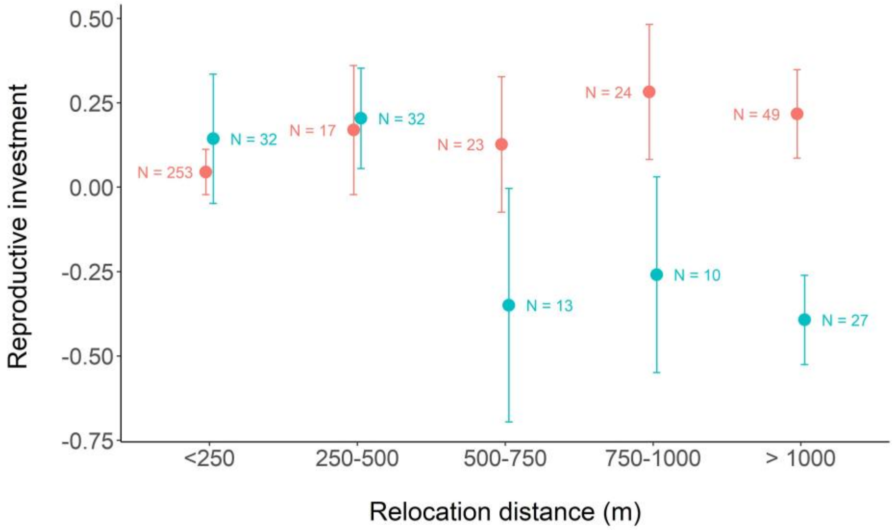

Fig. 2. The effect of the type of relocation (forced in blue and voluntary in red) on reproductive investment (year-corrected Z-scores) becomes larger for greater relocation distances. Data are binned into relocation distance intervals of 250 m. Dots represent mean values, and whiskers the standard deviations. Sample sizes are indicated by the numbers.

Likelihood of skipping a breeding season and probability of partner change

The likelihood of skipping a breeding season (Table 2) increased when a nest site relocation occurred ($\chi2 = 22.14$, $p = < 0.001$), although independently of the type of relocation ($Z = - 0.21$, $p = 0.97$). Furthermore, partner change increased the likelihood of skipping a breeding season ($\chi2 = 8.15$ $p < 0.01$). The likelihood of skipping a breeding was the same for males and females ($\chi2 = 0.16$, $p = 0.69$).

Table 2. Full generalized linear mixed models testing the effect of type of relocation, partner change and sex on (1.) the likelihood of skipping a breeding season and (2.) relocation distance. A third generalized mixed model (3.) was run to determine if the likelihood of partner change was affected by the type of relocation and sex. Models included all pairwise interactions. * = statistically significant.

	Chisq	d.f.	*p*
1. Likelihood of intermittent breeding			
Movement type	11.81	2	0.003*
Partner change	7.96	1	0.03*
Sex	0.01	1	0.9
Movement type * partner change	2.22	2	0.33
Movement type * Sex	0.004	2	0.99
Partner change * Sex	0.27	1	0.61
2. Distance			
Movement type	37.85	2	< 0.001*
Partner change	1	1	0.32
Sex	0.002	1	0.96
Movement type * partner change	0.46	1	0.49
Movement type * Sex	0.004	1	0.95
Partner change * Sex	0.002	1	0.96
3. Partner change			
Movement type	3.11	2	0.21
Sex	0.003	1	0.96
Movement type * Sex	0.96	2	0.62

The likelihood to change partner (Table 2) did not increase when birds were forced to relocate (χ2 = 2.41, p = 0.3), and did not differ between sexes (χ2 = 0.24, p = 0.62).

Distance and nest relocation

Over the course of this study, there were seven seasons where a part of the lesser black-backed gull population was forced to change nesting sites, while others voluntarily moved within the part of the colony that was still available (Fig. 3). When the previous nesting territories were available, voluntarily moving individuals relocated over significantly shorter distances (on average 441.2 metres) than when an area became unavailable (on average 564.6 metres). Neither partner change (χ^2 = 0.92, p = 0.33) nor sex (χ^2 = 0.00, p = 0.99) did affect the relocation distance.

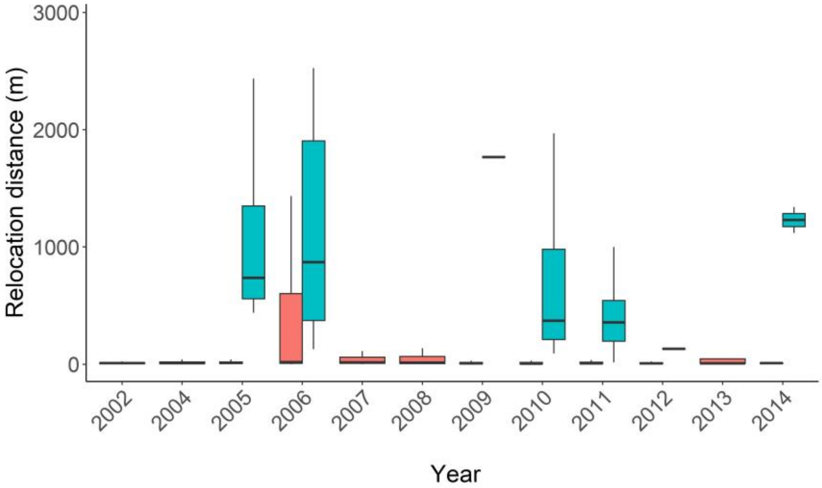

Fig. 3. The distance moved between breeding seasons from the original nest site to the new nest site. The 'not forced' category (red) included both sedentary and voluntary relocated birds, whereas the 'forced' category is represented in blue and includes only individuals that had lost their original nest site. Lines represent the median, and whiskers the 1.5 inter-quartile distance.

Discussion

Bird colonies are highly spatially and socially structured, and individuals often benefit from keeping the same breeding territory during successive years. However, habitat loss and degradation -whether or not due to anthropogenic activities- may force individuals to relocate to new breeding sites, at times over long distances. Yet, although breeding habitat loss often occurs, detailed studies on the consequences of nest site relocation for reproduction are scarce. In this study we provide clear evidence that losing a nesting territory and being forced to relocate to a new breeding spot comes at a reproductive cost in the site faithful lesser black-backed gull.

Costs for reproduction and relocation distance

We hypothesized that forced relocations that occur when the previous breeding location becomes unavailable or unsuitable would have a negative impact on reproduction, in contrast to voluntary changes of nesting sites as occur when individuals move to better-quality spots in the colony while their previous nest site is still available. To assess the impact of nest site relocations on reproductive investment, we measured clutch volumes as part of a longitudinal study, since egg size is an important parameter determining chick survival in birds (Parsons 1970; Krist 2011). We indeed found that forcedly relocated birds laid smaller eggs after relocation, indicating a reduced reproductive investment. The observed decrease in reproductive investment after changing nesting territories likely relates to the costs of losing a familiar nest site, as it has been shown that site fidelity covaries with higher reproductive success (Beletsky and Orians 1989; Piper et al. 2008; for a review of site familiarity, see Piper 2011). It may also reflect the costs of acquiring a new nest site, because of their limited availability or an increased unfamiliarity with neighbours and territories, both of which leading to higher, more escalated conflicts with new neighbours (‘dear-enemy’ phenomenon; Fisher 1954).

Intriguingly, we found a clear difference in reproductive investment between birds relocating voluntarily or forcedly. When pairs relocated in despite of having a previous territory available, they laid bigger eggs, even though those birds likely face costs of site unfamiliarity too. This suggests that birds voluntarily change their nesting sites when advantageous; for example, when relocating to a better territory with lower egg predation by conspecifics or less disturbance by human activities. Such an upgrading strategy may require some form of queuing, which could go along with an increase in reproductive performance due to increasing age. Indeed, age and breeding experience are well-known to increase individuals’ reproductive success (Wooller et al. 1990; Forslund and Pärt 1995; Limmer and Becker 2010; Bosman et al. 2013). However, in this study we were not able to control for age since very few individuals were ringed as juveniles in this colony or elsewhere. It could also be argued that individuals move voluntary when they are in better body condition to compete for new (and possibly better quality) nesting sites, which could also be reflected in a greater investment in their eggs. Unfortunately, body mass was only measured at the moment that the bird was ringed, so that we cannot capture the dynamics in body condition that could drive voluntary relocations. Yet, independent of the causes underlying nest site changes, we clearly prove that birds do not gain any of these benefits when forced to relocate – even though this occurred over comparatively small distances. Furthermore, our data show that forcedly relocated birds dispersed across greater distances than voluntary moving birds, and the further the forced but not the voluntary dispersing birds moved, the smaller their clutch volume.

It has also to be noted that all birds involved in this study kept breeding within the area, so it is very likely that they could maintain their foraging sites/habits. This reinforces the idea that nest site familiarity and a stable social environment are key factors for the reproduction of lesser black-backed gulls and probably many other long-lived colonial birds.

Likelihood of intermittent breeding and partner change

Settling in a new territory appears to be difficult, as we could show that after a nest site relocation there is an increased chance that birds skip a breeding season, whereas sedentary birds are more likely to be found breeding every year. In long-lived species, individuals may decide to skip one or more breeding season to increase their future reproductive success in case current conditions are suboptimal (Roff 1992). Our data are in line with the idea that birds can improve their reproductive investment by intermittent breeding. In fact, intermittent breeding has been found in several seabird species (Calladine and Harris 1997; Bruinzeel 2007; Cubaynes et al. 2010), but here we show that this appears to be triggered by nest site relocations. Nevertheless, non-breeding relocated birds may benefit from prospecting at the new breeding site, thus getting familiar with the site and neighbours, and consequently decreasing the costs on reproduction associated with changing nesting territories. Indeed, when birds started to breed again after two years, these birds had a higher clutch volume than individuals breeding in the immediate year after a forced relocation. Having skipped a breeding season, individuals might have built up site familiarity. However, the increase in clutch volume was like that of sedentary birds suggesting that higher body condition because of spared costs of reproduction or gained age and experience, could play a significant role too.

Finally, losing breeding territories might come at the cost of increased partner change rates since nesting sites can function as meeting points for pairs (Morse and Kress 1984; Cézilly et al. 2000). This is especially relevant when birds are forced to move over very long distances. However, this study was carried out in a limited context of an industrial area where birds could still have ample opportunities to meet, which is likely the reason why we did not find that relocation affected the rate of partner change. Moreover, changing partner might imply losing the benefits of increased pair bond duration on reproductive success (Coulson 1966; Sanchez-Macouzet et al. 2014). In fact, we found that skipping a breeding season is beneficial for reproductive investment when individuals stayed with their previous partner, yet when partner change occurs, those benefits were lost.

Implications for conservation

Anthropogenic habitat destruction and degradation has dramatic effects on wildlife and biodiversity worldwide (Grimm et al. 2008; Sih et al. 2011), but lesser black-backed gulls were considered an example of an opportunistic species that can successfully adapt to anthropogenic environments - for breeding and foraging. More recently, however, these positive population trends have reversed. While this decrease initially concerned coastal colonies (Camphuysen et al. 2010; Ross-Smith et al. 2014), now population declines dismayingly affect lesser black-backed gull populations in urban environments. For example, our study population has declined by about 75% over the past ten years (from 4484 to 956; Stienen et al. 2018, Stienen personal communication).

The causes of the decline are likely complex, which in conjunction with their intimate association with the urban environment hampers successful conservation strategies. Here, we show that forced relocations due to loss of breeding habitat not only impinge on the likelihood of breeding, and therewith reproductive output, but also has subtle long-term negative effects on egg volume and thus offspring quality. Both can contribute to the observed negative population trends (Stienen et al. 2018). Moreover, these effects should be taken into account when implementing control measures to reduce urban gull populations, such as removal of nests and eggs, which are likely to have similar consequences. Finally, forced relocations may also affect other colonial gull species, such as the herring gull, which has similar ecological requirements and often co-habits with lesser black-backed gulls in the same breeding colonies. In fact, the herring gull is already listed as “Near Threatened” by the IUCN in their last European assessment in 2015, which underlines the need for better knowledge and systematic monitoring of urban colonies.

Conclusions

In this study, we show that forced relocations due to nest site loss have a negative impact on the reproduction of a colonial seabird species breeding in an urban environment where anthropogenic disturbances are one of the drivers leading to permanent relocations of breeding sites. The resulting dynamics potentially disrupt a stable social environment, affecting reproductive effort and partner fidelity. Thus far, this has insufficiently been taken into account when implementing conservation strategies for this and other colonial breeding seabirds’ species.

Authors' contributions

RS: Conceptualization, Formal analysis, Writing - original draft. WM: Conceptualization, Supervision, Writing - review & editing. HV: Data curation. LL: Conceptualization, Writing - review & editing. ES: Conceptualization, Data curation, Supervision, Writing - review & editing.

Deployment of a GPS tracker on a Lesser black-backed gull.

CHAPTER 3

Territoriality constrains foraging activity and has carry-over effects[1] on reproductive investment

Salas R., Baert J., Stienen E., Lens L., Müller W.

Marine Biology (2022), **169** (87)

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[1] Effects that arise during the early territorial establishment period that affect egg laying, i.e., the consecutive reproductive phase.

Abstract

Colonial breeding provides benefits such as reduced predation risk, but also entails costs due to the enhanced levels of competition. In particular, it may require a significant amount of time and energy to establish a territory at the onset of reproduction, which in turn can impose carry-over effects on subsequent reproductive investments. Here we made use of GPS tracking devices to test how a colonial breeder, the lesser black-backed gull (*Larus fuscus*), balances its time investment between territorial and foraging activities throughout the pre-laying period, and investigated possible fitness consequences. As hypothesized, individuals that spent more time in their territories reduced their foraging time, foraged closer to the colony, and spent less time commuting during foraging trips. Although males initially invested more time in establishing a territory, both sexes gradually spent more time in their territory as the onset of egg laying, an energetically demanding period, approached. Furthermore, males that exhibited a higher territory attendance alleviated the females' time constraints for foraging and their partners laid larger eggs. Our results highlight the importance of quantifying carry-over effects related to time-budgets during the (often understudied) pre-laying period, in order to better comprehend fitness consequences of colonial breeding.

Introduction

Colonial breeding is a widespread phenomenon in nature, occurring in a variety of taxa such as spiders (Uetz et al. 2002), reptiles (Trillmich and Trillmich 1984) and mammals (Campagna et al. 1992). It is also very common in seabirds, where about 95% of the species breed in colonies (Wittenberger and Hunt 1985). Aggregating in breeding colonies provides a variety of benefits, such as easier access to potential mates (McCarthy 1997; Dubois et al. 1998), higher foraging efficiency as information on profitable foraging locations can be shared between individuals (Ward and Zahavi 1973; Emlen and Demong 1975; Weimerskirch et al. 2010) and an improved anti-predator defence (Götmark and Andersson 1984; Arroyo et al. 2001; Hernández-Matías et al. 2003; Jungwirth et al. 2015). However, colonial breeding also entails costs, such as high levels of competition for nesting sites (Potts et al. 1980; Coulson 2001; Hamer et al. 2001; Kokko et al. 2004), intra-specific predation of eggs and nestlings (Davis and Dunn 1976), and a density-dependent depletion of food resources within the vicinity of the colony due to high competition (Furness and Birkhead 1984; Lewis et al. 2001; Ballance et al. 2009; Lamb et al. 2017), which in turn can negatively affect offspring condition and survival (Hunt et al. 1986, Bonal and Aparicio 2008; Szostek et al. 2014).

Reproductive costs of colonial breeding have been typically studied during the post-hatching period. Nonetheless, the period of territorial establishment is equally essential for reproduction, yet it has been rarely investigated. Under strong competition pressure, individuals risk not being able to breed if they are not capable of acquiring and maintaining a territory in the colony (Danchin and Cam, 2002). Consequently, many seabird species arrive in their breeding colonies long before the start of the breeding season (del Hoyo et al. 1996).

Furthermore, it is common that individuals have to prospect in the year(s) before obtaining a first territory (Schjørring et al. 1999) or even queue before a territory becomes vacant (Ens et al. 1995) before being able to reproduce. The fitness costs of acquiring and defending a territory become particularly evident when birds are forced to settle in a new colony. Relocated birds have been shown to reduce clutch investment by laying smaller eggs (Salas et al. 2020), produce fewer fledglings (Barbraud and Delord 2021), and/or their offspring exhibit a reduced growth (Kavelaars et al. 2020).

Obtaining and defending a territory likely imposes a trade-off for individuals between time allocated to nest defence and other relevant activities like foraging. During the pre-laying period this might be particularly relevant for females because they need to accumulate resources for clutch production. In birds for example, it is known that females in better body condition lay larger eggs (Wendeln 1997; Reynolds et al. 2003), which is in turn associated with a higher reproductive success (Blomqvist et al. 1997; Krist 2011). Yet for females, having to attend the territory may limit their opportunities to obtain relevant resources and enhance their body condition. Males might compensate for that, e.g., by courtship feeding (males feeding their partner) which positively influences egg size (Nisbet 1973; Salzer and Larkin 1990), yet it may not be sufficient to outweigh the costs of territorial attendance of their female partner.

Furthermore, the time and energy costs that individuals are willing to spend on nest defence may vary within a colony. Commonly, high breeding density areas are associated with higher levels of agonistic interactions among individuals (Butler and Trivelpiece 1981; Hill et al. 1997; Hötker 2000; Ashbrook et al. 2008). In turn, high levels of competition for breeding sites may prevent low quality individuals from occupying territories in preferred (high density) areas (Coulson 1968), where the risk of heterospecific predation on offspring is lower (Pratte et al. 2016). Moreover, physical attributes of the nest site such as vegetation cover are known to positively influence breeding success in ground nesting species (Pierotti 1982; Kim and Monaghan 2005), and may co-vary with time investment in territorial defence. This implies that the costs of territoriality depend on the competitive abilities of the individual. Because body size is related with an individual’s competitive ability (Johnsson et al. 1999; Serrano-Meneses 2007), and since most seabirds are sexually dimorphic, agonistic interactions are predominantly performed by the larger sex, often males. Individuals of the larger sex play a major role in acquiring and defending nesting sites (Tinbergen 1956; Butler and Janes-Butler 1983; Paredes and Insley 2010). In Northern gannets, the larger males sometimes invest so much in territorial defence that they even lose more body weight than females do during egg laying (Montevecchi and Porter 1980). In turn, females often contribute passively in territorial defence by their mere presence in the territory.

Therefore, individuals of colonial breeding species are likely facing a trade-off between acquiring and holding a site for nesting and the necessity to accumulate resources for self-maintenance and reproduction, which may vary between sexes and with individual or territory quality. However, little is known about how individuals balance foraging for self-maintenance and reproductive investment, and territorial activity. Quantifying an individual’s presence in the territory along with its foraging activity was as yet virtually impossible, but recent technological innovations in miniaturized, remote-sensing devices offer novel and exciting opportunities for addressing such questions (Kays et al. 2015; Hertel et al. 2020).

In this study, we used the lesser black-backed gull (*Larus fuscus*), a migratory, colonial breeding seabird as a model species to get a better understanding of the costs of holding a territory, here focusing on time investment. We analysed high-resolution tracking data of 20 adult breeders to quantify the time each bird spent inside its territory throughout the 30 days prior to egg laying. We hypothesized that birds would increasingly spend more time in their territories as egg laying approaches, since the value of successfully retaining a territory increases over time. We further studied the impact of territory quality (expressed as local breeding densities) and individual quality (expressed as body size) on the time spent in the breeding colony during the territory establishment period (30 to 15 days to egg-laying date).We also analysed whether a greater time investment in territorial guard influenced their foraging activity, hypothesizing that birds would shorten their foraging and commuting time, along with their foraging distance travelled, with increasing investment in territory defence. Finally, we analysed if a high time expenditure inside territories affects reproductive investment. Since resource accumulation prior to laying is likely related to egg size, we hypothesized that females spending more time inside territories would lay smaller eggs as they might be limited in their foraging activity.

