A comparison of egg investment in lesser black-backed gulls (*Larus fuscus*) from urban and non-urban colonies

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Abstract

While the increasing worldwide urbanization generally has negative effects on biodiversity, some animals, like roof nesting gulls, are able to take advantage of these areas and have generated large populations in a number of cities. This increase is thought to result from the favorable living conditions urban systems can provide, such as high food densities, warmer temperatures, lower predation rates, and ample nesting sites. However, few studies have focused on the urbanization of gulls. To help fill this knowledge gap, I compared egg investment between three lesser black-backed gull colonies that experience different amounts of predation pressure: one urban colony, one rural colony and one control colony with assumed intermediate predation levels relative to the others. Urban systems often have lower predation risk and provide a natural contrast for studying the effect of predation on reproductive strategies. The aim of this study was to investigate the effect of decreased predation on egg investment to better understand the mechanics behind the influx of birds to urban systems. I found that the three colonies showed a divergence in reproductive strategies where the urban colony invested more in their offspring overall, and laid significantly bigger clutches (mean$\pm$SD, Realfagstaket=2.84$\pm$0.41, Lyngøy=2.3$\pm$0.81, Ågotnes=2.45$\pm$0.82), but the rural colony laid significantly larger eggs (mean volume$\pm$SD, Realfagstaket=67.0$\pm$6.01 cm^3, Lyngøy=71.81$\pm$7.81 cm^3, Ågotnes=70.94$\pm$7.33 cm^3). The findings suggest that the lower amount of predation in urban areas provides advantageous conditions in which parent birds are able invest more in reproduction. However, further research is needed to separate the effects of predation from other potential differences between the colonies, and to see the potential consequences of these findings.

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Introduction

At present, over half of the human population lives in urban areas, and the trend is increasing. By 2050 it is expected that two-thirds of the population will have relocated to cities, leading to a vast expansion of urban areas (Ritchie, 2018). This rapid urbanization can be detrimental for many species of animals, but also potentially advantageous for others (McKinney, 2008). While gulls usually exploit coastal areas and islands for breeding, many now utilize the urban environment. Currently, the global urban-nesting populations of gulls have experienced swift population increases and many species, including the lesser black-backed gull (*Larus fuscus*) and herring gull (*Larus argentatus*), now have substantial urban populations across Europe (Belant, 1997; Spelt et al., 2019). However, along with this increase in urban areas, many natural populations of lesser black-backed gulls are now declining at the same time (Balmer et al., 2007; Ross-Smith et al., 2015). This can be seen in the United Kingdom (UK), where urban gull populations have experienced an increase during the last 40 years, while the non-urban populations have experienced declines in the same period (Eaton et al., 2015; Spelt et al., 2019).

The exact reason for the gull´s success in urban systems is uncertain but could be a potential result of high food densities, warmer temperatures, lower predation rates, and ample nesting sites (Rock, 2005; Spelt et al., 2019, 2021). Gulls often have high plasticity in both foraging and nest-site selection, making them able to take advantage of novel habitats like urban areas for nesting (Fuirst et al., 2018; Ross-Smith et al., 2014). Due to their adaptable nature, they provide useful opportunities to study how the urban environment impacts behavior and reproductive strategies. Especially the impact of predation is of interest, due to the low predation rates in many urban systems (Eötvös et al., 2018). In these systems, urban gulls represent a useful natural contrast for studying the effect of reduced predation. As nest predation is the primary source of reproductive failure for the majority of wild bird populations, it represents an important driver of natural selection (Fontaine & Martin, 2006; Lima, 2009). Predation can have direct effects through mortality and consumption, and indirect effects through associated predation risk that can influence the behavior and reproductive strategies of their prey (Hua et al., 2014).