Materials and methods

GPS tracking and data treatment

We used the movement data of 20 individuals (7 females and 13 males) breeding in four sub-colonies situated in the harbour of Vlissingen, The

Netherlands (51.45N, 3.69 E). Data was collected between April and May 2017, 2018 and 2020. In Belgium and in the South of the Netherlands, first birds are seen in the colony at the beginning of March with males and females arriving at the colony at the same time (Bosman et al. 2012). Egg laying starts about 2 months after first arrivals, with first eggs generally found during the last week of April (Baert et al. 2021). Repeated measures across years were available for two males, and three couples were simultaneously tracked during the 2018 breeding season. Individuals were sexed molecularly (Griffiths et al. 1998), and morphometric body measurements were taken before deploying 18g UvA-BiTS solar-powered tracking devices on the birds collecting both GPS and acceleration data. Loggers were attached with a Teflon wing harness, and the total combined weight was less than 3% of the bird's body mass (the devices measured 61 × 25 × 10 mm and weighed 13.5 g + 5 g harness, for more detailed information see Bouten et al. 2013 and Thaxter et al. 2014). As lesser black-backed gulls are difficult to catch before egg laying, they were caught on the nest during the egg incubation period using walk-in traps and fitted with tracking devices. Therefore, data of the pre-laying period could not be collected until the breeding season of the following year. GPS fixes were taken every 6 minutes inside the colony and every 20 minutes outside of it. Still, for unknown reasons, we detected two major data gaps, where data was missing for more than 24 hours during the study period. GPS spatial resolution was at least of 10 m accuracy (Bouten et al. 2013). Four individuals had a 20 minutes resolution inside the colony, since battery levels were not sufficient to sample at high temporal resolution. Since we only had the body mass measure in the year prior to our measurements, we decided to use head-bill length, a morphometric size measure that is unlikely to change much between years, as a proxy for competitive capacities. We therefore measured the maximum distance from the bill tip to the back of the skull with a digital calliper (to the nearest 0.1 mm) when fitting the GPS tracker on a bird.

Reproductive investment and breeding densities

The colony was visited three times a week, and we recorded laying dates from the onset of breeding onwards (± 25th of April). Lesser black-backed gulls clutches generally consist of three eggs that are laid every other day. Visiting the colony three days per week ensured an accurate determination of laying dates. Egg length and width were assessed to the nearest 0.1 mm employing a digital calliper. For each egg, the volume was estimated as $0.476 * \text{height} * \text{width}^2 / 1000$ (Harris 1964). To account for incomplete three-eggs clutches due to commonly occurring intra-specific egg predation, we used mean egg volume as a measure for reproductive investment.

Distance to the three nearest neighbours (m) was recorded within 5 days after clutch completion using a distance meter tape. Distance was measured from the centre of the focal nest to the centre of the three nearest active neighbouring nests. The average distance to the three nearest neighbours was subsequently used as a proxy for local breeding density (Figure S3).

Territory size and time budgets

To delineate territory boundaries, we used the tracking data during the two weeks prior to egg laying, when birds likely have already established their breeding territory. To do so, we created polygons delimiting each of the four sub-colonies, which resulted in four areas of 2.6 km^2, 7.4 km^2, 12.8 km^2 and 49.9 km^2. Subsequently, we selected the GPS fixes that overlapped with such polygons and estimated the territory as being the 75% utilization distribution kernel using a 150 meter bandwidth (Figures S1 and S2).

Once we determined the territory boundaries for all individuals, we calculated how much time each individual spent inside (i.e., their individual kernel polygon) per day (=24 h) during the 30 days prior to the start of egg laying.

Foraging behaviour

We used a random forest classifier (Ho 1998) to identify three main types of behaviour during foraging trips: resting, flying and foraging (see Baert et al. 2021 for details). However, possibly due to memory space or power issues of the trackers when collecting acceleration data at the beginning of the field season, 25% of the behavioural annotation would have been lost if we would have used the acceleration profile as input information for the classifier (Baert et al. 2021). We therefore adjusted and subsequently trained the random forest classifier of Baert et al. 2021, as such that acceleration data were not further required. This classifier uses a combination of path geometry and habitat type to infer these three behaviours from the tracking data. Information on path geometry was included as the step length between consecutive GPS positions, and the turning angle between consecutive steps. Habitat type associated with each GPS was inferred from the MODIS Land Cover 500-m Yearly Combined (Type 1) dataset, which was extracted from the Env-data annotation system in Movebank (Wikelski et al. 2021). In addition, random forest models also used a 3-point moving input window to be able to exploit information that lies in specific movement sequences. This means that models were not only trained on the parameter values for each GPS position, but also for the previous and consecutive positions. We trained separate models to infer behaviours from the 5-minute and 20-minute resolution data due to inherent differences in the distributions of step-lengths and turning angles between resolutions. Models were trained and validated based on 128 annotated days of tracking data (64 individuals, 2 days for each individual), where each GPS position was assigned to either ‘resting’, ‘flying’ or ‘foraging’ by expert researchers, based on their knowledge in the field and in tracking data analyses. Half of these annotated days were used for model training, the other half for model validation. Each day assigned to either the training or validation dataset at random. The predictive power of our classifier was very similar to the one of Baert et al. 2021: our overall accuracy of the 5-minute resolution model was 84% (Cohen’s kappa 75). Our accuracy of the estimated behaviours was 93% for flying, 73% for foraging and 85% for resting. For the 20-minute resolution data, the overall accuracy of our model was 83% (Cohen’s kappa 75), and the accuracy to estimate the different type of behaviours were similar to the 5-minute resolution model, except for the resting behaviour, which had an accuracy of 84%. Models were fitted using the RandomForest package in R (Liaw and Wiener 2002).

We defined a trip as foraging trip when the following criteria were met: (i) the sequence of positions occurred outside the colony boundaries (a single polygon containing all sub-colonies mentioned above), and (ii) it included two or more consecutive fixes that were classified as foraging behaviour. Moreover, we omitted trips of less than 1 km of distance (N=52 out of 652), since resources close to the colony are scarce, and we did not observe birds foraging in this area of the industrial port (pers. observation). Furthermore, these trips had a very short duration (on average 12 minutes), so it is unlikely that birds were foraging within 1km of the colony. In total, we quantified 1064 trips outside the colony, of which 56.4% were classified as foraging trips. The remaining trips outside the colony were resting or exploratory trips. We only considered foraging trips in further analysis (N=600). For each individual, we calculated the following parameters on a daily basis: (i) furthest distance from the colony during a foraging trip (henceforth 'maximum distance travelled'), (ii) cumulative time between foraging bouts based on GPS fixes classified as flying ('commuting time'), and (iii) cumulative time spent foraging during a trip based on GPS fixes classified as foraging ('foraging time'). These parameters allowed us to explore whether time spent in the colony forces individuals to forage closer to the colony, as it may limit the time for commuting, and whether it limits foraging time and hence the opportunities for resource accumulation across the pre-laying period.

Data analyses

Since we focused on time investment (as presence in a territory is required to defend it), we fitted a linear mixed model (N_{ind}=20) to estimate how daily time spent inside the territory varied over the course of the pre-laying period, in relation to average distance to neighbours (estimate for local breeding density), head-bill length (estimate for competitiveness), sex, and year. To test for differences in temporal patterns between sexes, we also included a pairwise interaction between day and sex in the model. To account for pseudo-replication and temporal dependence in our data, bird ID nested in pair ID (an individual is not independent from its partner) was included as random effects, as well as a first order temporal autocorrelation structure.

To infer which parameters influenced time investment required for establishing a territory, we fitted a second linear mixed model for males (N_{ind}=13) during the first half of the 30 days before egg laying (i.e., day 30 to day 15 before egg laying). Males are hypothesized to play a key role in territorial defence, since mating activities rarely take place during that period, as females did not yet enter their fertile period, and nest-building activities are not frequent at such an early stage of the breeding season (Brown 1967; O'Connel et al. 1997). This ensured that the time spent inside the territory was mainly related to territorial activities. Daily time spent inside the territory was modelled as dependent variable, whereas average distance to neighbours, head-bill length, day and year were included as fixed factors. Individual ID was included as random effect to account for repeated measures, and a temporal autocorrelation structure was fitted.

To test whether time spent inside the territory affected the time birds spent foraging, we fitted a linear mixed model for all birds (N_{ind}=20) with daily foraging time as a response variable, and daily time spent in the territory, year, sex, and the interaction between daily time spent in the territory and sex as fixed effects. Individual ID nested in pair ID were included as random factors, as well as a temporal autocorrelation structure. We also re-ran the same model with (i) commuting time (square root transformed) and (ii) maximum daily distance travelled as dependent variable.

Finally, we fitted a linear mixed model (N_{ind}=20) to explore whether mean egg volume was affected by territorial attendance. We focused on the 14 days prior to egg laying (i.e., day 14 to day 1), as the mating activities and accumulation of resources for egg production in females starts around two weeks before laying. Here, head-bill length, year, sex, time investment (averaged individual values based on the 14 days prior to egg laying) and the interaction between time investment and sex were included as fixed effects. Individual and pair ID were selected as random factors.

Linear mixed models were fitted using the ‘nlme’ package (Pinheiro and Bates 2018) in R (R Core Development Team 2020). Normality, independence and homoscedasticity were explored by analysing model residuals. Package ‘ggplot2’ was used for visualization of results (Wickham 2016). Statistical significance was set at a critical α level of 0.05.

Results

Time-budgets

When establishing and defending a breeding territory, that is during the entire period of 30 days prior to egg laying, lesser black-backed gulls spent on average about 40% of their time in their breeding territory (males: 10.80 ± 0.20 h.day^{-1} (SE); females: 9.99 ± 0.35 h.day^{-1} [SE]). For both males and females time spent in the territory increased as egg laying approached (Figure 1), so that in the week before egg laying, both spent up to 58% of their time in the territory (males: 13.35 ± 0.39 (SE) h; females: 13.85 ± 0.56 (SE) h). As indicated by the significant interaction between day and sex in the full model ($p < 0.001$, Table 1), this temporal pattern differed between sexes: both sexes gradually increased their time investment inside the territory, but males already invested more time than females during the early phase when the territory was established (Figure 1). This pattern was very similar when taking into account only daylight data (Figure S4).

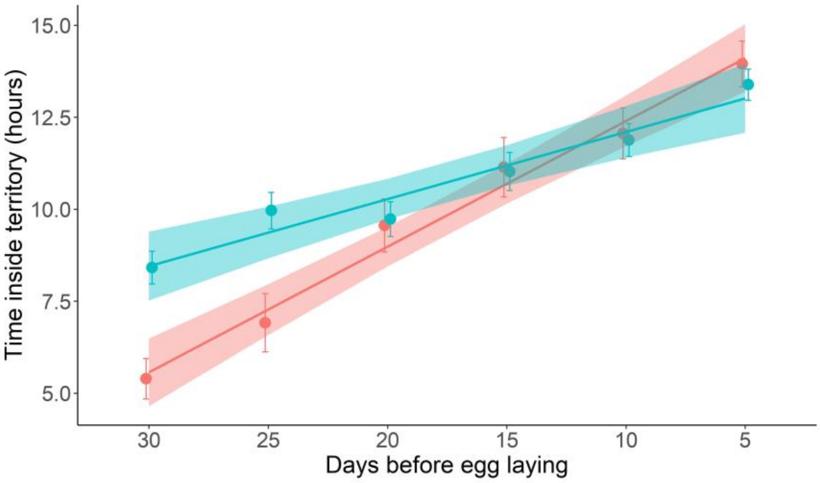

Figure 1. Time spent inside the territory across the 30 days prior to egg laying (binned in 5-day interval) for males (blue) and females (red). Dots represent the mean values, whiskers the standard error, and bands represent the 95% confidence interval.

During the territorial establishment period (from day 30 to day 15 before egg laying), males spent significantly more time in their own territory when distances to neighbouring nests were smaller (p-value = 0.01; Table 1), Their size also significantly influenced the time spent inside their territory, with bigger individuals spending more time than smaller ones (p-value < 0.01; Table 1).

Table 1. Full linear mixed models (1.) testing the effect of body size, local breeding density, sex and number of days before egg laying on the time investment inside the territory throughout 30 days before egg laying. A similar model (2.) was fitted to test the effect of body size, local breeding density and number of days before egg laying on the time males invested inside the territory during the period of territorial establishment (days 30 to 15 prior to laying).

	Coefficient	**SE**	**Chisq**	**d.f.**	**p-values**
1. Time in territory					
Year	-0.54	0.42	1.66	1	0.20
Day	-0.35	0.04	78,63	1	<0.001
Sex	-2.03	1.16	3,10	1	0.08
Distance to neighbours	-0.00	-0.00	3.02	1	0.08
Head-bill length	0.12	0.10	1.37	1	0.24
Day * Sex	0.16	0.05	10,99	1	<0.001
2. Time in territory during territorial establishment (males)					
Year	-1.31	0.57	5.27	1	0.02
Day	-0.10	0.05	3.59	1	0.06
Distance to neighbours	-0.00	0.00	6.06	1	0.01
Head-bill length	0.58	0.22	6.96	1	<0.01

Foraging behaviour and egg size in function of time investment inside territories

During the 30 days before egg laying, the daily time spent foraging (cumulative daily time considering only GPS fixes classified as foraging behaviour) was significantly shorter when birds spent more time in their territories, (Figure 2, Table 2). At the onset of the pre-breeding period (four weeks before egg laying), birds spent on average 5.06 ± 0.25 (SE) hours per day foraging, whereas in the week prior to egg laying, the foraging time decreased to an average of 2.99 ± 0.24 (SE) hours per day (Figure 2). No significant differences were found between males and females for the time spent foraging in both pre-breeding and prior to egg laying periods (Table 2). Likewise, the daily time spent on commuting during foraging trips was significantly reduced when birds invested more time in their territories, with males commuting significantly longer than females (males: 3.81 ± 0.10 (SE); females: 2.98 ± 0.16 (SE) h, Table 2). The daily maximum distance travelled during foraging trips was negatively related with the time spent inside territories, and males travelled further away from the colony compared to females (males: 51.13 ± 1.19 (SE) km; females: 41.19 ± 1.92 (SE) km, Table 2).

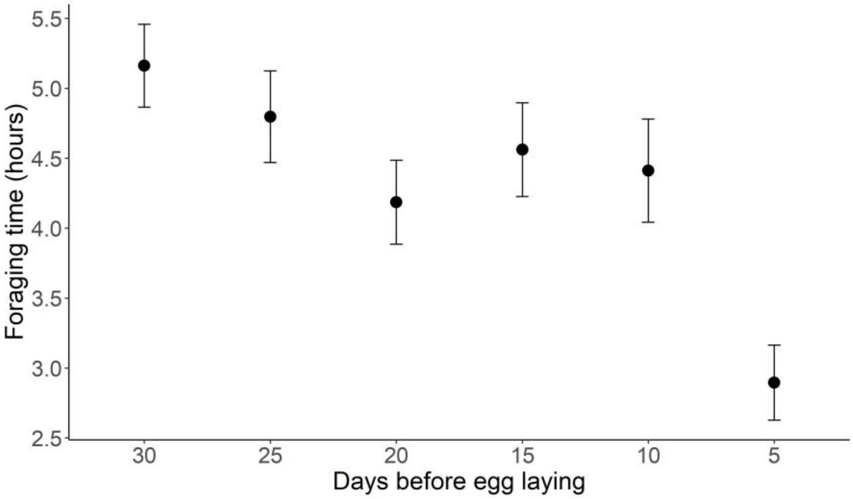

Figure 2. Daily time spent actively foraging across the 30 days prior to egg laying, for visualisation binned in 5-day intervals. Dots represent the mean values, and whiskers the standard error.

Table 2. Linear mixed models testing the effect of sex and time spent inside the territories on (1.) maximum foraging distance, (2.) foraging time, and (3.) commuting time during the 30 days before egg laying. A fourth linear mixed model (4.) was run to determine whether body size, sex and average time spent inside the territory during the 14 days prior to laying affected the reproductive investment (mean egg volumes).

	Coefficient	**SE**	**Chisq**	**d.f.**	**p-values**
1. Maximum foraging distance					
Year	-7.10	2.90	6.02	1	0.01
Sex	21.78	4.91	19.69	1	<0.001
Hours inside territory	-1.47	0.33	19.84	1	<0.001
Hours inside territory * Sex	-1.07	0.40	7.04	1	<0.01
2. Foraging time					
Year	-0.72	0.41	3.07	1	0.08
Sex	0.34	0.73	0.21	1	0.64
Hours inside territory	-0.35	0.04	66.09	1	<0.001
Hours inside territory * Sex	0.08	0.05	2.51	1	0.11
3. Commuting time					
Year	-0.16	0.05	10.61	1	<0.01
Sex	0.38	0.13	7.78	1	<0.01
Hours inside territory	-0.04	0.00	19.42	1	<0.001
Hours inside territory * Sex	-0.00	0.01	0.23	1	0.63
4. Mean egg volume					
Year	-1.20	0.91	1.72	1	0.19
Sex	-22.42	9.65	5.39	1	0.02
Head-bill length	0.38	0.27	2.01	1	0.16
Hours inside territory	-0.68	0.61	1.27	1	0.26
Hours inside territory * Sex	1.52	0.77	3.85	1	0.05

Finally, a significant interaction effect of time investment inside the territory and sex on mean egg volume was found showing that there are sex specific relationships (p= 0.05, Table 2, Figure 3). To further interpret such interaction, we performed separate linear model and linear mixed model for each sex, with mean egg volume as response variable, average time spent inside the territories as fixed effect, and bird ID as a random factor to control for repeated measures in males. When males spent more time in the territory during the two weeks prior to egg laying, their partner laid significantly larger eggs (linear mixed model estimate ± standard error = 0.97 ± 0.42; Chisq: 5.24, p = 0.02), while the opposite pattern, a negative effect of time spent inside the territory on egg volume was observed for females, even though this was statistically not significant (linear model estimate ± standard error = -0.96 ± 0.79; F-value: 1.48, p = 0.28), possibly because of the lack of power.

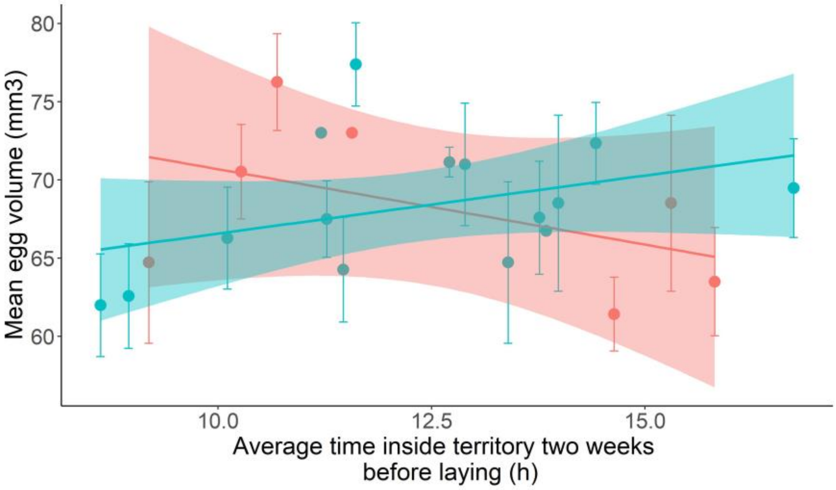

Figure 3. Effect of average time spent in the territories on mean egg volume for males (blue circles, standard error and regression line) and females (red circles, standard error and regression line). Bands represent the 95% confidence interval.

Discussion

In this study, the use of GPS tracking devices showed that in the 30 days before egg-laying, lesser black-backed gulls spent a significant amount of time inside their territories, which systematically varied across the pre-laying period and among sexes. Males significantly invested more time than females particularly during the period of territory establishment (30 to 15 days pre-laying). We also show that as egg laying approaches, birds spent more time in the territory and changed their foraging behaviour, which in turn might be the cause of the observed sex specific relationship between time invested in territoriality and resource allocation to the eggs. This high-resolution (in space and time) exploration of individual daily activities before egg laying allowed us to discuss novel insights into the costs of territoriality in colonial breeders.

Time investment in territoriality: temporal patterns and sex differences

Lesser black-backed gulls spent a substantial amount of their time (on average nearly 60%) inside their territory close to the egg laying period. The increased time investment when egg laying approaches, is likely due to the fact that losing a nesting site at a later stage might imply to lose the opportunity to breed in that year. Competing for a new nesting site might be impossible because of time constraints or become very costly, and it could go along with the loss of the breeding partner (Cézilly et al. 2000).

The high time investment of males during the early phase of the pre-laying period is likely relevant for territorial establishment (Tinbergen 1956; Butler and Janes-Butler 1983; Paredes and Insley 2010). Gulls show high levels of aggression during territorial defence, where larger sized males are likely in advantage. Indeed, males are more involved in agonistic interactions, while females typically contribute passively by their presence in the territory (Tinbergen 1956; Pierotti 1981; Burger 1984). Agonistic interactions between individuals (i.e., behavioural investment), which is in turn related to the energetic costs of defending a territory, could not be quantified in this study. However, presence in the territory (i.e., time investment), likely co-varies with such number of territorial activities, since the more time birds are physically present in their territories, the higher the chances to engage in territorial activities with other conspecifics.

Furthermore, we also showed that the amount of time spent by males to establish a territory was positively related to local nest density, suggesting that males have to invest more time in territory defence when in closer proximity to neighbours (Butler and Trivelpiece 1981; Hill et al. 1997; Hötker 2000; Ashbrook et al. 2008). Breeding in high density areas is beneficial due to reduced heterospecific predation of eggs and chicks (Pratte, et al. 2016), but involves higher competition costs and thus higher time investment as we can show. Moreover, it can be argued that higher quality males are able to allocate significantly more time and energy in territorial defence. This is indeed supported by our data, showing that larger males spent more time in their territory. Such relationships may result from the fact that larger males have higher competitive abilities, and hence, a higher resource holding potential (Parker 1974; Lindström 1988; Serrano-Meneses 2007), and possibly also because they are more efficient in (competitive) foraging and can therefore better withstand the costs of territoriality. Lastly, for ground nesting birds, vegetation cover around the nest site is also an important feature of the local habitat, which is positively related with breeding performance (Pierotti 1982; Kim and Monaghan 2005). This might in turn influence the time investment needed to establish and maintain territories with such physical attributes. However, our study colony was located in an industrial port, where the habitat was highly homogenous.

Time investment in territoriality: consequences for foraging and reproduction

As the time available during a day is obviously limited, allocating time in territoriality will likely constrain the time available for other activities, the most prominent one being foraging. Foraging is key for resource accumulation certainly for females during the pre-laying period. As expected, the time spent in the territory negatively varied with the time allocated to foraging activities. Birds changed their foraging behaviour, spent less time commuting, and foraged at shorter distances from the colony as egg-laying came closer. Furthermore, birds that foraged closer to the colony may have encountered greater competition. The fact that these closer foraging sites were not visited earlier during the pre-breeding season may also indicate that these are potentially poorer quality habitats (for more information on foraging specialisation in breeding females please see Baert et al. 2021). While time limitations could force birds to forage in close proximity of the nest, birds could also preferentially choose food resources with a predictable timing, such as urban resources (Baert et al. 2021).

Intriguingly, territory attendance increased for both sexes as egg laying approached, together with a decrease in time spent foraging. We hypothesized that a reduced foraging activity could directly influence the abilities of accumulating resources for egg production, in particular during the last two weeks before egg laying when egg production is ongoing. Males of lesser black-backed gulls are known to contribute to egg quality through courtship feeding, which is known to strongly increase over the 7-10 days before egg laying (Brown 1967), and to positively influence clutch size and egg volume (Nisbet 1973; Salzer and Larkin 1990). Nevertheless, we show here that a greater investment in territorial presence of males positively affected the egg investment of their partner. This relationship is most likely reversed in females but the lower sample size did not allow to capture statistically significant results. A possible reason for the observed larger egg volumes could be that good quality males are very efficient in foraging and courtship feeding, while still being able to spend more time in the territory. The marginal negative relationship between territory attendance and egg volume in females indicates that a high male presence could free females from having to attend the territory, which could ultimately be reflected in an increase in their own foraging opportunities and associated accumulation of resources for egg production. These findings suggest that courtship feeding would be more important for pair-bonding and mate selection, only constituting a complementary food source for females whilst they are capable of accumulating resources more efficiently by their own. However, this has to be interpreted cautiously given the relatively small sample size per sex and the difficulty to track both breeding partners simultaneously. While the negative relationship between foraging time and time spent in territory strongly suggest that the reproductive costs of territoriality might be a time cost, spending time in the territory might also entail an energetic cost, if time spent in the territory co-varies with the number of territorial disputes. These two aspects cannot be fully separated here since, as mentioned above, agonistic behaviour could not be quantified in this study.

Conclusions

For colonial breeders, holding a territory is required to reproduce, yet competition for nesting sites entails multiple costs as shown in our study. Birds have to allocate a significant amount of time in territory defence to an extent that they even had to limit their foraging activities. This seemed to compromise all aspects of foraging behaviour, i.e., time spent foraging, time spent commuting and the maximum distance they travelled for foraging. We argue that this likely generates a carry-over effect on the reproductive investment in egg size with possible fitness consequences. Our detailed insights into the costs of territory guarding provide significant knowledge on the costs and benefits of colonial breeding, and might be particularly relevant in the context of breeding habitat loss due to anthropogenic activities. Establishing a territory in a new colony might imply higher costs in terms of time investment, and therefore a negative effect on reproductive success. While this study focused on time investment in territoriality of resident birds, in a next step, studies should aim at increasing female and couple sample sizes, and integrate aspects of energy expenditure that might arise from the agonistic interactions during nest defence.

Authors’ contributions

RS and WM conceived and design the study. RS collected the data. RS and JB analysed the data. RS and WM wrote the manuscript. ES, LL and JB contributed with reviewing and provided critical scientific advice to improve the manuscript. All authors have contributed significantly to the development of this work.

The set-up for the behavioural testing of the chicks in Zeebrugge.

CHAPTER 4

Growing up in a crowd: social environment shapes the offspring's early exploratory phenotype in a colonial breeding species

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Abstract

In colonial breeding species, the number of adverse social interactions during early-life typically varies with breeding density. Phenotypic plasticity can help dealing with this social context, by allowing offspring to adjust their behaviour. Furthermore, offspring may not be unprepared since mothers can allocate resources to their embryos that may pre-adjust them to the post-hatching conditions. Thus, we hypothesize that lesser black-backed gull chicks raised in dense breeding areas, with greater exposure to intra-specific aggression, show higher levels of anxiety and lower levels of exploration compared to chicks in low density areas, and that this is facilitated by pre-natal effects. To test this, we cross-fostered clutches within and across pre-defined high- and low-breeding density areas. We measured chicks' anxiety and exploration-activity in an open field test that included a novel and a familiar object. We found that both pre- and post-natal social environment contributed nearly equally and shaped the offspring's exploratory behaviour, but not its anxiety, in an additive way. Post-natal effects could reflect a learned avoidance of intra-specific aggression, yet identifying the pathways of the pre-natal effects will require further study.

Introduction

When organisms are born, they are faced with a new, variable and challenging natal environment. Phenotypic plasticity, i.e., the ability of one genotype to express a range of different phenotypes across an environmental gradient, can help offspring to survive and optimally perform in a range of hostile environments. The latter can also be facilitated through pre-natal effects, such as maternal effects whereby the mother transmits environmental information to her offspring, which serves as an important cue to offspring development (Champagne 2008). When the mother correctly anticipates the post-natal environment, pre-natal effects can prepare offspring for environments they are likely to encounter (i.e., anticipatory maternal effects; Ward and Weisz, 1980; Schwabl 1996; Schwabl et al. 1997; Ketterson and Nolan, 1999; von Engelhardt and Groothuis, 2011). In other words, the perceived environment is translated into adaptive phenotypic variation in the offspring (Mousseau and Fox 1998), maximizing offspring performance via developmental plasticity (Marshall & Uller 2007; Bateson et al. 2014). However, the adaptive significance of such maternal canalization of offspring development hinges on the predictability of the conditions after birth. If the post-natal environment deviates from the predicted environment, then the phenotype can be mismatched which will negatively affect offspring performance. The pre-natal and post-natal context can therefore drive phenotypic adjustments to environmental conditions, and can become an instructive factor during development (Gilbert 2001). Recently, a lot of attention has been paid to the social component of the early-life environment, as the number and type of social interactions that newly-born individuals have with their parents, siblings or other conspecifics ("interacting phenotypes" sensu Moore et al. 1997) can have a major impact on a suite of behavioural traits such as exploratory behaviour, aggressive behaviour, sociability, anxiety, learning ability, and personality traits (Ferdman et al., 2007; Stamps and Groothuis 2010; Hunt et al. 2018; Laubach et al., 2021; Lambert and Guillette 2021).

The early-life social environment may play a particularly prominent role in colonial breeding species, since variation in breeding densities within colonies of ground-nesting species can cause strong variation in the social conditions to which offspring are exposed. For example, in colonies of Larus gulls, central parts with high nest densities are typically surrounded by more dispersed, isolated territories (Minias et al., 2013) where levels of aggressive interactions among individuals are generally lower (Butler and Trivelpiece 1981; Danchin and Wagner 1997; Hill et al. 1997; Hötker 2000). Chicks that cross into a neighbouring territory, which is more likely to occur at higher breeding densities, may experience (possibly lethal) rates of aggression from neighbouring adults (Hunt and McLoon 1975; Ashbrook et al. 2008). When establishing a breeding territory in a colony, parents therefore already set their offspring's social environment, which can have important fitness consequences for the latter. Yet, the social environment experienced by the female during laying likewise affects the deposition of maternal hormones in her eggs (Whittingham and Schwabl 2002; Mazuc et al. 2003; Pilz and Smith 2004). This, in turn, may pre-adjust their offspring to match post-natal (social) conditions at a given breeding density (Welberg and Seckl 2001, Groothuis et al. 2005, Müller et al. 2009), e.g., through epigenetic effects that may result in altered hormone receptor densities, modified hormone production or morphological and muscular changes (Groothuis and Schwabl 2008).

In this study, we investigated to what extent levels of anxiety and exploratory activity in the offspring of colonial breeding, semi-precocial lesser black-backed gulls vary with their early-life social environment, and whether this is modulated by pre-natal effects. We hypothesized that negative (i.e., aggressive) social interactions with conspecifics, which are more common at higher breeding densities, trigger more anxious and less explorative phenotypes (Sterlemann et al., 2008; Sachser et al., 2013; French and Carp, 2016, Hope et al., 2020). We divided our study colony into different plots of equal size, with high-density plots hosting twice as many nests as low-density ones. We then cross-fostered full clutches with the same laying dates between and within high- and low-density plots. This allowed us to separate pre-natal and post-natal effects on the behavioural phenotype of the chicks, given that further adjustments of the maternally-set embryonic environment are no longer possible once the eggs are laid.

Chicks were tested near fledging age using a modified open-field test. Open field tests have been extensively used in behavioural research to study locomotor activity, exploration, and anxiety (Hall and Ballachey 1932; Hall 1934; Hall 1936; Walsh and Cummins 1976; Verbeek et al. 1994; Carducci and Jakob 2000; Rodenburg et al. 2003; Gould et al. 2009). In our version of the open field test, we measured the behaviour of an individual after it was released into an open unfamiliar arena, which included a novel object and a familiar hiding place, to test for individual differences in exploration and anxiety. The experiment was conducted during two consecutive breeding seasons (2020 and 2021). We hypothesized that chicks reared in more dense breeding areas would be less explorative and exhibit higher levels of anxiety, and that pre-natal effects would reinforce such behaviour in an additive way.

Materials and methods

Density assessment and cross-fostering

Our study colony was located in the port of Zeebrugge, Belgium (51°20’56.2”N 3°10’25.0”E), and hosted 181 and 282 lesser black-backed gull breeding pairs over the studied seasons of 2020 and 2021, respectively. In order to manipulate the early-life social environment, we created 8 plots of similar size (~ 850 m^2) by installing 50cm high plastic mesh fences for separation. We aimed to experimentally create plots with contrasting breeding densities, i.e., plots differing in number of nests. So in 2020, we placed 15 U-shaped concrete blocks in plots that were supposed to become “low-density” (LD) plots and 25 blocks as shelter in those plots that should become “high-density” (HD) plots. The concrete blocks serve as favourable breeding spots in our population and hence attract breeding pairs. In our colony, 60% of the breeding pairs chose a territory with an artificial block, and those that did not were provided with a shelter just before chick-hatching. In total, we placed 150 concrete elements in 2020, and 71 more in 2021. The concrete blocks are hence present in all plots and all chicks were familiar with them. During the breeding season of 2020, LD plots held on average 17.34 ± 3.79 nests, while HD plots held on average 35 ± 1.41 nests. In 2021, when the overall number breeding pairs increased substantially, LD plots held on average 20.68 ± 10.41 nests vs 43 nests in the only HD plot used in 2021. Densities significantly differed between years ($\chi2 = 206.77$, $p < 0.001$) and plots ($\chi2 = 9.52$, $p < 0.01$).

To determine laying dates and number of nests, we visited the colony three times per week from the onset of breeding onwards (± 25th of April). Typically, the peak of egg-laying is in mid-May and lasts around two weeks. The cross-fostering was carried out about one week before hatching, that is about 3 weeks after laying of the first egg. Not all nests were used for the experiment, as only nests where clutches could be matched for their laying dates and that were laid in a restricted time window (see below) were selected. In the breeding season of 2020, we cross-fostered a total of 108 nests within and between three LD and two HD plots. In 2021 we used three LD and one HD plot and cross-fostered 78 nests. Three of those plots (two LD and one HD) were used in both years. Clutches were cross-fostered both within the same plot and among other plots with similar or contrasting density. By cross-fostering we created four experimental groups: clutches laid in low density (LD) plots that were cross-fostered to nests located (1) in LD plots (matching a low density early-life environment) or (2) in high density (HD) plots (mismatching as chicks were being raised in a more dense early-life environment); and clutches laid in HD plots that were cross-fostered to nests located (3) in LD plots (mismatching as chicks were being raised in a less dense environment) or (4) in HD areas (matching a high density environment) (Figure 1).

Experimental chicks were individually labelled with numbered tape strips that were fitted around the tarsus at their first nest control after hatching (nests were checked three days a week), ensuring an accurate determination of chick origin and age. At hatch down feathers were collected for molecular sex determination (Griffiths et al. 1998).

Behavioural testing and measurements

To reduce the impact of disturbance in the colony, all tests were performed over two consecutive days and we selected chicks that were 20 ± 5 days old to control for age effects. We tested a total of 90 experimental chicks (N_{2020} = 46;

N_{2021} = 44). Only one individual per nest (usually the first-hatched chick) was tested. The sample sizes among cross-foster groups and between years were as follows: $N_{\text{LD to LD}}$ = 13_{2020} and 11_{2021}; $N_{\text{HD to LD}}$ = 12_{2020} and 13_{2021}; $N_{\text{LD to HD}}$ = 11_{2020} and 11_{2021} and $N_{\text{HD to HD}}$ = 10_{2020} and 9_{2021}.

In both years, we performed open field tests in a 3x3 m arena, which had a familiar U-shaped concrete block as a familiar shelter, and a 1x1 m red carpet as novel object in the middle of the testing arena (Figure 1). We tested each chick individually after an acclimation period of three minutes inside an opaque box that was placed in the arena at the opposite site of the shelter. After removing the box, we video recorded the chick's behaviour for 10 minutes. We focused on the following parameters: (i) latency to enter the shelter; (ii) time spent in the shelter; (iii) latency to enter the carpet; (iv) time spent on the carpet; and finally, (v) time spent moving and exploring (inactivity was defined to start after 5 seconds without movements). Each year, three testing arenas were set-up in an undisturbed area nearby the colony.

After the open field test was performed, we took morphometric measurements of chicks' head and tarsus length to the nearest 0.1 mm using a calliper, and body weight to the nearest 0.1 g using an electronic balance. We then calculated the body size (age corrected) per chick by using the residuals of a linear regression of head-bill length against age, to account for any possible effects of size. After testing and measuring, chicks were returned to their nests.

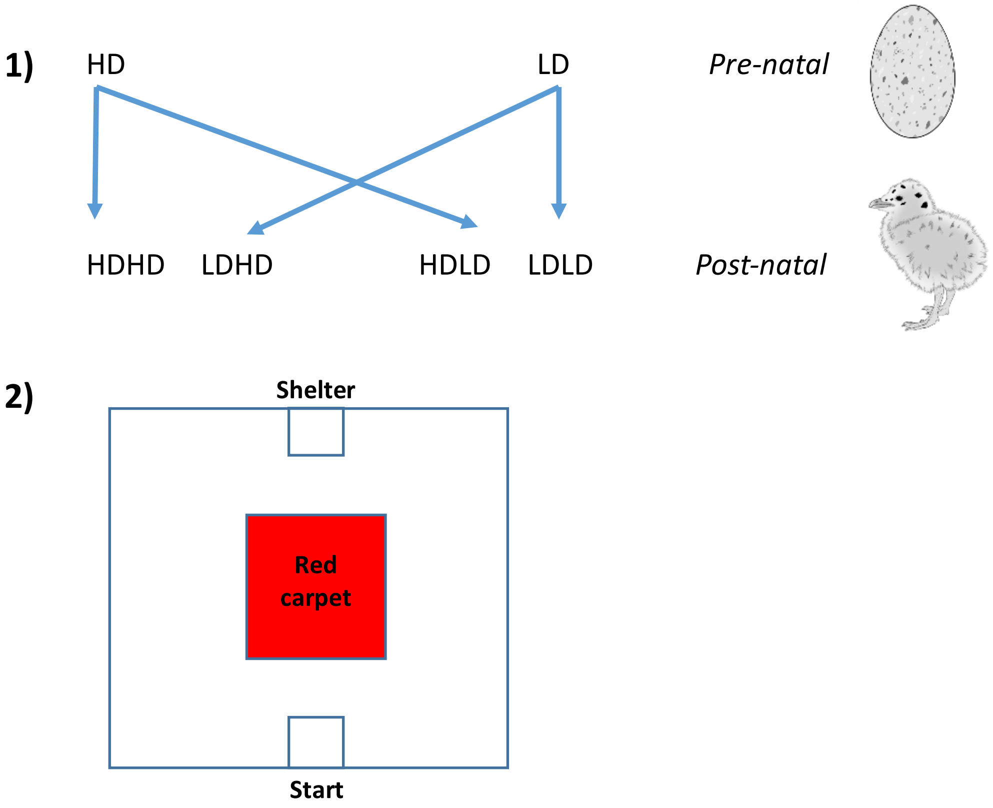

Figure 1. Scheme of the experimental design: 1) Cross-fostering between (=mismatching pre- and post-natal environment) and within breeding densities (=Matching pre- and post-natal environment) and 2) Open field test set-up that included a familiar hiding spot, the concrete block, and a red carpet as central novel object. Drawings by Reyes Reguera Rosal.