An expanding amount of research now show that breeding birds are able to assess the level of predation risk and respond adaptively in ecological time through changes in egg and brood size (Lima, 2009). Several hypotheses have been suggested to explain this observed variation in investment. The nest predation hypothesis states that birds experiencing a high degree of nesting failure due to predation or other factors should lay smaller clutches and therefore invest less than birds who experience a lower degree of nesting failure (Slagsvold, 1984). This hypothesis has gained support through multiple experiments, including predator removal experiments wherein safer environments, parents increased investment in their offspring through increased egg size and clutch size, as well as higher feeding rates for the nestlings (Fontaine & Martin, 2006; Lavers et al., 2010). Other experiments have shown that even the perception of predation risk alone, only playbacks of predator calls, was enough to reduce the number of offspring produced by 40% (Zanette et al., 2011). The absence of this selection factor in some urban systems is therefore likely to affect the reproductive investment of birds and might allude to why some might immigrate to or even thrive in urban environments.

While it is clear that predation plays a significant role in reproductive strategies, the individual circumstance of the prey also plays a large role. The production of eggs is a demanding process in terms of both energy and nutrient demands and can potentially influence the subsequent performance of both parent and offspring (Pat Monaghan & Nager, 1997; Nager et al., 2000; Verboven et al., 2009). Because the developing embryo is entirely dependent on the resources allocated to the egg, the amount and quality of the egg components can heavily affect its viability (Pat Monaghan & Nager, 1997; Verboven et al., 2009). The mother can influence individual offspring fitness by both egg size and egg quality, two traits that have been shown to correlate (Amundsen & Stockland, 1990). Egg size has been found to positively correlate with offspring traits across nearly all life stages and often breeds offspring of larger size, which is advantageous in early hatching stages (Bolton, 1991; Krist, 2011). However, due to the high energy requirements of reproduction, there exists a trade-off between both the number and size of the eggs and current and future reproduction (Krist, 2011; Magnhagen, 1991). As central parts of life-history theory, both trade-offs have been extensively studied and supported through increased egg formation research where later laid eggs were progressively poorer in quality (P. Monaghan et al., 1998; Nager et al., 2000), and parent females were both less likely to be resighted at the breeding ground and produce a clutch the following year (Nager et al., 2001).

Despite being so prominent in urban habitats, relatively few studies focused on the urbanization of gulls (Hirvonen, 2019). Ecologists typically focus their research on the impact on wildlife in natural environments, leaving studies of animal behavior in urban environments more limited (Fuirst et al., 2018). In order to inform management and further conservation decisions, more research about their behavior and success in urban habitats is therefore needed. To contribute to this topic, this research will focus on the aspect of reproduction in urban areas and make use of the natural contrast urban gulls provide by comparing egg and clutch sizes of lesser black-backed gulls in three mixed gull colonies in Vestland, Norway. In Norway, the lesser black-backed gulls have previously been in decline (50% decrease from 2005 to 2013) but remained relatively stable since (Fauchald et al., 2015). The colonies were chosen based on their close proximity and their different levels of exposure to predation. One is located on the roof of a building in the city center with no observed predation pressure, one on a natural island with many potential predators, and one control in an industrial area with assumed intermediate predation relative to the other colonies. Due to their proximity, this study operated on the assumption that the colonies experience the same climatic conditions and have access to the same foraging areas, making predation the primary external difference. The size of the eggs and clutch were treated as indicators of investment and compared between the colonies. Based on the theory presented above, I expect to find higher amounts of investment, seen through an increase in the number and or size of eggs, in the urban colony experiencing less predation.

Materials & methods

Study sites

Lyngøy nature reserve:

Lyngøy is an island and nature reserve in Tysnes commune in Vestland, Norway (60°04'34"N 5°30'57"E). The 62daa big island is situated 3,3km from closest shore and approximately 35km from the city center in airline. It houses the biggest mixed seabird colony in the region, with approximately 60 Breeding pairs of lesser black-backed gulls and 300 pairs of herring gulls each year. It is an older colony that has been recorded since the 1960s and is now in slight decline. Other species found on the island include the great black-backed gull *(Larus marinus*), the common eider (*Somateria mollissima*), and the Eurasian oystercatcher (*Haematopus ostralegus*), among others. The island contains a variety of different terrains, making it suitable for many species: flatter areas with grass, tufts, and swamps, as well as rocky hills, cliffs, and beachside. The lesser black-backed gulls mainly utilize the flat terrain in the middle of the island, laying their eggs between tufts of grass in the swamp area. Due to its proximity to land, the island is also accessible to a number of predators. Both the golden eagle (*Aquila chrysaetos*) and the white-tailed eagle (*Haliaeetus albicilla*) have been observed on-site during the breeding season, as well as the hooded crow (*Corvus cornix*) and eurasian otter (*Lutra lutra)*. The greater black-backed gull, while an inhabitant of the colony, is also a potential nest predator of both eggs and fledglings (Veitch et al., 2016). The American mink (*Neovison vison*) was previously found on the island but was removed in 2015 and has not been observed there since. The island is only accessible by boat and is off-limits to humans within a 50m range in the breeding period (15th of April to 31st of July). (SEAPOP, n.d.).

RFB:

Realfagsbygget (RFB) is the roof of one of the biggest stand-alone buildings in Norway and is located in Bergen city center (60°23'05.5"N 5°19'41.9"E). The flat roof covers an area of 6700 m^2 and is the breeding ground for around 90 mating pairs of gulls, the majority of them being lesser black-backed gulls (approx. 76 pairs) and a couple of herring gulls. Due to its height and location, it is inaccessible for land-bound predators, and observations of avian predators are rare. While the hooded crow is present in the city and the peregrine falcon (*Falco pelegrinus*) has been observed, no predator incidents have ever been observed in this colony (either through cameras or observations of predated eggs). Even though it is located in an urban area, RFB close to the coastline (<10km), and the birds have access to both anthropogenic refuse and oceanic feeding opportunities. The roof is covered by gravel with no railing along the sides, and the birds make their nests with twigs and foliage. It is a relatively young colony that was first established in 2011 with four pairs of lesser black-backed gulls and has since had yearly growth.

Ågotnes:

The Ågotnes colony is located in the middle of an industrial area (60°24'42.4"N 5°00'31.9"E) with birds hatching in close human vicinity. The colony consists of mainly three species of gull, the great black-backed gull, the herring gull and the lesser black-backed gull. It is located on the coastline of Bergen, approximately 17km from the city center in airline. The birds in this colony lay their eggs on the side of roads, parking lots, and the few areas of tufts and grass located around the facility. Due to it being an industrial area, the colony is in many ways protected from predators because of fences surrounding the location, as well as human noise. However, predators like the American mink and great black-backed gull are still potential sources of nest predation. There are no population estimations for this colony due to restrictions of the facility and inaccessible nesting sites. The gulls here are thought to feed mainly in marine habitats and at a landfill site close by.