Data analysis

Videos were analysed using the Solomon coder software to extract the behavioural parameters of interest (Peter, 2019). We then performed a Principal Component Analysis to reduce the number of behavioural traits and to account for correlations among them. The first two Principal Components

(PC) had eigenvalues higher than one and were used for subsequent analyses. Specifically, to assess the effect of the early-life social environment on the chicks' behavioural phenotype, we fitted two linear mixed models using the square-rooted PC1 (to obtain normally distributed residuals, transformed by adding the maximum negative value and a constant of 1) and PC2 respectively as response variables, and sex, year, chick hatching order (two-level factor: A or B chick), age-corrected body size, pre-natal environment (two-level factor: low and high density), post-natal environment (two-level factor: low and high density), the interaction between pre-natal and post-natal environment, and the interactions between both the pre- and the post-natal environment and year as fixed effects. Finally, plot ID was included as random factor. Non-significant interactions were removed from the statistical models.

To assess which factors influenced chick size, we performed another linear mixed model with age-corrected body size as a response variable, and post-natal environment (two-level factor: low and high density), pre-natal environment (two-level factor: low and high density), sex, year, the interaction between pre-natal and post-natal environment, and the interactions between both the pre- and the post-natal environment and year as explanatory variables. Again, plot ID was included as random effect.

All linear mixed models were fitted using the 'nlme' package (Pinheiro and Bates 2018) using R (R Core Development Team 2022). Normality, independence and homoscedasticity were explored by analysing model residuals. Package 'ggplot2' was used for visualization of results (Wickham 2016). Effect sizes were estimated using the 'emmeans' (Lenth et al., 2018) package, and statistical significance was set at a critical α level of 0.05.

Results

Chick size and social environment

Chicks' size (age-corrected, taken after the open field test) was significantly larger in 2021 compared to 2020 (χ2 = 15.43, p <0.001), and males were larger than females (χ2 = 77.89, p = <0.001). However, we found no significant interactions, nor effects of the pre- (χ2 = 1.31, p = 0.25) and post-natal social environment (χ2 = 0.07, p = 0.79) on chick size after removing non-significant interactions.

Principal Components

PC1 explained 40.53 % of the variance and was related to anxiety behaviours (shelter use duration and latency to shelter; Table 1). Lower values of PC1 indicate higher anxiety levels. PC2 explained 36.72% of the variance, and was related to exploratory behaviours (time active, carpet use duration and latency to carpet; Table 1). Lower values of PC2 are indicative of higher levels of exploration activity. Results of our PCA thus confirms that the open field test measures two distinct behavioural components, namely anxiety and exploration (Walsh and Cummins 1976; Gould et al. 2009).

Table 1. Output of the principal component analysis showing the loadings of the two principal components with eigenvalues higher than one for each behavioural trait extracted from the open field test.

	PC1	**PC2**
Loadings		
Latency to shelter	**0.93**	0.21
Shelter use duration	**-0.96**	-0.09
Time active	0.32	**-0.71**
Latency to carpet	0.20	**0.87**
Carpet use duration	0.31	**-0.72**

Behavioural phenotypes and social environment

We found no significant effect of any of our explanatory variables on PC1, which reflects anxiety (Table 2, S1). Regarding PC2, which reflects exploration activity, there was a significant effect of both the pre-natal ($\chi2 = 3.90$, $p = 0.05$) and the post-natal social environment ($\chi2 = 6.10$, $p = 0.01$) after removing interactions in the model, as they were non-significant (Table 2, S1). Chicks that were prenatally predetermined for LD were significantly more exploratory than the ones programmed for HD (Table 2). Chicks that were raised in LD post-hatching exhibited a significantly higher exploration activity (Table 2). Chicks that were raised in mismatching pre- and post-natal conditions (LDHD and HDLD) exhibited intermediate phenotypes (Figure 2). This effect was consistent in both years (Table 2).

Table 2. Full linear mixed models excluding non-significant interactions (1.) testing the effect of sex, year, chick size, pre-natal and post-natal conditions, and the interaction between the pre-natal and post-natal conditions on the Principal Component 1 ("anxiety"). A similar model (2.) was fitted to investigate the effects on Principal Component 2 ("exploration activity"). The reference levels of comparison were: LD for pre- and post-natal densities, 2020 for year, females for sex, and A chick for chick hatching order.

	Coefficient	**SE**	**Chisq**	**d.f.**	**p-values**	***Effect size ± SE***
1. Principal Component 1						
Pre-natal density	-0.05	0.08	0.40	1	0.53	*0.13 ± 0.21*
Post-natal density	0.01	0.10	0.02	1	0.89	*-0.04 ± 0.27*
Year	-0.07	0.09	0.63	1	0.43	*0.19 ± 0.23*
Sex	0.00	0.11	0.00	1	0.98	*-0.01 ± 0.30*
Chick size	0.02	0.01	2.06	1	0.15	
Chick order	0.01	0.09	0.00	1	0.95	*-0.01 ± 0.23*
2. Principal Component 2						
Pre-natal density	0.55	0.28	3.90	1	0.05	*-0.42 ± 0.21*
Post-natal density	0.70	0.28	6.1	1	0.01	*-0.54 ± 0.22*
Year	0.24	0.30	0.67	1	0.41	*0.05 ± 0.07*
Sex	0.47	0.39	1.46	1	0.23	*-0.00 ± 0.09*
Chick size	-0.00	0.05	0.00	1	0.98	
Chick order	0.19	0.30	0.40	1	0.53	*-0.00 ± 0.07*

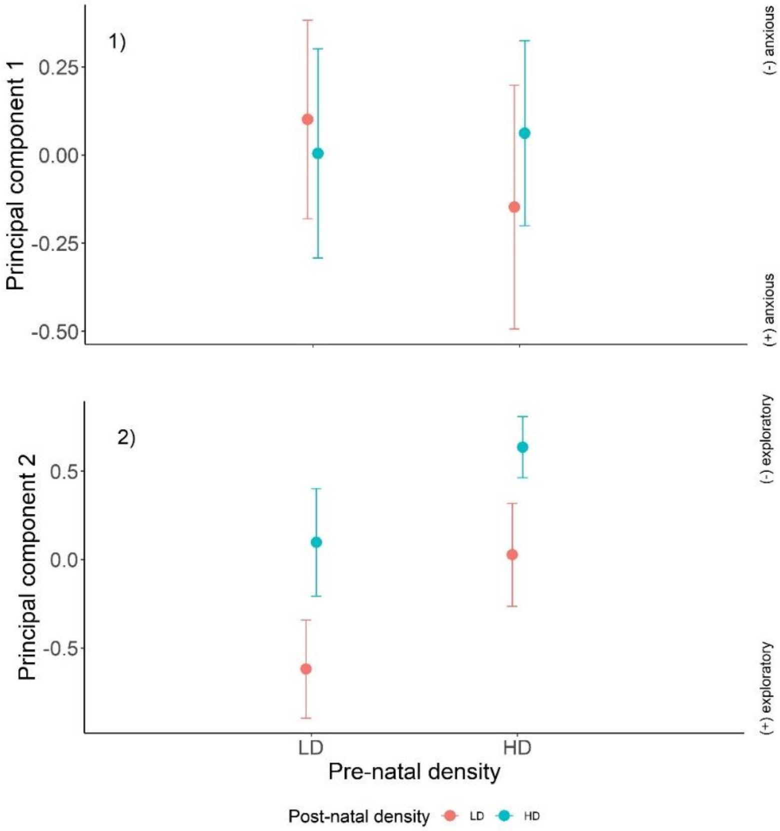

Figure 2. Values of 1) Principal Component 1 representing anxiety and 2) Principal Component 2 representing exploration, according to pre-natal and post-natal social environments (i.e., low and high breeding densities). Dots represent the mean values, and whiskers the standard errors.

Discussion

An important component of the early life environment that most animal species must cope with is the social environment. Animals might hence -from the moment they are born- have to adapt to the social context via phenotypic plasticity to increase their performance and to reduce their chances of mortality. Here we indeed show that the behavioural phenotype of lesser black-backed gull chicks is significantly altered in relation to their post-hatching social environment, consistently so over two consecutive years. Furthermore, this phenotypic effect was supported by the contribution of pre-natal effects, as such that the pre-natal effects had an additive effect on the offspring's phenotype. Below we discuss our results against the background of developmental plasticity, which might play an important role in shaping behavioural differences, possibly with long-lasting consequences.

Post-natal effects

The adult breeding territory of colonial breeding lesser black-backed gulls determines the offspring's early-life social environment, and we hypothesized that it affects the expression of their behaviour, as it is sensitive to and modulated by environmental conditions. Thus, growing up in territories in more dense areas should trigger more anxious and less explorative offspring phenotypes, as they experience more aggressive interactions from neighbouring breeding pairs and/or their chicks (Hunt and McLoon 1975; Butler and Trivelpiece 1981; Hill et al. 1997; Ashbrook et al. 2008). Consistent with this hypothesis, the post-natal breeding density to which a chick was exposed explained a significant amount of variation in its exploration activity, with chicks being raised in HD areas showing reduced exploration activity. Lesser black-backed gulls are semi-precocial, and their chicks start moving around when about 5-7 days old. As we tested the chicks when they were about three weeks old, it is likely that chicks might have learned to reduce their exploration activity through social experience. That is in particular by aversive feedback learning, as they might have encountered aggressive interactions with neighbouring birds when moving beyond their own territory borders. Chicks raised in HD areas would benefit most strongly from being less explorative and hence from avoiding conflicts, as their territories are probably smaller and encounters with neighbours more likely. Unfortunately, we do not have reliable estimates of chick mortality in our colony, and we obviously do not have the behavioural profile of chicks that died before the testing, while this could have provided relevant information on the adaptive significance of a given behavioural phenotype in a certain social context.

Furthermore, the observed behavioural differences among chicks raised in low and high breeding plots could also be related to the behaviour of their foster parents. The amount and quality of parental care during development have been correlated with offspring behaviour in general (Budaev et al. 1999; Francis et al. 1999; Arnold et al. 2007; Perkeybile et al. 2013; Tang et al. 2014; Van Oers et al. 2015), and here specifically one parental behaviour, the parental presence at the nest, could be of importance. Gull chicks tend to stay in close proximity to their parents, and via alarm calls parents may force their chicks to remain quiet and hide in safe spots (here: the concrete nest blocks) (Impekoven 1976; Magrath et al. 2010). This would result in an enhanced protection of the offspring from intra-specific aggression through reduced exploration activity, again likely through learning even though here chicks might not have experienced aggression.

Intriguingly, we did not find effects of the post-hatching social environment on chick anxiety. The anxiety of the chicks raised in HD areas was comparable to that of chicks raised in LD areas. At current, we can only speculate that anxiety could be a less plastic trait. Possibly because anxiety is a key trait so that all chicks in the colony show similar intrinsic tendencies to hide when left alone by their parents and in potential danger, as it might enhance survival. However, we do observe among individual variation in anxiety, yet we could not identify the underlying drivers (see also below), we only could rule out an effect of the post-natal social environment.

Pre-natal effects

We further hypothesized that chick behaviour might be pre-adjusted by the pre-natal (social) conditions. This hypothesis was also supported by our data as pre-natal breeding density significantly predicted the exploration activity by the offspring, explaining about 50% of the variation. More specifically, chicks born from eggs laid by females breeding in HD plots, but raised in LD ones, showed similar exploration activity levels as chicks born from eggs laid by females in LD plots but raised in HD ones. Moreover, their level of exploration activity was intermediate to that of chicks raised from clutches that had been cross-fostered within high- or low-density plots. We did not find any significant interaction between pre- and post-natal environments on offspring's behavioural phenotype, but only two significant main effects. Thus, pre- and post-natal effects were about equal strength and shaped offspring phenotype in a similar way, i.e., they were additive. This suggests that offspring may benefit from the prenatal programming when the post-hatching conditions are similar to the pre-natal conditions, thus in a matching environment.

From a proximate perspective, maternal yolk androgens constitute a prime candidate for pre-adjusting offspring behaviour to the social conditions experienced after hatching (Groothuis et al. 2005). Breeding density as experienced by the mother when laying her eggs (here referred to as the social environment) has earlier been shown to alter maternal androgen deposition into the egg yolk (Schwabl 1997; Gil 2008; Oliveira 2004; Pilz and Smith 2004; Hargitai et al, 2009). Maternal yolk androgens are known to affect a variety of offspring traits (Groothuis et al. 2005, Eising et al., 2006), such as begging, exploratory and territorial behaviour (Eising and Groothuis 2003; Müller et al. 2009; Ruuskanen and Laaksonen 2010). The latter could hence serve as functional explanations for the fact that yolk androgen levels often co-vary with breeding densities. However, we found a lower exploration activity in high breeding densities, where yolk androgens levels are supposed to be high, which contrasts the still limited current evidence (Eising and Groothuis 2003, Daisley et al. 2005, Ruuskanen and Laaksinen 2010).

Other maternally derived hormones might be involved, such as corticosterone (Almasi et al. 2012) which is involved in stress responses, and high breeding density environments could affect maternal stress levels. However, their transmission to the egg by the mother is still debated (Rettenbacher et al. 2005). If deposited by the female, they should induce greater levels of fearfulness and anxiety in the offspring (Guibert et al. 2010; Guibert et al. 2011, but see Hartmann and Schmidt, 2020), yet we did not find a pre-natal effect on anxiety. Finally, the pre-natal effects might also reflect genetic differences in exploratory behaviour (see e.g., Dingemanse et al. 2002; Stirling et al., 2002; Drent et al. 2003; Van Oers et al. 2004; Van Oers et al. 2005). While a low exploration activity is likely adaptive for the offspring in high-density areas, it remains puzzling how this could be adaptive in adults.

Other non-mutually exclusive pre-natal mechanisms with potential effects on offspring behaviour include more disrupted incubation patterns in HD areas due to more frequent interactions with neighbouring pairs (DuRant et al. 2010, Hopkins et al. 2011), or vocal cues (i.e., alarm calls) experienced during the embryonic phase, which would be more present in HD areas (Noguera and Velando 2019). We could have underestimated the role of pre-natal cues, as some clutches were already cross-fostered days before hatching (cross-fostering of all clutches was synchronized to avoid disturbance after chicks had hatched). However, there were no differences in the average time (i.e., days after cross-fostering) clutches spent in their foster plots relative to their hatching day and according to cross-foster category ($\chi2 = 2.33$, $p = 0.51$). Thus, further studies are necessary to unravel the proximate mechanisms underlying pre-natal effects.

Conclusions

We provide key evidence that the early-life social environment plays a fundamental role in shaping the offspring's behavioural phenotype in our study species. Pre-natal effects, i.e., maternal effects, and post-natal effects, i.e., learning through social interactions or parental care, contribute equally and uni-directionally to variation in exploration activity. The fact that both pre- and post-natal stages impact on offspring phenotype implies that the timeframe during which developmental plasticity and adjustment to the prevailing social environmental context can occur, is extensive. Understanding the adaptive significance of the observed patterns will ultimately require a better understanding of the mechanisms, i.e., the contribution of maternal effects and genes to offspring performance, as well as of potentially long-lasting effects during adulthood.

Authors’ contributions

R.S.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft; L.L.: conceptualization, methodology, supervision, writing—review and editing; E.S.: conceptualization, data curation, methodology, writing—review and editing; F.V.: conceptualization, methodology, writing—review and editing; W.M.: conceptualization, investigation, methodology, supervision, writing—review and editing.

Study plot in Zeebrugge.

CHAPTER 5

A hostile social environment restricts territory size, movement activity and social associations in the Lesser black-backed gull

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To be submitted

Abstract

There is significant variation in the early-life social environment for offspring of colonial breeding species. While in the peripheral parts nests are spaced as such that chicks can keep distance, more central parts of the colonies typically show much higher concentrations of nests and shorter inter-nest distances, which increases the number of social interactions. In lesser black-backed gulls, chicks raised in such dense areas are additionally exposed to high levels of intra-specific aggression. This has consequences for the offspring, who presumably have to adjust their movements and social behaviour to avoid conflicts in socially dense environments. To further increase chick survival, mothers can pre-adjust the offspring's behaviour to the conditions they will experience post-hatching by means of maternal effects, so that the chicks' movement and social behaviour is pre-adjusted to the social conditions after hatching. Taken together, we hypothesize that lesser black-backed gull chicks raised in areas with a greater proximity to neighbouring nests exhibit a reduced movement activity, avoid social encounters and have smaller territories. These differences could develop post-hatching through experience, facilitated anticipatory maternal effects.

To test for pre- and post-natal effects of breeding density on the chicks' movement, territorial and social behaviour, we first cross-fostered full clutches to disentangle pre-natal from post-natal effects. We then deployed ultra-wide band (UWB) trackers to 81 chicks over a period of three days, when the chicks were between 15-25 days old, from which we derived information on movement activity, territory size and social avoidance (via social network analyses). In line with our predictions, we found that chicks raised in dense areas showed a lower movement activity and had smaller territories, likely due

to an enhanced intra-specific aggression with increasing breeding density. Yet pre-natal effects had no significant effect. Chicks raised in dense areas associated with more neighbouring chicks, which could, however, be explained by a higher chance of unintentionally encountering other chicks in close proximity rather than reflecting active choices. The number of social associations with neighbouring chicks was surprisingly low which underlines the hostility of the early social environment in our model system, which strongly influences the offspring’s movement behaviour.

Introduction

Colonial breeding is a widespread phenomenon in nature (Trillmich and Trillmich, 1984; Campagna et al., 1992; Uetz et al., 2002), and is especially remarkable in seabirds, where about 95% of the species breed in colonies (Wittenberger & Hunt, 1985). Aggregating in colonies during the breeding period involves a variety of benefits, such as easier access to potential mates (McCarthy 1997; Dubois et al. 1998), higher food-finding efficiency with colonies acting as 'information centres' (Ward and Zahavi 1973; Emlen and Demong 1975; Weimerskirch et al. 2010) or improved anti-predator defence (Götmark and Andersson 1984; Arroyo et al. 2001; Hernández-Matías et al. 2003; Jungwirth et al. 2015). However, colonial breeding also entails costs associated with high levels of competition, particularly for food resources within the vicinity of the colony (Furness & Birkhead, 1984; Lewis et al., 2001; Ballance et al., 2009; Lamb et al., 2017) and nesting sites (Hötker,2000; Kokko et al., 2004), as well as intra-specific predation of eggs and nestlings (Davis and Dunn 1976).

The costs and benefits of avian colonial breeding are typically studied from the adult's perspective, while it is the offspring that is exposed to the colonial context during a critical stage. When establishing a breeding territory in a colony, parents already set their offspring's social environment, which can have important consequences for the offspring behavioural development during the post-hatching period. For example, in colonies of Larus gulls, chicks that cross into a neighbouring territory often experience high rates of (possibly lethal) aggression from neighbouring adults (Hunt and McLoon 1975; Ashbrook et al. 2008). It is well documented that this happens more often in high density areas, where neighbouring territories are smaller and closer together (Butler and Trivelpiece 1981; Danchin and Wagner 1997; Hill et al. 1997; Hötker 2000). In order to deal with their social environment, chicks can adjust their exploratory behaviour (Salas et al. 2022), aggressive behaviour (Rittschof et al. 2015), or anxiety (Laubach et al., 2021).