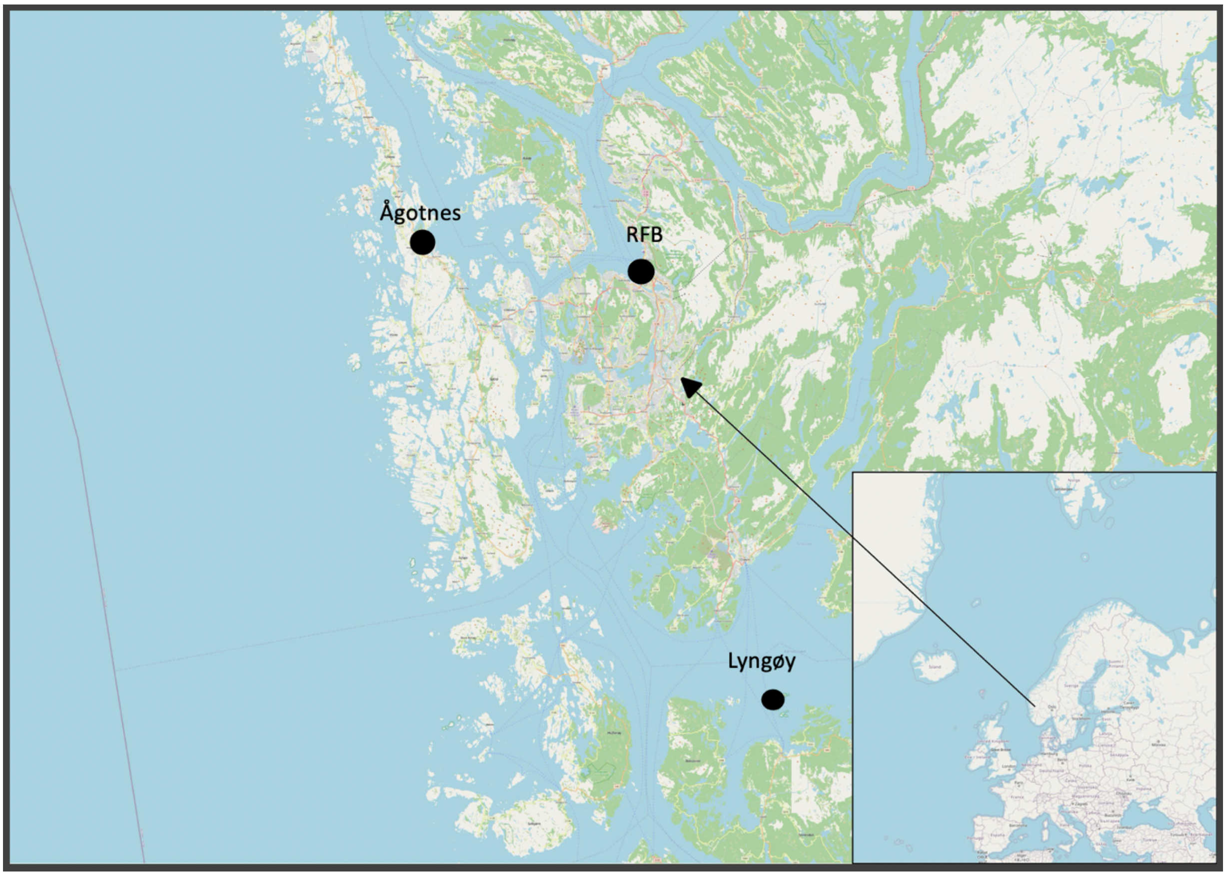

Figure 1: Map showing the location three lesser black-backed gull colonies in Vestland, Norway. Made using QGIS Geographic Information System (QGIS.org, 2021).

Study species

The lesser black-backed gull is a species of large seagull that is commonly found in the northern hemisphere. During the breeding season, the species is mainly distributed around coastal areas in western Europe, from north-central Russia to Spain (BirdLife International, 2021). The global population estimate is between 940,000-2,070,000 adult individuals, and the trend is increasing (BirdLife International, 2021). In Norway, it is a relatively common species of gull with around 26 000 breeding pairs per 2015 (Shimmings & Jostein Øien, 2015). The two subspecies breeding in Norway are *Larus fuscus intermedius,* which is more numerous and the one researched in this study, and *Larus f. fuscus,* which predominately breeds in the north (Helberg et al., 2009).

The lesser black-backed gulls start breeding at four years old and lay 1-4 eggs in May-June with an incubation period of approximately four weeks (Burger et al., 2020). In good conditions, they can breed every year and even replace eggs lost early in the breeding season (Parsons, 1976). The species nest either in colonies or spread out depending on individual conditions, but often in mixed colonies with herring gull (Ross-Smith et al., 2014). Lesser black-backed gulls generally prefer some type of nest cover (i.e., grass & shrubs) (Calladine, 1997), but they have the capacity to exploit a multitude of breeding habitats, including urban rooftops. When a nest site is chosen, both parents contribute with incubation and feeding, and given the survival of both parents, they usually return to the same site each year (Ross-Smith et al., 2014). When it comes to predation, the lesser black-backed gull has several potential predators during the breeding season. Both aerial predators, land mammals, and neighbor cannibalism by other gulls are common sources of mortality in the young (Harris, 1964).

It is a migratory species that usually spend the winter months in areas south of its breeding colonies. The Norwegian intermedius has been shown to consistently overwinter around Iberian Peninsula, West Mediterranean, and West Africa (Helberg et al., 2009), where they leave in autumn and return in the spring. The species are both flight style and feeding generalists, which means they can travel long distances and find suitable feeding habitat virtually anywhere along their migratory route (Klaassen et al., 2012). They therefore have diverse diet consisting of both fish and aquatic invertebrates, as well as eggs, chicks, rodents and human waste (Burger et al., 2020). Due to their flexibility, they are also able to fly great distances on foraging trips, with some colonies averaging at 30km per trip, and individual trips being up to 135km away from the colony (Corman et al., 2016; Garthe et al., 2016; Klaassen et al., 2012).

Data collection

Samples were acquired during trips to each colony in May 2020 (Lyngøy 18.05.20, RFB 21.05.20, and Ågotnes 29.05.20)**.** Every lesser black-backed gull nest was attempted located by three people walking slowly through the colony. For every nest found, the number of eggs were counted, and the nest was given an id and GPS point to avoid recounting. An approximately random selection of these nests was selected for egg measurements.

Variable's weight, length, width, and brood size was measured for each sampled brood at each location. The weight was measured using a portable digital scale (to nearest 0,01g), and the length and width were measured using a digital caliper (to nearest 0.01mm).

In order to discriminate between the species of specific nests, we relied on previous knowledge, observations, and species-specific preferences in nesting sites. The island has been closely monitored since 2009 (SEAPOP, n.d.), and the areas where the different species nest tend to correlate between years. Previous studies have also shown that the two species have some differences in preference when it comes to nesting; the herring gulls tend to nest in more rocky areas with vantage points versus the lesser black-backed gull who, tend to nest in flat areas with nearby vegetation (Calladine, 1997). When in doubt, real-time observations of birds leaving and reclaiming nests, as well as cameras in the different locations, were used to confirm speciation. The nests were considered to be fully laid and non-predated when we arrived at the colonies. This was mainly due to previous knowledge of the timing of egg-laying in the colonies, but a recount of a selection of nests during a second visit was also conducted and no difference in clutch size was found.

Data manipulation

To get a unified measure of investment, egg length and width was converted to volume using a standard equation for egg volume: volume (cm^3) = kLW^2 where L=maximum length (mm), W=maximum width (mm) and k=constant. There are multiple values for the constant (k), but I will be using k=0.0005035, which is based on 12 herring gull eggs as done in Camphuijsen (2013).

In order to gain insight into the difference of egg laying in the colonies, weight, and volume were used to determine the rate between egg weight and volume using the equation: rate = W/V, where W = weight (g) and V = volume (cm^3). Developing eggs lose weight during incubation due to evaporation, meaning we can use this relationship to compare egg-laying between locations. In this case, a lower rate will equal to earlier laid eggs, but not give an exact laying date. However, since the measurements on Lyngøy and RFB were taken three days apart (approximately 10% of the incubation time and 1.68g of total weight loss)

(Morgan et al., 1978; Rahn & Dawson, 1979), this difference was accounted for before proceeding with analyses.