Intriguingly, one trait that has been poorly studied is the movement behaviour of the chicks, even though it is a trait directly influenced by the social environment. Movement behaviour is furthermore related to space use and home range size, can enhance memory and learning early in life (Van Praag 2008; Erickson et al., 2011; Lambert and Guillette 2021), and constitutes the basis for exploratory behaviour, which has been shown to be affected by the early social environment (Salas et al. 2022). Furthermore, the aggression rates that offspring is subjected to early in life (Hunt and McLoon 1975; Ashbrook et al. 2008) are likely driven by their movement behaviour and the spatial proximity to other neighbouring territories, and it can thus be expected that the social environment could constrain chick movement activity in dense areas of the colony. At current it is not known whether chicks adjust their movement activity to the social context, and if so whether it is sufficient to reduce the number of social interactions.

However, in dense areas of the colony even minimal movements could result in a social interaction, simply because of the proximity to neighbouring nests. If these associations involve aggression, chicks with a greater competitive ability, i.e., larger chicks or male chicks (larid gulls are sexually dimorphic; see Johnsson et al. 1999; Serrano-Meneses 2007), should be able to better withstand conflicts with neighbours. Thus, the consequences of higher breeding density on the number of social associations should vary with body size, at least if movement is constrained by competitive abilities.

Measuring movement and social parameters in small animals such as gull offspring was virtually impossible until very recently. The development of ultra-wide band tracking devices that can be deployed on live birds, now allows us to individually follow e.g., free ranging birds in natural conditions with temporal and spatial accuracies as never seen before (Rahayu et al. 2008; Li et al. 2021). Ultra-wide band tracking is spatio-temporally more accurate than GPS tracking, with spatial accuracy under 0.5 m (Stadig et al. 2018).

In this study, we investigated the impact of the early-life social environment on the movement activity and social associations of lesser black backed gull (*Larus fuscus*) chicks during the nestling period. Because lesser black-backed gulls are semi-precocial, and their chicks start moving around when about 5-7 days old, we hypothesize that chicks raised in high density areas, where neighbouring nests are more clustered together, would have smaller home ranges and would restrict their movement activity - to reduce conflicts with neighbouring birds. However, the chances of social encounters will still be greater when the distances to neighbouring territories are shorter. If these associations with neighbouring chicks are predominantly aggressive, we would expect that their duration depends on the competitive ability of a chick, i.e. chick size. To investigate this, chicks were tracked around fledging with ultra-wide band loggers during three consecutive days, where we quantified daily movement activity, territory size and number of social associations among chicks. In addition, we cross-fostered full clutches within similar and dissimilar breeding densities to disentangle pre-natal from post-natal effects on movement and social behaviour, since mothers can pre-adjust their offspring’s behaviour to match post-natal (social) conditions (Welberg and Seckl 2001; Salas et al. 2022).

Material and methods

Social environment and cross-fostering

Our study site was located in the port of Zeebrugge, Belgium (51°20’56.2”N 3°10’25.0”E), and hosted 282 lesser black-backed gull breeding pairs in 2021. The site was completely fenced-off to prevent fox predation, and we created 8 plots of similar size (850 m^2) by installing 50 cm high plastic mesh fences for further subdivision. Since our movement and social parameters could be affected by the presence of an infrastructure, we included a categorical variable that took into account whether nests were in close proximity to the fence, i.e., fence being present less than 1.32 meters from a given nest. The threshold value was calculated based on the average distance travelled by all chicks (0.91 ± 0.41 meters), where only 8 nests were affected by the presence of a fence.

In 2021, 221 U-shaped of concrete blocks were placed in separated plots of the colony to create plots that differ in the number of breeding pairs. In order to disentangle pre-natal from post-natal effects, we cross-fostered full clutches within and between high and low breeding density plots based on the number of nests present in each plot (see Salas et al. 2022 for a more detailed description of the experimental set-up). Subsequently, we used the pre- and post-natal inter-nest distances to the three nearest neighbours as a quantitative measurement of the social densities. The average distance to the three nearest neighbours in our tracked nests significantly differed between high- (2.96 ± 0.78 meters) and low-density plots (4.11 ± 1.66 meters, $\chi^2 = 4.68$, $p = 0.03$).

From the start of egg laying onwards (± 25th of April), we visited the colony three times per week, which allowed an accurate determination of laying dates. The cross-fostering was performed before any eggs had hatched in the colony, where we selected nests based on the peak of egg-laying and matched clutches by their laying dates. By cross-fostering a total of 78 nests, within and between density plots, we thus created nests with a range of differences between pre- and post-natal environment. Experimental chicks were individually labelled at the first control after hatching, ensuring an accurate determination of chick origin and age. At hatch down feathers were collected for molecular sex determination (Griffiths et al. 1998).

UWB tracking and data treatment

We placed UWB trackers (commercialized by iMec) on a total of 81 chicks from 51 nests that were between 15 and 25 days old. Tracking lasted over a period of three consecutive days, where we did not visit the colony to avoid disturbances. A total of 8 trackers did not collect movement information, and we omitted the data of 5 chicks who cross-fostered themselves to a different nest. From the remaining 68 tracked chicks, 59% were sibling pairs of the same nest (N = 20 nests). Before deploying the UWB trackers, morphometric measurements of head and tarsus length were taken using a digital calliper to the nearest 0.1 mm, along with the body weight using an electronic balance to the nearest 0.1 g. To account for the age differences among chicks, for later analysis we calculated a chick’s body size index by using the residuals of a linear regression of tarsus length (relevant for movement) against age. After the morphometric measurements, we deployed 20.3 g ultra-wide band tracking devices on the chicks, and attached them with an elastic wing harness. We ensured that the total combined weight of the tracker and the harness was between 3% and 5% of the bird's body mass (the minimum body mass of a chick with a deployed tracker was 411 g). After three days of consecutive tracking, we recovered 100% of the deployed trackers. The data was remotely stored by a grid of receivers placed throughout the colony. Those devices collected accurate spatial and temporal data based on triangulation of very short pulses emitted by the trackers in relation to a grid of antennas placed in the colony. The tags were programmed to collect data every 30 seconds, and we left some stationary loggers (N = 10) to estimate the spatial accuracy in the field.

We excluded unrealistic data points that occurred outside our colony grid/fence when beyond 0.5 meters (to account for spatial errors of the trackers), and with a speed higher than 0.2 m/s (i.e., distance between consecutive points divided by the time elapsed between those positions, Figure S1). Moreover, by visually exploring the data, we could detect the presence of some artificial straight lines. Such artefacts could be clearly identified because of the consecutive repetition of specific X coordinates, and were removed for further analyses.

Movement activity and territory size

To calculate movement activity, we resampled the tracking data to a temporal resolution of 5 minutes, to ensure that the number of tracking recordings per chicks was constant and similar between chicks. We then calculated the total average movement activity over the entire tracking period, i.e., the average distance travelled between consecutive spatial positions. We also calculated the daily average movement in order to calculate the movement repeatability (see data analyses). Moreover, we used the tracking data to calculate the territory size of each chick, that was defined as the 95% utilization distribution kernel with reference bandwidth selection.

Social associations

For the social network analyses, we did not temporally resample the dataset to maximize the likelihood of detecting associations. We established that a social association occurred when two individuals were at a distance of less than 60 cm from each other (thus accounting for spatial resolution errors, see below) at the same time, where timestamp was round to the closest 30 seconds (over 80% of the fixes were collected every 30 seconds, Figure S2). With this information, we performed social network analyses to derive 1) the degree centrality i.e., the number of individuals that chicks had contact with, and 2) the strength of such associations, i.e., the individuals' total number of social associations over the course of the 3-day tracking period. For this, we used the R package ggraph (Pedersen 2022).

Data analyses

To assess whether chick movements were consistent over the tracking period, we calculated the repeatability of the daily (square-rooted) average movement with the "rptR" package (Stoffel et al. 2017) against chick ID, with a bootstrapping of 1000.

To investigate the effect of the early-life social environment on the chick movement, we fitted two linear mixed models using the logarithm of the square-rooted movement activity, and the square-rooted territory size respectively as response variables. Sex, age-corrected chick body size, pre-natal average distance to the three nearest neighbours, post-natal average distance to the three nearest neighbour and proximity to the fence (calculated as a categorical variable), as well as the interaction between pre-natal and post-natal social environment were used as fixed effects. Finally, chick ID nested in plot ID was included as random factor.

Regarding the chicks' social associations, and because associations with neighbouring, untracked chicks are uncaptured, we only used nests in which at least one chick was tracked in order to calculate the average distance to the three nearest neighbours (i.e., post-natal social environment). To test whether the early-life social environment affected the chick's social associations, we thus fitted a linear mixed model using degree centrality as response variable, and sex, age-corrected body size, pre-natal average distance to the three nearest neighbours, post-natal average distance to the three nearest tracked neighbours and proximity to the fence, as well as the interaction between pre-natal and post-natal social environment as fixed effects. Regarding the strength of the social associations, we winsorized one outlier to minimize the influence of that data point (i.e., by replacing the outlier with the next most extreme value of strength) (Quinn & Keough 2002). Also note that analysing the non-winsorized data leads to qualitative similar results. We then fitted a similar model with the square-rooted, winsorized strength as response variable. Chick ID nested in plot ID were included as random factor.

We fitted the linear mixed models using the 'nlme' package (Pinheiro and Bates 2018) in R (R Core Development Team 2022). Normality, independence and homoscedasticity were assessed by analysing model residuals. Package 'ggplot2' was used for visualization of results (Wickham 2016), and statistical significance was set at a critical α level of 0.05.

Results

Accuracy of UWB tracker

The spatial accuracy of the UWB trackers was 33 cm ± 14 (mean ± sd, N=10). This spatial accuracy is remarkably high, and provides evidence that UWB technology is a powerful method to study animal movement activity at small scales and suitable for the aims of this study.

Movement activity and social environment

We tracked the movements of 68 chicks over three consecutive days, where daily movements had a repeatability of 0.71, indicating a highly consistent movement activity of chicks. We consequently used the average movement over the three consecutive days as estimate for further analysis. After removing non-significant interactions, we found that chicks moved significantly less when the average distance to the three closest neighbouring nests was smaller ($\chi^2 = 18.22$, $p < 0.001$, Figure 2A), but only the post-natal, and not the pre-natal average distance to the three closest neighbouring nests affected chick movements (Table 1). We found that the movement activity of siblings from the same nest was strongly correlated ($r = 0.94$, $p < 0.001$).

Regarding the territory size, after removing non-significant interactions we found that chicks raised in areas where neighbouring nests were closer by had smaller territories ($\chi^2 = 20.43$, $p < 0.001$, Figure 2B). Moreover, we found that chicks also had smaller territories when the subdivision fences were closer by ($\chi^2 = 4.84$, $p = 0.03$). The territory size was also highly correlated among siblings ($r = 0.92$, $p < 0.001$).

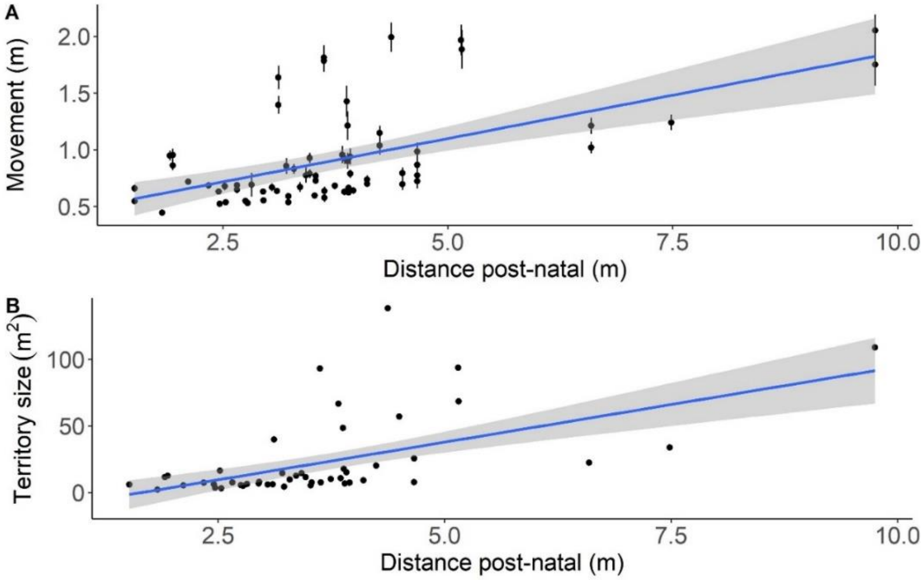


Figure 2. Effect of average distance to the three nearest neighbours on (A) movement activity (m) and (B) territory size (m^2). Bands represent the 95% confidence interval.

Table 1. Full linear mixed models (1.) testing the effect of sex, year, chick body size, pre-natal and post-natal conditions, and the interaction between the pre-natal and post-natal conditions on the movement activity. Similar models were fitted to investigate the effects on (2.) territory size, (3.) degree centrality and (4.) strength of social associations.

	Coefficient	**SE**	**Chisq**	**d.f.**	**p-values**
1. Movement activity					
Pre-natal distance to neighbours	-0.13	0.07	0.57	1	0.45
Post-natal distance to neighbours	-0.03	0.07	23.18	1	< 0.001
Sex	-0.02	0.02	0.62	1	0.43
Chick size	0.00	0.00	2.09	1	0.15
Fence category	0.08	0.01	1.85	1	0.17
Pre-natal * Post-natal	0.04	0.02	2.90	1	0.09
2. Territory size					
Pre-natal distance to neighbours	-1.45	0.92	0.13	1	0.72
Post-natal distance to neighbours	-0.18	0.92	28.12	1	< 0.001
Sex	0.19	0.34	0.30	1	0.58
Chick size	0.01	0.06	0.03	1	0.86
Fence category	-1.67	0.77	4.74	1	0.03
Pre-natal * Post-natal	0.42	0.27	2.37	1	0.12
3. Degree centrality					
Pre-natal distance to neighbours	-0.20	0.44	0.30	1	0.58
Post-natal distance to tracked neighbours	-0.47	0.33	2.67	1	0.10
Sex	0.98	0.53	1.63	1	0.20
Chick size	-0.06	0.09	0.42	1	0.51
Fence category	-0.07	0.10	0.50	1	0.48
Pre-natal * Post-natal	0.04	0.06	0.47	1	0.49
4. Strength interactions					
Pre-natal distance to neighbours	-0.73	1.20	0.02	1	0.88
Post-natal distance to tracked neighbours	-1.67	0.90	5.92	1	0.01
Sex	2.10	1.00	4.37	1	0.04
Chick size	-0.30	0.19	2.50	1	0.11
Fence category	7.63	2.31	10.89	1	< 0.001
Pre-natal * Post-natal	0.12	0.17	0.50	1	0.48

Social associations and social environment

For the social network analyses, we used the average distance to the three nearest tracked neighbours, which was strongly correlated with the one considering all nests in each plot ($r = 0.73$, $p < 0.001$). Most associations occurred among siblings, where on average, a chick had 4445.92 ± 1823.06 social associations with its sibling, compared to on average 115.69 ± 46.19 with 2.98 ± 2.48 neighbouring chicks. When only considering the social associations with non-sibling chicks (Figure 3), and after removing non-significant interactions, we found a significant effect of post-natal density, where chicks interacted with more individuals when the distance to the three nearest tracked neighbours was smaller (i.e., degree centrality, $\chi^2 = 4.10$, $p = 0.04$).

When considering the strength of the social associations, and again after removing non-significant interactions, we found that males had a significantly higher number of social associations than females (males: 124.14 ± 34.09, females: 95.05 ± 23.65; $\chi^2 = 4.55$, $p = 0.03$), and we also found a significant effect of post-natal density, where chicks had higher number of associations when neighbouring tracked nests were closer by ($\chi^2 = 6.00$, $p = 0.01$). Finally, chicks also had higher number of associations when the fences were closer by ($\chi^2 = 10.89$, $p < 0.001$)

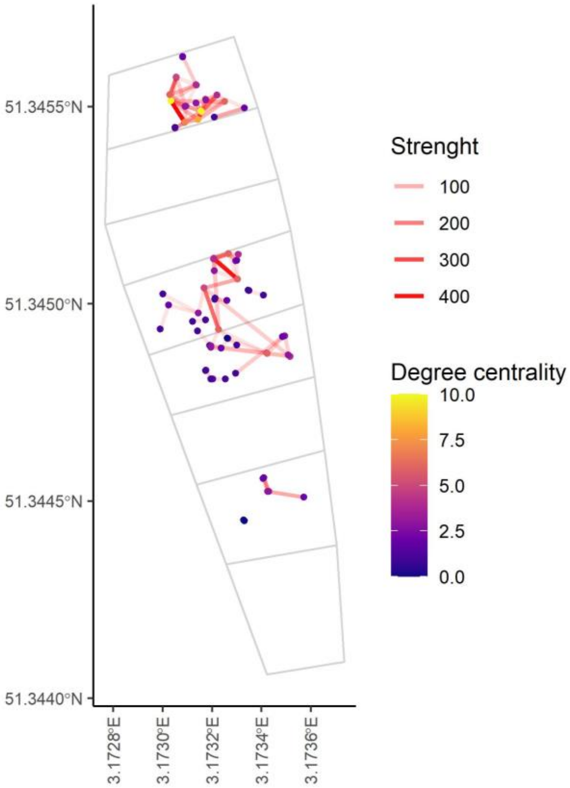


Figure 3. Spatial map displaying the social network of the tracked chicks. Dots represent the average spatial location of each chick during the three days of tracking, and their colour is related to the degree centrality. The thickness of the lines connecting chicks represent the strength of the associations. Fences delimiting plots are plotted as grey lines.

Discussion

The early-life social environment represents a fundamental component that offspring should adapt to. In colonial breeding species, the social environment is defined by the breeding density, as a high number of individuals aggregate to breed in close proximity. Here we indeed show that the movement activity and social associations of lesser black-backed gull chicks are significantly altered in relation to the inter-nest densities. Below we discuss these findings against the background of the adversity of the early-life social environment.

Post-natal effects on movement activity

In colonial breeding lesser black-backed gulls, offspring experience aggressive interactions from adults of neighbouring breeding pairs and/or their chicks (Hunt and McLoon 1975; Butler and Trivelpiece 1981; Hill et al. 1997; Ashbrook et al. 2008). Growing up in territories where the neighbouring nests are more close-by could hence affect the movement behaviour and space use, i.e., territory size of the offspring. We indeed found that chicks that were raised in closer proximity to neighbours showed a reduced movement activity and had smaller territories. As we measured movement activity towards the end of the nestling period, this is likely because offspring could have learned to avoid conflicts with neighbours by aversive feedback learning, as they might have encountered aggressive interactions when crossing into a neighbouring territory. Having neighbours on average closer by limits thus the space available for chicks, and hence the territory size. This is also supported by the fact that the presence of infrastructure (i.e., fences separating the plots), negatively influenced the territory size by restricting the available space. These findings are in line with our previous study in which chicks showed higher levels of exploration activity when raised in low-density areas of the colony (Salas et al. 2022).

The observed patterns likely represent an adaptation to the social context a chick currently experiences. Typically, offspring raised in low density areas suffer higher predation risk (Krebs and Davies 1978; Hötker 2000), and by being more explorative in low densities (Salas et al. 2022) chicks might enhance their ability to escape from predators. These chicks might gain a better spatial knowledge of the hiding areas surrounding their territories. In contrast, in dense areas of the colony the risk of intra-specific aggression dominates.

Moving and exploring in high density areas can even be lethal for the chicks. However, during early-life individuals integrate environmental information into a canalized adult phenotype (Williams 1957; English et al. 2016), so it is possible that early-life environmental effects on trait development can have lasting consequences. Movement behaviour can for example enhance memory and learning (Van Praag 2008; Erickson et al., 2011), and hence impinge on the development of spatial cognition. Being raised in complex social environments could influence the development of inhibitory control, i.e., the ability to intentionally supress inappropriate, dominant actions and instead exhibit an alternative behaviour which ultimately attains a reward (Aron 2007; Frijda 2010; Diamond 2013). Stopping an inappropriate action is likely adaptive in crowded social environments where levels of aggression are high. However, at current this remains highly speculative, as nothing is known about lasting effects. Furthermore, if for example the chicks' movement behaviour early in life affects spatial cognition, these effects may be restricted to species-specific time-windows during development. Because movements in altricial species or for instance, in cliff-nesting species, where chicks avoid moving to not fall out from the nest and drown in the sea, movement in early life is unlikely to determine spatial cognition.

Parental and maternal effects

The fact that chicks do not freely move around and that territory sizes are limited by the proximity to neighbours indicates that territories as established by the parents remain functional during the chick rearing period. Furthermore, at least one lesser black-backed gull parent is constantly present in the territory (Kavelaars et al. 2021). And since chicks tend to stay in proximity of their parents, the parental movement behaviour inside the territories could in turn influence the movement behaviour of their offspring and parents may also interact with chicks from neighbouring territories. However, here only chick movements were tracked, and we do not have any information to what extend the movement patterns that we observe are related to such parental effects. While this aspect is highly interesting, it will require further technical progress to address this.

In contrast to a previous study (Salas et al. 2022), the pre-natal environment did not affect any of the traits measured here, and we can only speculate about the causes thereof. Contrary to the previous study which tested the chicks in an experimental setup, here chicks were followed in their post-hatching social environment. It is thus possible that we cannot observe any pre-natal effects due to the critical importance of adapting movement behaviour to the post-natal social environment for the offspring.

Post-natal effects and social associations

As predicted, most of the social associations happened among siblings, with only 2% of the chicks' associations occurring with chicks from neighbouring territories. This indicates that chicks not only remain in their territory, but that they also closely associate with their sibling, which might provide additional safety. However, our data only inform about the spatial proximity of the siblings, and it will require further study to identify the nature of these contacts. Concerning the social associations that occurred with neighbouring chicks, we hypothesized that chicks raised in dense areas, would have a higher degree centrality (i.e., interacted with more neighbouring chicks) because of a closer proximity to (more) neighbouring nests. We indeed found such an effect, showing that the social environment as chosen by the parents potentially impacts on the social life of their offspring. These contacts may reflect active interactions, e.g., in the context of territorial defence, but could also be driven by passive associations that occurred unintentionally and in very low frequency when chicks run into each other in dense areas.

A similar pattern was found regarding the strength of the social associations, where chicks in dense areas had a higher number of associations with other neighbouring tracked chicks. Again, this could be explained by a higher chance of unintentionally encountering neighbouring chicks. Interestingly, sex also influenced the number of social associations, which suggests that interacting with other chicks is likely facilitated by the competitive abilities of the chicks. The competitive abilities of an individual are related with size, where lesser black-backed gulls males are typically bigger than females. The larger size may allow them to win conflicts with neighbouring birds, so they rather remain in contact than escaping or avoiding it. Alternatively, if chicks are involved in territorial aggression (Groothuis 1989a, Groothuis 1989b, Müller et al. 2009) this can be regulated by testosterone (Ros et al. 2002). It is possible that the sex differences in the strength of the social associations are driven by sex-related differences in testosterone levels. However, this has to be interpreted cautiously since we do not have information regarding the nature of the social associations.

Conclusions

Using a novel, high resolution tracking technology we can show that parents, by choosing their breeding territory within a colony, determine the (social) environment of their offspring. We show that with shorter inter-nest distances, the available space and the movement activity became increasingly restricted. In addition to being adaptive in the short-term, the complexity of the early-life social environment could have lasting consequences e.g., for cognitive development. Our social network analyses further show that coming in contact with neighbouring chicks is very uncommon and kept to a minimum. Overall, our study shows that the behavioural demands that gull offspring must meet in order to adapt to a colonial life are far more complex than previously thought.

Authors’ contributions

R.S.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft; W.M.: conceptualization, investigation, methodology, supervision, writing—review and editing; E.S.: conceptualization, data curation, methodology, writing—review and editing; H.M.: data curation, methodology; F.V.: conceptualization, writing—review and editing; L.L.: conceptualization, methodology, supervision, writing—review and editing.

Two hatched Lesser black-backed gull chicks and one pipping egg.

CHAPTER 6

General discussion

In the past decades, lesser black-backed gulls have opportunistically invaded (sub)urban areas along the coasts of Europe as breeding grounds. Yet, urban areas are also a hotspot for anthropogenic activities, and birds breeding in such areas are exposed to higher rates of habitat destruction than birds breeding in natural habitats, which can force the former to repeatedly relocate for breeding. However, the costs of forcedly relocating to a new nesting site were as yet largely unexplored, among others because of a lack of knowledge about the costs of obtaining and maintaining a territory, as well as about the significance of territories for the offspring. Using lesser black-backed gulls as study species, I here aimed to fill these knowledge gaps. To achieve this, I combined a number of different approaches. First, I analysed highly valuable long-term breeding records to study the **reproductive costs of relocations**. Second, I used GPS tracking technologies to explore **time costs of territoriality**. Finally, I combined behavioural testing and novel UWB tracking technology to investigate **how territory choice affects chick behaviour**. This integration of approaches allowed us to advance our knowledge of the costs of colonial breeding in a human-induced rapidly changing environment from the adults' perspective, and could unravel as yet unknown and possibly long-lasting consequences for the behavioural phenotype of their offspring.

Keeping up with anthropogenic change - territoriality in urban colonies

The number of lesser black-backed gulls breeding in traditional gull colonies has steeply decreased over the past century (Camphuysen et al. 2010; Ross-Smith et al. 2014). On land, this was mainly driven by breeding failures related to persistent predation, especially by foxes (Southern et al. 1985; Spaans 1998).

At the same time, the high and predictable levels of anthropogenic food sources attracted gulls to the urban landscapes, which ultimately promoted roof-tops and industrial areas as breeding grounds. However, gulls are site-faithful and tend to occupy the same nesting site over consecutive seasons, while when breeding in anthropogenic environments they suffer from high and rapid rates of habitat loss due to human activities. Thus, as a first step it was crucial to get a more detailed understanding of possible reproductive costs associated to anthropogenic-derived loss of nesting areas. In **Chapter 2** I could indeed show that there are several effects of relocations on reproduction: birds that were forced to relocate exhibited a higher probability of intermittent breeding. This could be due to the fact that mass relocations of birds increase competition costs for nesting sites when a large number of individuals need to simultaneously settle in a new sub-colony. Furthermore, when birds bred in the season immediately following the one in which they had lost their nesting site, they showed a reduced reproductive investment as expressed by a smaller clutch volume. This effect was negatively correlated with relocation distance, suggesting that an increased unfamiliarity with sites (Beletsky and Orians 1989; Piper et al. 2008; for a review of site familiarity, see Piper 2011) and/or neighbours (Fisher 1954) inversely affected egg volume and thus offspring quality. Birds could limit these costs by skipping a breeding season, probably gaining more familiarity with the new site, but at the expense of losing one reproductive season.

Relocation thus induces a reproductive cost that was related to the nature and distance of the nest site switch. The existence of these costs could be the reason why most seabird species keep their nesting territories and mates over successive breeding seasons. In that context, it was often hypothesized that nest site fidelity evolved because it favours mate retention, since nests act as a meeting point for couples (Morse and Kress 1984; Cézilly et al. 2000). In turn, mate retention can be beneficial for breeding performance (Coulson 1966; van de Pol et al. 2006; Sanchez-Macouzet et al. 2014), as an increased familiarity with mates can lead to an enhanced parental coordination and a reduced allocation of time and energy in finding a new partner (Nelson 1972; Rowley 1983; Fowler 1995). However, I did not find that relocation affected the likelihood of partner change. In my study, this could be due to the fact that relocations happened at a very local scale, where birds relocated to other sub-colonies in the vicinity and still could have had opportunities to meet. It has also been argued that site fidelity can improve the foraging efficiency through an enhanced knowledge of foraging areas (Piper 2011; Rebstock et al. 2022). In a recent study on the same species, it has indeed been shown that familiarity is highly relevant for foraging behaviour, since individuals continued to use previous, more distant foraging areas after a forced nest site relocation (Kavelaars et al. 2020). In our study, individuals relocated over much shorter distances within the port of Zeebrugge, and most likely did not tend to exploit new foraging areas.

Taken together, the most probable reason why I found a cost of reproduction after a local-scale forced relocation is the loss of the advantages of familiarity with the neighbouring breeders. More specifically, my study suggests that the ‘dear-enemy phenomenon’ could be key for explaining nest site fidelity (Fisher 1954). The “dear enemy phenomenon” hypothesis states that individuals respond less aggressively to territorial intrusions from known neighbours than to non-neighbours (Heinze et al. 1996; Rosell and Bjørkøyli 2002; Lovell and Lein 2004; Jin et al. 2021; Werba et al. 2022), since previous fighting experiences help assessing the chances of winning or losing, and thus prevent escalated conflicts (Ydenberg et al. 1988; Temeles 1994). However, to ultimately prove that, it will be necessary to not only know the nest site history of the focal bird, but also that of its neighbours.

Keeping up with the neighbours – the burden of time for territoriality

As concluded before, the social environment is a prominent feature for colonial species, and coloniality can result in high levels of territorial aggression towards conspecifics. In lesser black-backed gulls, territorial defence is mainly related to the need of obtaining a nesting site in the colony in order to successfully reproduce. However, neighbouring conspecifics can predate on eggs and offspring, and therefore gulls keep a territory around their nesting site to prevent their conspecifics interfering with their reproduction. Competition for territories can also depend on the physical attributes of the site or location within the colony (Butler and Trivelpiece 1981; Hill et al. 1997; Hötker 2000; Ashbrook et al. 2008), e.g.. since some nesting sites can confer a higher protection against ground predators for the offspring (Pierotti 1982; Kim and Monaghan 2005; Pratte et al. 2016). Territorial disputes can be energetically costly, cause injuries and could negatively affect reproductive investment. To further investigate this, I performed a pilot study recording territorial behaviour during the breeding seasons of 2020 and 2021. Here, I focused on a total of 59 territories located in the main colony of Zeebrugge. In this pilot study, I found a trend that supports the idea that the number of agonistic interactions during territorial defence could be one of the underlying costs of reproduction after relocation (**Box 1**).

Box 1: Behavioural investment in territorial defence

I took 30-minute video recordings once per week in defined high and low density plots of the Zeebrugge colony during one month prior to egg-laying (similar time period as in **Chapter 3**). The aim was to annotate the territorial behaviour of the same 59 pairs (identified by block (=nest) number) over consecutive video recordings. We took the video recordings as such that we could see all individuals in a given plot, thus ensuring to account for all interactions received and displayed. 31 nests were analyzed in 2020, and 28 in 2021. I quantified the total number of territorial interactions that individuals exhibited over a period of 30 minutes for each weekly video recording, along with egg size measurements. The annotated territorial interactions were 1. **chasing** conspecifics away (without direct physical contact), 2. number of **attacks** (direct fight), 3. number of **redirected attacks** towards the ground (which mimics an actual attack towards an opponent, but without entering in direct conflict), and 4. **long calls** (for a detailed information on territorial behaviour of gulls see Tinbergen 1960).

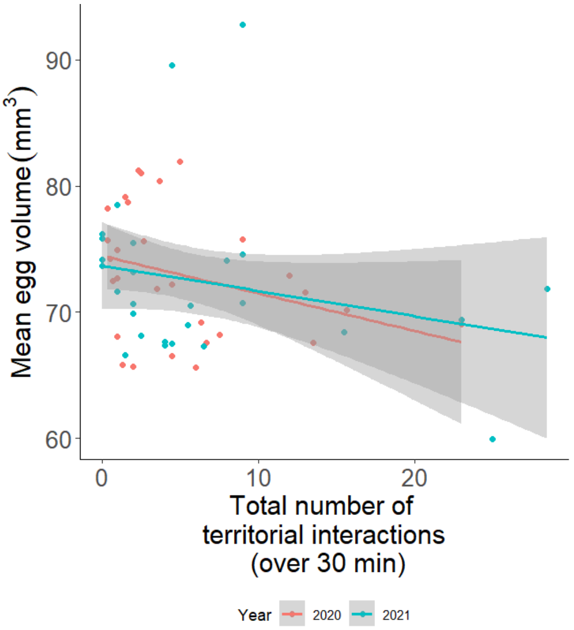


Figure B1. There was a negative effect of the total number of territorial interactions on reproductive investment (i.e., mean egg volume) in both years (LME, p = 0.05). The grey band represent the 95% confidence interval.

However, not only the costs of overt aggression might matter, investing time in territorial attendance and defence can impose carry-over effects with other relevant activities like foraging, which can in turn impinge on the reproductive investment. In **Chapter 3** I particularly focused on the time costs of territoriality. Lesser black-backed gull males initially invested more time than females in establishing a territory, which is likely related to the fact that males are more involved in territorial aggression (Tinbergen 1956; Pierotti 1981; Burger 1984). It is very likely that the more time birds were physically present in their territories, the higher the chances to engage in agonistic interactions with other conspecifics, but this was unfortunately not further studied. For males and females, spending time inside the territories was traded-off against the time individuals had for foraging activities, and thus limited the foraging time, foraging distance and commuting time during foraging trips. A reduced foraging activity during the pre-laying period could directly influence the accumulation of resources for egg production, affecting egg size, an important parameter influencing chick survival (Krist 2011). This could be especially relevant for females, since their body condition has been shown to be associated with egg size (Wendeln 1997; Reynolds et al. 2003). In fact, I found that territorial attendance indeed affected egg investment, where females that were more freed from the time constraints of attending the territory allocated more resources to the eggs, likely because they could increase their own foraging activities.

Territoriality in a changing world

The patterns as observed in **Chapter 2** suggest that a negative impact on reproductive investment after forcedly relocating is probably driven by the unfamiliarity with the social environment, while **Chapter 3** shows that the costs of maintaining a nesting site relate to time allocation trade-offs and possibly the number of agonistic interactions (**Box 1**). One might speculate that birds relocating to a different nesting area probably have to invest more time and energy in establishing and defending a territory. The idea that a reduced reproductive investment in relocated birds is due to a higher territorial investment remains speculative, as we did not explicitly test this hypothesis. However, I did find that time investment in territoriality can constrain the reproductive investment by reducing the accumulation of resources during the pre-laying period and hence *clutch volume*. And relocations negatively affected the *clutch volume* as well, which is highly suggestive. Unfortunately, I could not experimentally demonstrate that relocated birds incur higher time costs, since our study of forced relocations was carried out in the decade of the early 2000s, yet tracking of lesser black-backed gulls in our study populations started in 2013. This certainly remains an interesting and relevant question to answer in the future. Moreover, integrating aspects of energy expenditure that might arise from the agonistic interactions during nest defence is also an important step to better understand the costs of relocating to new breeding areas.

These competition costs could consequently affect the spatial structure as well as the social composition of a colony, which is still poorly understood. When faced with intense competition for nesting sites, low quality individuals are displaced to breed in low quality areas of the colony where breeding density and hence competition is lower (Fretwell and Lucas 1970; Potts et al. 1980; Rodenhouse et al. 1997). However, in low density areas egg and chick predation by ground predators could be higher (Krebs and Davies 1978; Hötker 2000), and available partners could be of lower quality (Coulson 1968), which can have implications for individual fitness. The quality and competitive ability of an individual thus determines its capacities to establish a territory in a particular (social) environment. However, this can as well be driven by habitat preference or by an animal's behavioural type (i.e., animal personality, Stamps and Groothuis 2010; Wolf and Weissing 2012), which could be set early in life (see below). For instance, individuals breeding in the most competitive, dense areas of the colony, also need to tolerate the close presence of neighbours in order to co-exist during the breeding period. This means that individuals need to be able to retreat from a conflict, or to down tune their levels of aggression towards their neighbours. Therefore, low density areas could not only be occupied by individuals with poorer competitive abilities, but also, and not mutually exclusively, by individuals with poorer social abilities. Yet it might be crucial to gain a better understanding of this. Interestingly, an interesting case of breeding at very low, almost isolated social conditions nesting on rooftops dramatically increases since the 1970s (Raven and Coulson 1997; François 2002; Soldatini et al. 2008; Ross-Smith et al. 2014). Rooftop nesting might allow successful reproduction of gulls independent of their quality or behavioural phenotype, due to the very low competition costs with conspecifics. It will be an important next step to investigate how changes in breeding conditions alter patterns of selection, and hence the evolution of a population.

The use of urban environments as breeding grounds increases the proximity to humans, which leads to an enhanced human-gull conflict (Belant 1997; Rock 2005). Breeding gulls are seen as nuisance species in the urban environment, and efforts are numerus to deter them. A common strategy to reduce such conflicts has been the removal of eggs, which would eventually lead to gull relocations to surrounding areas after several failed breeding attempts (Fairweather and Coulson 1995; Coulson and Coulson 2009). Even though such management activities typically affect a limited proportion of the breeding population (in contrast with the complete habitat loss and mass relocations derived from anthropogenic activities in colonies), they will still lead to reproductive failures for a prolonged period, likely followed by negative effects on reproductive investment after relocations, as I show in **Chapter 2**. The greater presence of ground predators in natural colonies, together with the persistent reproductive costs of relocation in urban and suburban areas likely explain why a generalist species such as the lesser black-backed gull is currently declining in numbers. Thus, providing sufficient suitable, undisrupted and predator-free habitat for breeding is likely the best solution to guarantee the continued existence of the species. A prime example for the success of this strategy is our study area in Zeebrugge, a sub-colony that is only used by gulls to breed. No anthropogenic activities can be carried out inside the sub-colony, and it is fenced to hold off ground predators. The colony at the entire port of Zeebrugge has dramatically decreased over the years, but in contrast, my study area showed a substantial increase in number of pairs over the two studied breeding seasons (from 181 in 2020 to 282 pairs in 2021). However, if no other suitable breeding areas are provided, this sub-colony will eventually saturate and promote individuals to breed in other surrounding areas (potentially rooftops), re-enforcing the human-gull conflict paradigm. While previously it appeared difficult to attract gulls to predetermined areas, we here show that by placing concrete blocks, one could likely attract breeding gulls to the desired suitable area, far enough from humans, to down tune the human-gull conflict. Moreover, such blocks can provide protection against unfavourable weather conditions, therefore increasing the survival of the offspring.

Keeping up with the neighbours - the early-life social environment

Parents choose and defend a territory, ultimately with the purpose of maximizing reproductive success. The costs of defending a territory should, therefore, ultimately be counterbalanced by benefits for the offspring. Thus far this has predominantly been studied by quantifying offspring survival, e.g., whether specific territories offer a higher protection from predators, either by physical attributes of the territory (i.e., vegetation cover), due to an avoidance of (ground) predators of dense areas, or due to a greater probability to survive heterospecific predation in high social densities (i.e., dilution effect, see Krebs and Davies 1978; Hötker 2000). However, considering that experiences during the early life can shape individual behaviour, we still do not fully understand the consequences of territory choice for the offspring. While colonial breeding indeed provides protection for the offspring, it also entails high levels of conspecific aggression against chicks (Hunt and McLoon 1975; Butler and Trivelpiece 1981; Hill et al. 1997; Ashbrook et al. 2008) or even predation of eggs. Sometimes chicks are also cannibalized (Parsons 1971; Davis and Dunn 1976; Wittenberg and Hunt 1985, Møller 1987). Furthermore, the offspring of this species is semi-precocial, and chicks start ranging around soon after birth. A resulting intrusion of chicks into neighbouring territories, which happens more often in dense areas, triggers the territorial aggression of the neighbouring adults (Hunt and McLoon 1975; Fetterolf 1983; Ashbrook 2008), and chicks are sometimes pecked repeatedly causing a substantial amount of mortality. Chicks can try to avoid conspecific aggression by moving less, so I hypothesized that growing up in territories in more dense areas should trigger lower levels of exploration activity in the offspring. Consistent with this hypothesis, I found that chicks being raised in high density (HD) areas showed reduced exploration activity, as measured in an Open Field Test (**Chapter 4**), probably because they benefit from avoiding conflicts, which is more relevant in dense areas where encounters with neighbours are more likely. I also found that chicks that were raised in closer proximity to neighbours showed a reduced movement activity and had smaller territories (**Chapter 5**), while siblings exhibited a high similarity in their movement patterns. As I measured exploration and movement activity towards the end of the nestling period, offspring could have learned to avoid conflicts with neighbours by aversive feedback learning. This means that chicks would have learnt from their previous interactions with neighbouring birds, by associating moving beyond their own territory borders with a negative stimulus (here, being aggressed).