Statistical analysis

The analyses were performed using the software R Studio (RStudio Team, 2020) version 1.3 with the additional use of package ´nlme´ (Pinheiro et al., 2021). Analyzes of egg size was run using a linear mixed effects model (lme) due to the clustering properties of the data. Nest id was here incorporated as a random effect, while volume and locations remained fixed effects. In order to see how clutch size affected the volume, a model selection was performed where clutch size was included as a covariate and either kept or excluded based on an Akaike´s Information Criterion test (AIC). To get a measure of total investment in the colonies, both sum of volume per nest and total number of eggs per nest was compared between locations using linear models (lm). In order to look at any differences in timing off egg laying, egg rate was compared between colonies using a linear mixed effects model after controlling for difference in timing of data collection. Nest id was again used as random effect, while rate and location remained fixed. Analysis of variance of volume between colonies was run using a variance test. All statistical tests had significance level of $p<0.05$. Any extreme outliers detected when exploring data was assumed to be either wrongly written in field or the cause of wrong speciation and removed prior to analyses.

Results:

There was an uneven distribution of the number of eggs laid in the different colonies. In the RFB colony, the vast majority of the clutches had three eggs (90%). On Lyngøy however, only about half of the clutches had three eggs (52%), meaning a substantial part of the clutches had one (21%) or two (27%) eggs. This resulted in a significantly lower average clutch size on Lyngøy (mean$\pm$SD, 2.3 $\pm$ 0.81) than RFB (2.85 $\pm$ 0.49, F=22.54, p<0.001). In the Ågotnes colony, only 11 nests were found and counted. This was due to difficulties finding/reaching the nests as they were laid on hillsides or inaccessible building roofs. Therefore, these data were not used in the analyses but rather as a reference point of a medium predation system. The birds in this colony mainly laid clutches with three eggs (64%) and had an average colony clutch size of 2.45$\pm$0.82 eggs (table 1).

Table 1: Sample sizes of lesser black-backed gull eggs from three colonies; RFB, Lyngøy and Ågotnes.

	Clutch size	RFB	Lyngøy	Ågotnes
Nests		73	56	-
	3	66	29	-
	2	3	15	-
	1	4	12	-
Measured nests		28	45	11
	3	24	26	7
	2	1	12	2
	1	3	7	2
Average clutch size		2.85	2.3	2.45

The size of the eggs varied both within and between the colonies, with Lyngøy having a bigger mean egg size range (58.5 cm^3 - 94.0 cm^3) than RFB (56.0 cm^3 - 76.3 cm^3) and Ågotnes (59.2cm^3 - 82.2 cm^3) (figure 2). However, the variability in mean egg size per nest was similar for all colonies, as indicated by a coefficient of variation of 11% and no significant difference in variance ($p>0.05$).