An important question when interpreting the movement data is whether the colony in Zeebrugge is comparable to more natural colonies. The behaviour of the chicks might have been influenced by (1) the lack of vegetation in the study colony of Zeebrugge, (2) the fact that we provided concrete blocks for shelter and (3) the range of breeding densities. With respect to the latter, the distance to three nearest neighbouring nests in Vlissingen in 2019 was 10.43 ± 4.76 m, while it was 3.68 ± 2.30 m in Zeebrugge in 2021. Thus, the colony in Zeebrugge is characterized by a very high breeding density, and that chicks moved so little has to be interpreted against this fact. Moreover, in presence of vegetation cover, chicks might receive less aggression as they are better visually hidden, which again could facilitate moving at least within the boundaries of the territory. Thus, now that the tools are available, we should study movement behaviour of the offspring over a greater range of densities and nest site characteristics. These data are urgently needed, also because most previous data about chicks' movement activity in seabirds were collected in the context of parental care, e.g., begging (Hunt and McLoon 1975; Eising and Groothuis 2003) and responses to parental calls (Impekoven 1976; Noguera and Velando 2019), which was not the case in my study. However, there are a number of studies in black-headed gulls, showing that chicks display territorial behaviour and that they defend their territory, also against adults (Groothuis 1989a; Ros et al. 2002; Müller et al. 2009). This at least suggests that I can interpret my movement and exploration data against a background of territoriality. Yet as mentioned, the limited number of studies on territoriality in chicks is partially due to the fact that accurately quantifying movement and territory size in the offspring is hardy possible without the use of (recently developed) tracking technologies.

This limited the possibilities for comparison, but it can be expected that the observed patterns reflect adaptations to the social environment. They likely increase the survival of the chicks, since received aggression can also likely lead to lethal attacks. Unfortunately, we did not accurately account for chick mortality in our study. First of all, we only followed on (the first) two chicks per nest, and second, the chick recovery rate in the field was not a 100%, as the plot was too big to find all chicks within a limited time frame. Therefore, it was impossible to fully distinguish between predation and failed attempt of recovery in the field, which could lead to a misinterpretation of chick survival. Despite these drawbacks, the data in **Box 2** indicate that chicks raised in dense areas suffer from a higher mortality risk, as would be expected if social density induces a survival cost. However, again, whether this mortality was related to aggression still remains to be shown. We did not monitor aggressive interactions towards the offspring, and we were not able to determine the cause of death. Furthermore, the observed mortality pattern might also be influenced by the artificial set up in my study colony, since it was fenced in order to avoid ground predators. In natural colonies, breeding success is higher in dense areas due to lower predation levels from ground predators (dilution effect, see Krebs and Davies 1978; Hötker 2000). Therefore, the pattern of higher mortality in dense areas in **Box 2** might then result from the exclusion of ground predators in Zeebrugge, skewing the focus to the higher levels of intra-specific aggression as the main cause of chick mortality. Still, adults exhibited a tendency to densely aggregate in the center of the colony, as in any natural situation this would have been the most optimal location. This remains as yet speculative, and will require studies comparing different types of colonies.

Box 2: Mortality and post-natal social environment

The mortality analysis comprised data of 288 experimental chicks (N=107 in low density areas, N = 181 in high density areas) with a maximum of two chicks that were followed per nest until the time of behavioural testing. In high density areas, the probability that a chick died or disappeared was 29%, while this probability was of 19% in low density areas, but these differences were not significant (binomial GLMM, t = 1.88, p = 0.06).

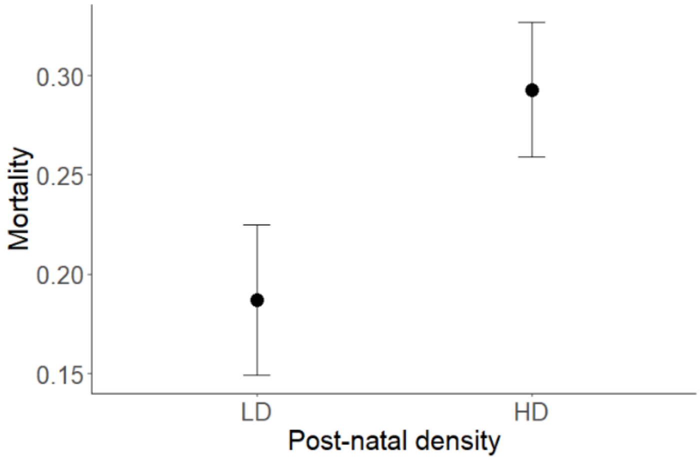


Figure B2. Plot illustrating mortality (=probability to die or disappear) according to post-natal social environments (LD = low breeding density, HD = high breeding density). Dots represent the average and whiskers the standard errors.

Another approach that I applied in order to understand the movement patterns was a social network analysis. Of course, this data does not give information about whether chicks really had interactions with each other and/or their nature, since UWB only gives information about locations in space and time. Still, I could quantify the associations and thus possible moments for interactions. As expected, chicks in dense areas interacted with more neighbouring chicks and had a higher number of associations with them, which could be explained by a higher chance of unintentionally encountering other neighbouring chicks in close proximity. However, these results have to be interpreted cautiously, because I found that only 2% of the chicks' associations occurred with chicks from neighbouring territories. That implies that the actual number of potential interactions is very low. However, here it has to be noted that not all individuals in the plot were tracked, i.e., no adults, only max. 2 chicks per nest (modal brood size is 2.3 chicks), and not the chicks of all nests. So, 2% interactions with neighbours are likely an underestimation, but it could still be indicative.

In summary, chicks were more exploratory in low density areas (**Chapter 4**), and moved more when other neighbours were further away (**Chapter 5**), as hypothesized. Thus, both effects might be mutually dependent. I tested this possibility for a subset of individuals (N= 36), as I had data about chicks that were tested in the open field test for exploration activity (**Chapter 4**) and afterwards their movements in the colony were followed via UWB trackers (**Chapter 5**). Movement and exploration activity were not correlated at the individual level (r = 0.12, p= 0.48), and at the moment, I can only speculate about the lack of such a relationship. The two traits may measure different aspects of the chicks' behavioural phenotype. While chicks tracked in the colony likely exhibit natural levels of movement activity, in the open field test they were tested in an artificial set-up that could also measure stress-related effects. Moreover, the environment during the open field test not only changed physically, but also socially as the chicks were tested in isolation away from their parents and other conspecifics. Thus, the non-social aspect of exploration (open field test) and social movement activity (UWB tracking) could reflect different, unrelated components of the chick's behavioural phenotype. Interestingly, I did not find a correlation between exploration activity and average distance to the three nearest neighbours (which defined the social environment in Chapter 5) ($r = 0.13$, $p = 0.44$), where such correlation was only found for movement activity. Similarly, exploration activity (PC2) varied with post-natal density category (which defined the social environment in Chapter 4) but movement activity did not ($\chi^2 = 0.38$, $p = 0.53$). This could indicate that exploration and movement activity are potentially explained by different aspects of the social environment. In one case the number of neighbours in a given plot matters and shapes the exploration phenotype, while the distance to neighbours affected social movement activity.

Keeping up with the neighbours – mothers' little helpers

As becomes clear from the above, right after hatching chicks encounter a partially hostile environment, but they are not necessarily unprepared for surviving in such a dense social environment. After hatching and throughout their first 1-2 weeks, they are quasi permanently guarded by their parents (Kavelaars et al. 2021), which is crucial to prevent predation. Since we tested chicks that were between 15 to 25 days old, it is likely that chicks learned over their first couple of weeks of life how to adjust to the social environment (Lougheed and Anderson 1999). In addition, parents and in particular mothers can pre-adjust offspring phenotype to the conditions the chicks likely will encounter in the post-natal environment. Such pre-natal maternal effects can have an anticipatory effect on offspring behavior, where the offspring may benefit from the prenatal programming when the post-hatching conditions are similar to the pre-natal (maternally anticipated) conditions (Groothuis et al. 2005; Marshall and Uller 2007). There is indeed evidence that social conditions are translated to the offspring via maternal effects. The breeding density as experienced by the mother when laying her eggs (i.e., the social environment) has for example been shown to alter maternal androgen deposition into the egg yolk (Schwabl 1997; Gil 2008; Oliveira 2004; Pilz and Smith 2004; Hargitai et al, 2009), which can in turn pre-adjust offspring behaviour to the social conditions experienced after hatching (Groothuis et al. 2005, Müller et al. 2009). This is because maternal yolk androgens are known to affect a variety of offspring traits (Groothuis et al. 2005, Eising et al., 2006), such as begging and territorial behaviour (Eising and Groothuis 2003; Müller et al. 2009). As mentioned above, these studies predominantly focus on the context of parental care. In contrast, there is hardly any evidence of how yolk androgens affect exploratory and movement behaviour, although it has been shown that embryonic exposure to androgens has a long-term effect on exploratory behaviour in male flycatchers when tested in a novel environment (Ruuskanen and Laaksinen 2010), and it resulted in more active and faster individuals when exploring new environments in quails (Daisley et al. 2005).

I thus hypothesized that chick behaviour might be pre-adjusted by the pre-natal (social) conditions, and I indeed found that the pre-natal environment significantly affected the exploration activity of the offspring in **Chapter 4**. However, a lower exploration activity was found in high breeding densities, where yolk androgens levels are supposed to be high (Schwabl 1997; Gil 2008; Oliveira 2004; Pilz and Smith 2004; Hargitai et al, 2009), which should have resulted in a higher exploration activity according to the limited evidence available (Daisley et al. 2005; Ruuskanen and Laaksinen 2010). The discrepancy in results is difficult to explain due to the limited experimental evidence. Other non-mutually exclusive mechanisms with potential effects on offspring behaviour include genetic effects (Dingemanse et al. 2002; Stirling et al., 2002; Drent et al; 2003; Van Oers et al. 2004; Van Oers et al. 2005), or vocal cues (i.e., alarm calls) experienced during the embryonic phase, which would be more present in high density areas (Noguera and Velando 2019). Still, the mechanisms underlying pre-natal effects on exploratory behaviour are unclear and require further study.

In **Chapter 5**, I also hypothesized that movement behaviour could be influenced by pre-natal effects. For instance, pre-natal effects can affect muscle development and skeleton size (Ashton et al. 2005, DuRant et al. 2010, Hopkins et al. 2011; Romano et al. 2021), and ultimately the ability to move. Less disrupted patterns of incubation due to less frequent interactions with neighbours could also influence the locomotor development of the offspring (DuRant et al. 2010; Hopkins et al. 2011; Belnap et al. 2019). Interestingly, I found that pre-natal densities significantly affected chick size (i.e., tarsus length, age-corrected, $\chi^2 = 5.32$, $p = 0.02$, **Box 3**). Chicks that hatched from eggs that were laid in nests where the neighbours were further away were bigger. However, I did not find effects of the pre-natal breeding densities nor chick size on movement behaviour (**Chapter 5**). This suggests that, even when chicks have larger tarsi and are possibly able to move more, their movement behaviour is instead determined by the social environment post-hatching.

Interestingly, chick size was not affected by the post-natal densities (χ^2 = 0.11, p = 0.73), even though it is typically assumed that only better birds, with a higher parental quality, will be able to obtain a territory in a high social density (see above). This clearly requires further study.

Box 3: Pre-natal effects on movement behaviour

Pre-natal effects for chicks equipped with UWB trackers in 2021 in Zeebrugge (N= 76). Tarsus length in males was on average 63.54 ± 3.68 (N = 34), and for females 60.57 ± 2.87 (N= 42). As a measure of chick size, the age-corrected tarsus length was calculated by using the residuals of a linear model of tarsus size against age of the chicks, as not all chicks were measured at the same age. There was a significant effect of the pre-natal social environment (distance to the three nearest neighbours) on chick size (χ^2 = 5.32, p = 0.02), and male chicks were also bigger than females (χ^2 = 35.60, p < 0.001).

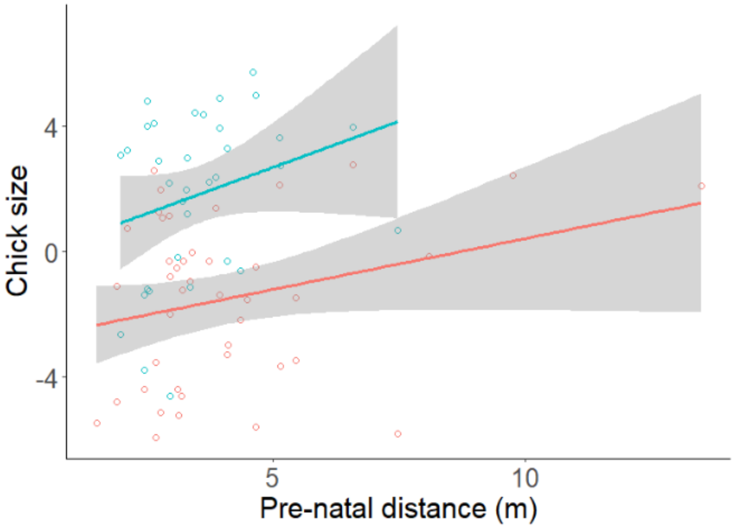


Figure B3. Plot illustrating the relationship between chick size and pre-natal social environments for males (blue circles and regression line) and females (red circles and regression line). The grey band represent the 95% confidence interval.

Traces of the social environment – long-lasting effects?

Pre-natal maternal effects as well as post-natal environmental effects acting during early life have been shown to have long-lasting effects on phenotypic traits (Lindström 1999). This makes it likely that the individual differences in exploration and movement behaviour, which I only measured close to fledging and during a short time period in **Chapter 4** and **Chapter 5**, may have a range of long-term effects as well as ecological implications for lesser black-backed gulls during adulthood. Individuals, for example, are predicted to select ecological niches that fit with their own behavioural phenotype. It could then be hypothesized that any effects on the exploration and movement traits that I found during early-life, if long-lasting, could affect foraging behaviour, and the choice of wintering or breeding sites. In that regard, chicks raised in low density environments, which showed a higher exploration and movement activity, could also show a faster exploration of foraging patches, potentially making use of a broader variety of foraging resources (i.e., thus becoming generalist individuals later in life), or could exhibit a better ability to locate and remember a higher number of foraging patches (i.e., higher spatial cognitive abilities).

Regarding migration, lesser black-backed gulls, although highly consistent at the individual level, exhibit a high inter-individual variation of migratory routes, stop-over and wintering sites (Baert et al. 2018). The development of the different migration strategies in lesser black-backed gulls could potentially be explained by the recently proposed ‘exploration-refinement’ mechanism (Guilford et al. 2011), where immature individuals (lesser black-backed gulls reach reproductive maturity at 4 years old) explore wintering grounds in their first years, and gradually refine their migratory route as they age. For instance, Campioni et al. in 2020 found that migratory routes of immature Cory’s shearwater (*Calonectris borealis*) become gradually less explorative as individuals aged. Direct evidence supporting the 'exploration-refinement' mechanism is very scarce, since it is challenging to track juvenile individuals (i.e., high mortality over the first year of life, long-term tracking over the entire immature period of an individual). If lesser black-backed gulls use this strategy, individuals raised in low density areas could potentially be more explorative and hence more variable in defining their migration routes and wintering sites later in life, possibly also migrating to wintering areas further away.

Interestingly, exploration has been shown to be correlated with boldness and aggression (Sih et al. 2004; Réale et al. 2007; Dingemanse et al. 2007; Sih and Bell 2008), which has been shown to influence foraging behaviour, where bolder birds foraged closer to the colony (Patrick and Weimerskirch 2014) and were more repeatable in their use of foraging areas (Harris et al. 2019). But those traits could be relevant for colonial breeding (Réale et al. 2010). As I hypothesized above, individuals that are too bold and aggressive could be incompatible for breeding in dense social conditions, since bolder individuals might withdraw less from conflicts and have a lower sociability (Magurran and Seghers 1991; Lacasse and Aubin-Horth 2014). For instance, it has been shown that bolder females in chestnut thrushes (*Turdus rubrocanus*) prefer to nest further away from other neighbours (Zhao et al. 2016) and although there are very little studies measuring personality in seabirds, interestingly Patrick et al. (2013) have shown in adult wandering albatrosses (*Diomeda exulans*) that birds were shyer in a dense colony compared to those at lower densities. This could ultimately mean that if lesser black-backed gulls chicks raised in low density areas are also more explorative later in life, and if this correlates with boldness and aggression, individuals could favour to breed in similar low density social conditions as experienced during their own development.

The fact that the social early life environment could have lasting effects on phenotypic traits at adulthood is speculative and tailored to the biology of my study species. Other seabird species move very little during the pre-fledging period compared to lesser black-backed gulls, but still cover long distances during their annual life cycle, which requires strong navigational and spatial skills. In such species, the experiences post-fledging thus likely play a more important role for their cognitive development. Thus, either the sensitive windows for cognitive development differ among species, or the adaptive significance of the observed reduced movement and exploratory activity of the offspring on dense breeding densities relates predominantly to the pre-fledging period. As part of another on-going PhD project, some GPS trackers were fitted to a subset of lesser black-backed gulls for which I measured behaviour early in life, in order to follow their movements during their first years of life. Therefore, whether or not the early-life social environment has long-lasting effects on the offspring phenotype at adulthood will hopefully be answered in the near future.

Final remarks

Colonial breeding species experience significant variation in their social environment, where the social interactions that individuals have early in life can profoundly shape their own phenotype, a phenomenon known as “interacting phenotypes” (Moore et al. 1997), possibly with long-lasting consequences. Understanding how individuals cope with and adapt to their early-life environment can thus provide fundamental insights into the drivers of behavioural variation and how it evolves. Here, I provide evidence that the early-life social environment plays a key role in shaping the exploration and movement behaviour in lesser black-backed gull offspring, but understanding its adaptive significance will require further studies on whether and how there is selection against less well adapted phenotypes early in life, and whether these behavioural patterns are maintained later in life and relate to fitness. This is of particular importance in order to understand the consequences of anthropogenic change. To predict how organisms respond to it, it is fundamental to know whether there are phenotypic changes in response to experiencing novel environments. To take an example, being raised in isolation on a rooftop could have lasting effects on the offspring's phenotype, which might lose their social competence as the development of inhibitory control could likely be impaired. If so, the unprecedented current levels of habitat and environmental change, which implies often neglected changes in the social environment, could have the potential to shift the (behavioural) phenotypes of future gull generations, with as yet unknown consequences.

Set-up for recordings of adult behaviour during the pre-breeding season in Zeebrugge.