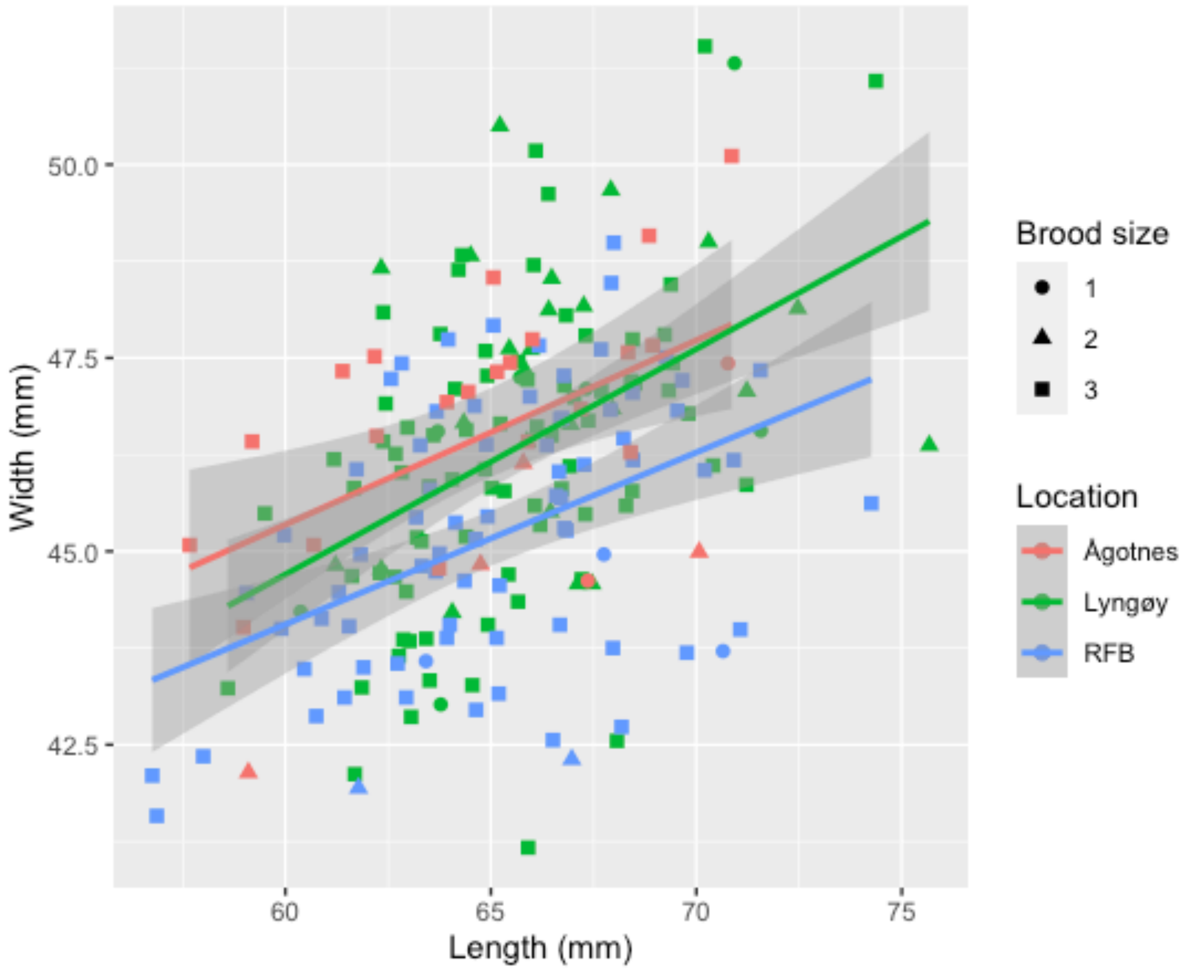

Figure 2: Egg length and width of lesser black-backed gulls from three different colonies. Each point represents an egg with color and shape indicating the colony and clutch size.

The eggs were significantly larger in the Lyngøy colony than the RFB colony ($F= 7.612$, $p<0.01$), and the size of the clutch had no significant effect on the volume of the eggs ($p>0.05$) (table 2). Ågotnes generally had intermediate levels of volume relative to the other colonies (figure 3).

Table 2: Variation in egg volume from lesser black-backed gulls within and between three colonies; RFB, Lyngøy and Ågotnes.

	Mean volume (mean ± SD)		
Clutch size	**RFB**	**Lyngøy**	**Ågotnes**
1	65,85 ± 4,54 cm^3	72,80 ± 11,93cm^3	73,84 ± 8,93 cm^3
2	57,54 ± 3,40 cm^3	74,67 ± 6,94 cm^3	65,07 ± 8,56 cm^3
3	67,52 ± 7,43 cm^3	70,22 ± 7,90 cm^3	71,78 ± 7,75 cm^3
Total	67.0± 6.01cm^3	71.81± 7.81 cm^3	70.94± 7.33 cm^3