Supplementary information

Supplementary information Chapter 3

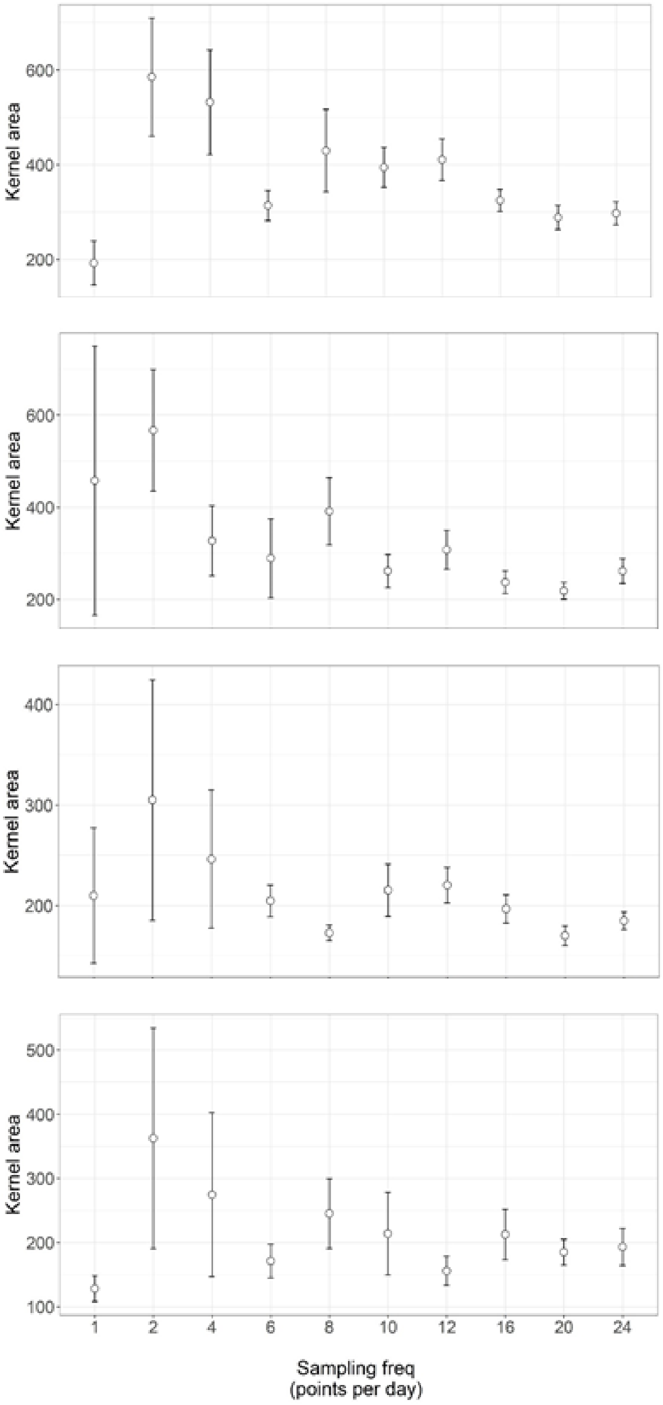


Figure S1. Bootstrapping for the estimation of kernel size based on sampling frequency using the data of four individuals. A sampling frequency of 12 GPS fixes per day or more is sufficient to accurately estimate kernel size. Each simulation was run 10 times.

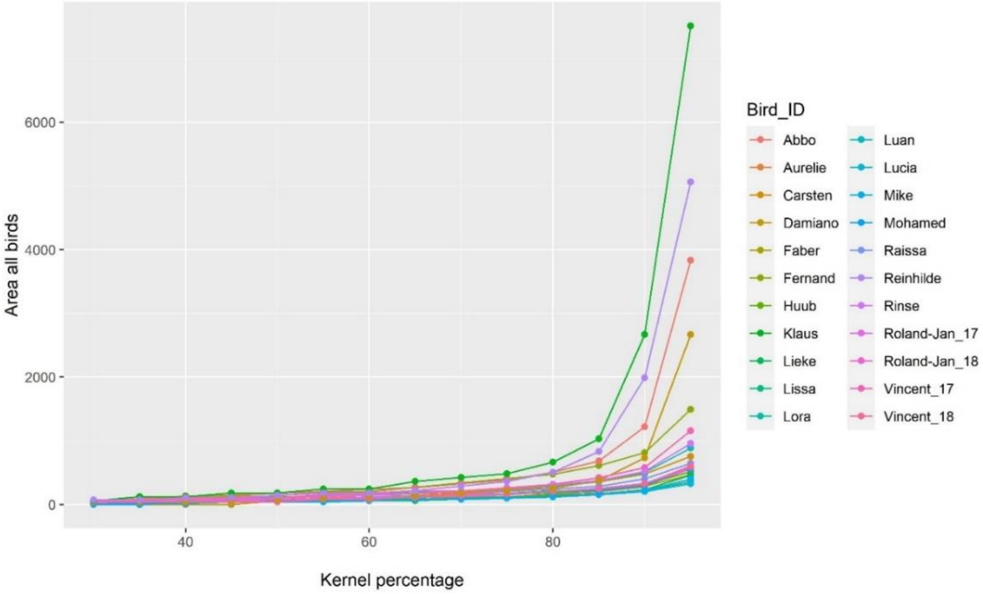


Figure S2. Kernel area based on kernel UD percentages for all birds; a 75% kernel UD represents a conservative estimate for territory size in our population.

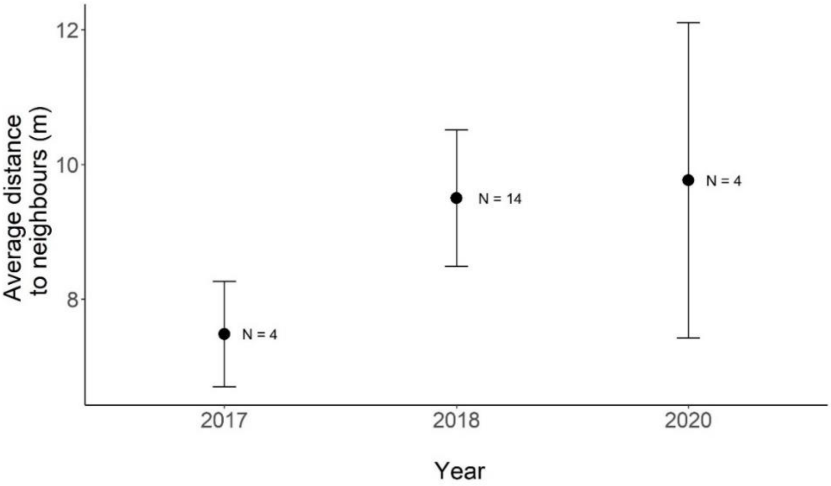
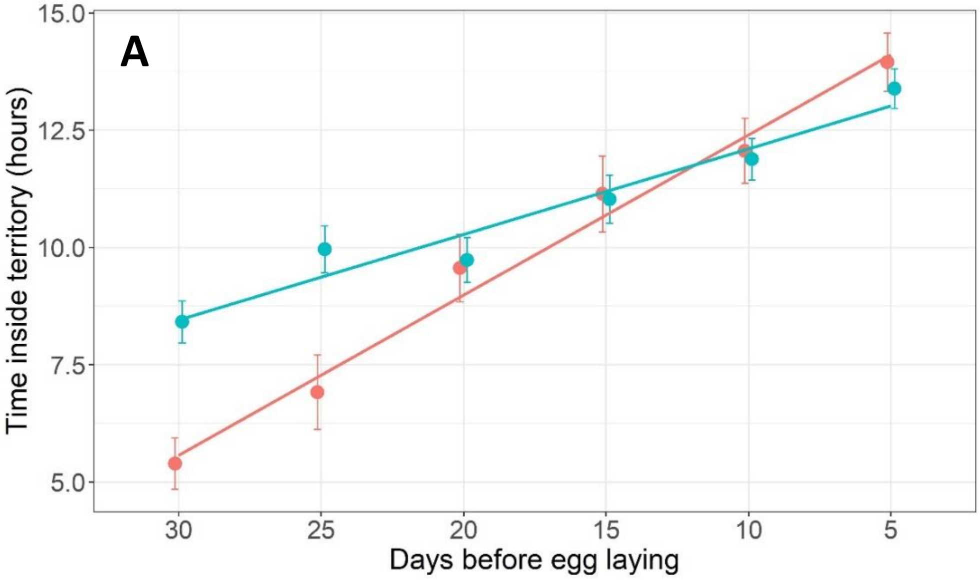


Figure S3. Average distance to the three nearest neighbours (m) per year. Dots represent the mean values, and whiskers the standard error.



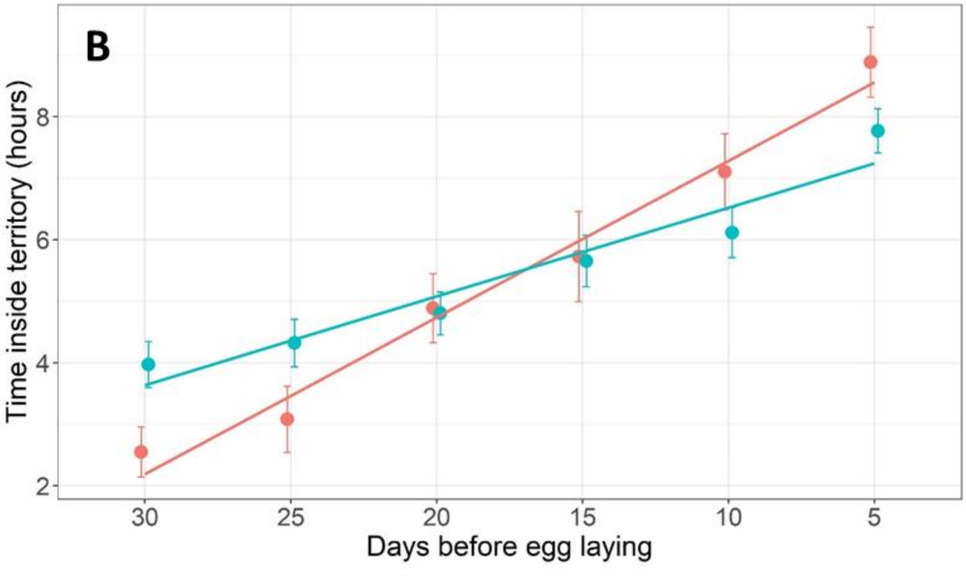
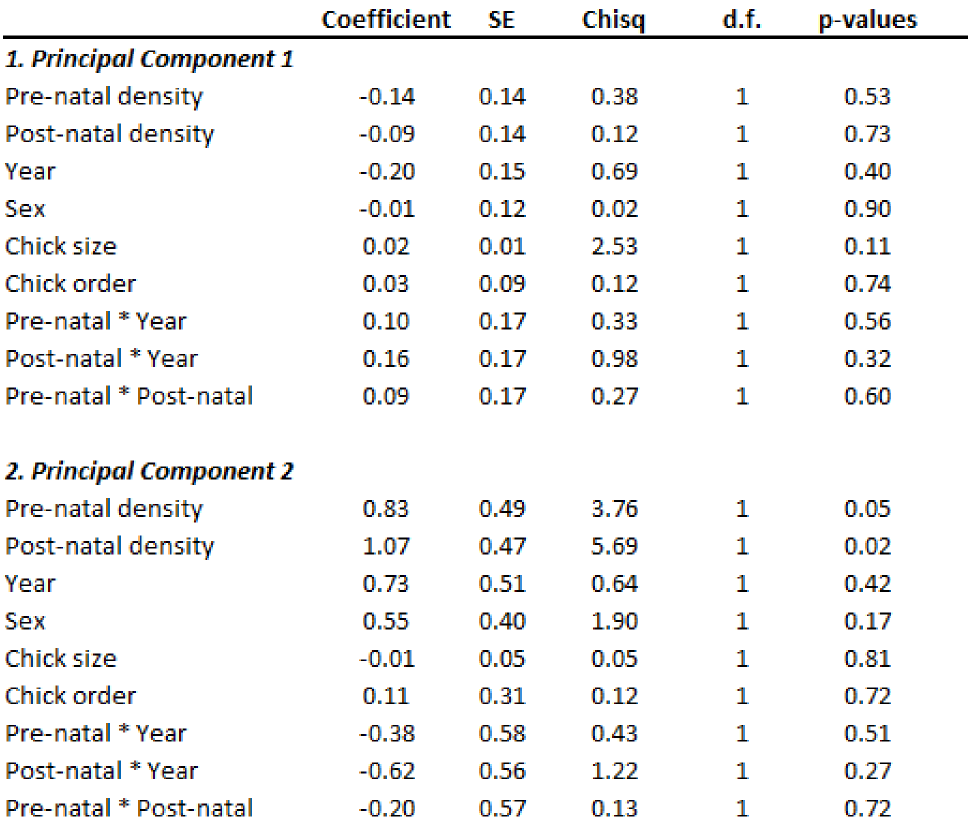


Figure S4. Time spent inside the territory across the 30 days prior to egg laying (binned in 5-day interval) for males (blue) and females (red). A) comprises data during day and night and B) only the daylight period (extracted using the suncalc package in R). Dots represent the mean values, and whiskers the standard error.

Supplementary information Chapter 4



	Coefficient	SE	Chisq	d.f.	p-values
1. Principal Component 1					
Pre-natal density	-0.14	0.14	0.38	1	0.53
Post-natal density	-0.09	0.14	0.12	1	0.73
Year	-0.20	0.15	0.69	1	0.40
Sex	-0.01	0.12	0.02	1	0.90
Chick size	0.02	0.01	2.53	1	0.11
Chick order	0.03	0.09	0.12	1	0.74
Pre-natal * Year	0.10	0.17	0.33	1	0.56
Post-natal * Year	0.16	0.17	0.98	1	0.32
Pre-natal * Post-natal	0.09	0.17	0.27	1	0.60
2. Principal Component 2					
Pre-natal density	0.83	0.49	3.76	1	0.05
Post-natal density	1.07	0.47	5.69	1	0.02
Year	0.73	0.51	0.64	1	0.42
Sex	0.55	0.40	1.90	1	0.17
Chick size	-0.01	0.05	0.05	1	0.81
Chick order	0.11	0.31	0.12	1	0.72
Pre-natal * Year	-0.38	0.58	0.43	1	0.51
Post-natal * Year	-0.62	0.56	1.22	1	0.27
Pre-natal * Post-natal	-0.20	0.57	0.13	1	0.72

Table S1. Full linear mixed models (1.) testing the effect of sex, year, chick size, pre-natal and post-natal conditions, and the interaction between the pre-natal and post-natal conditions on the Principal Component 1 (“anxiety”). A similar model (2.) was fitted to investigate the effects on Principal Component 2 (“exploration activity”).

Supplementary information Chapter 5

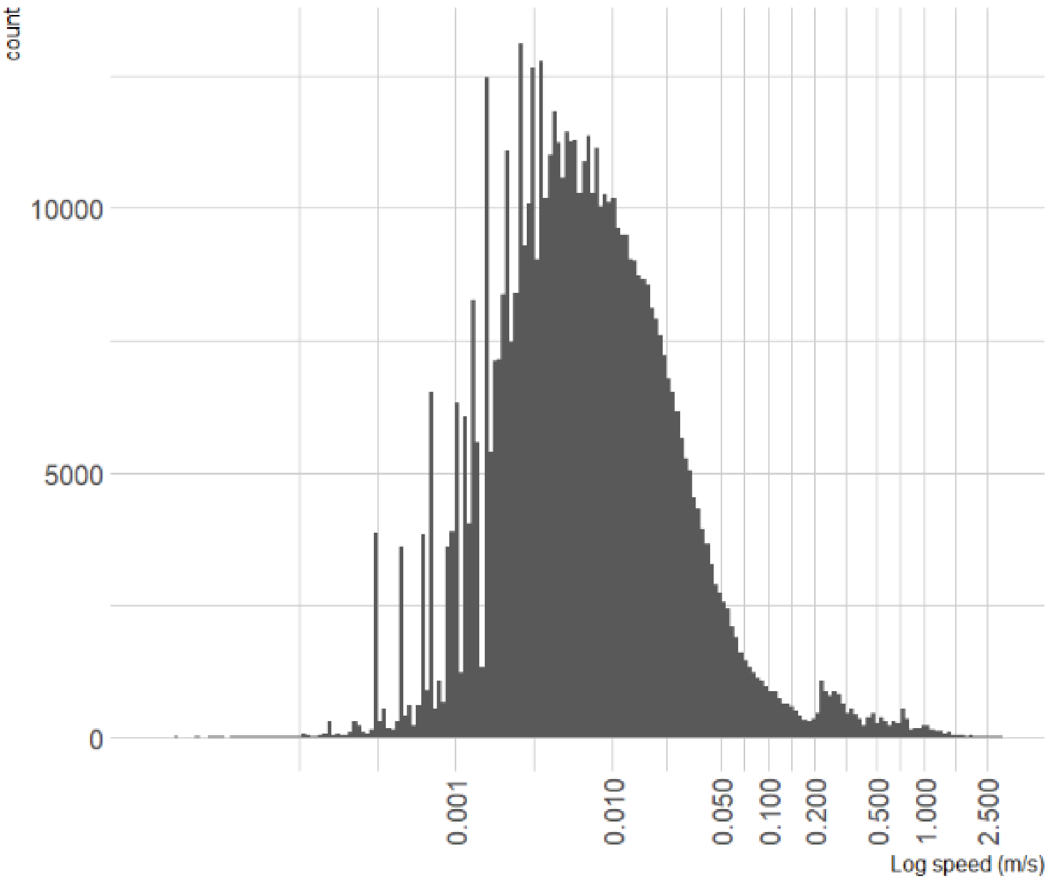


Figure S1. Density plot speed (distance/time elapsed) to next spatial position.

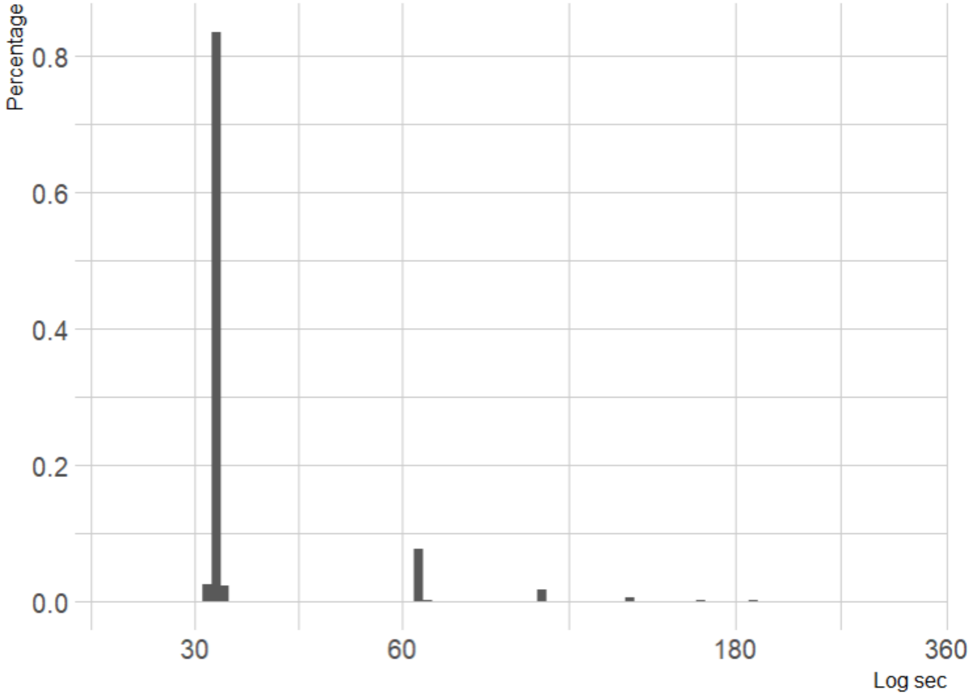


Figure S2. Density plot time (seconds) to next spatial position.

Anthropogenic activities carried out in a subcolony in Vlissingen.

References

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Lesser black-backed gull chick.

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