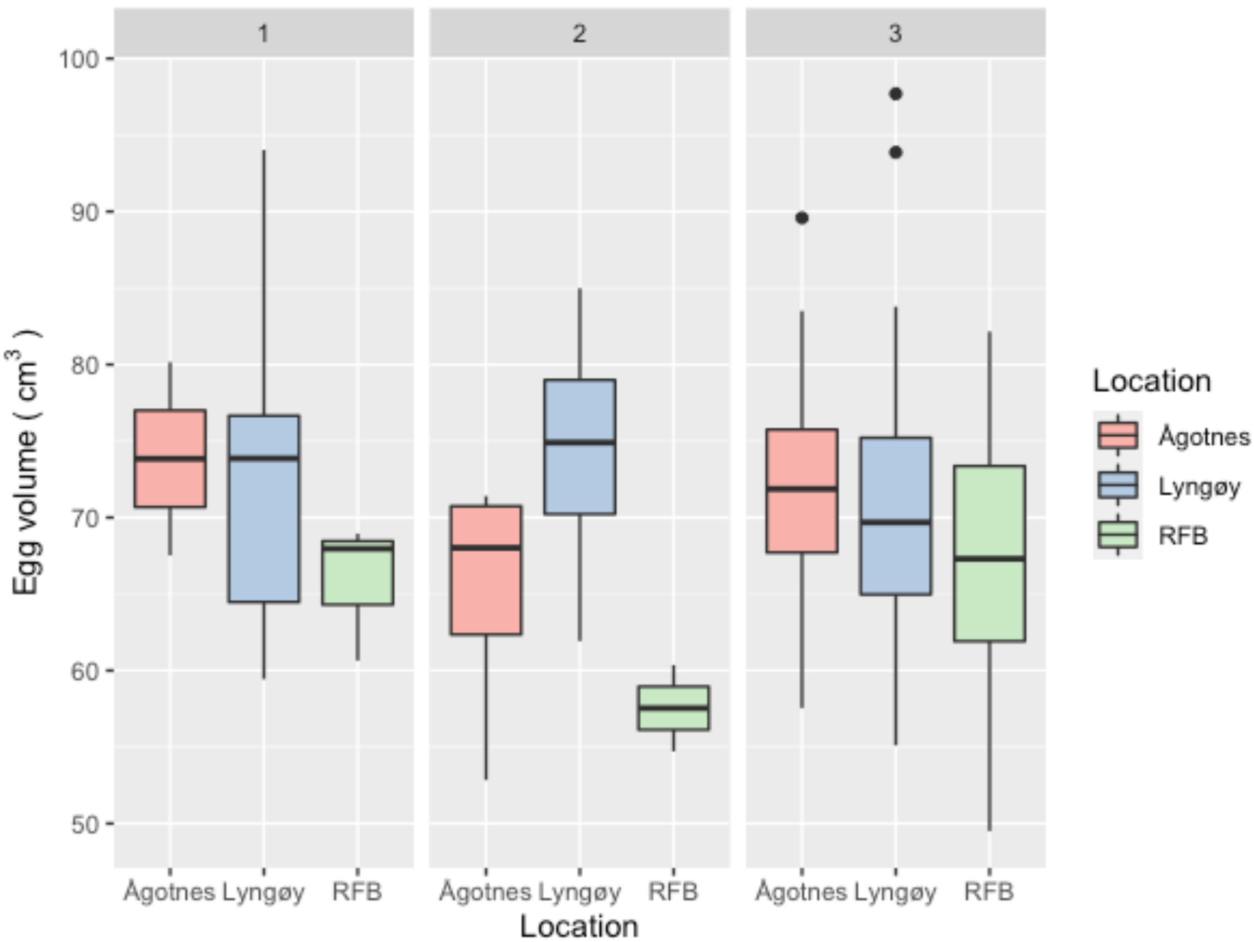

Figure 3: Volume of lesser black-backed gull eggs from nests with different clutch size (1,2 & 3) from three colonies; Ågotnes, Lyngøy and RFB.

The sum of volume per brood was lower for the birds on Lyngøy (mean ± SD: 172,9±53.8 cm^3) than for those at RFB (184,8±48.1 cm^3), but not significantly so ($p>0.05$) (figure 4). The birds at Ågotnes colony had intermediate levels relative to the other colonies (174±62,38 cm^3).

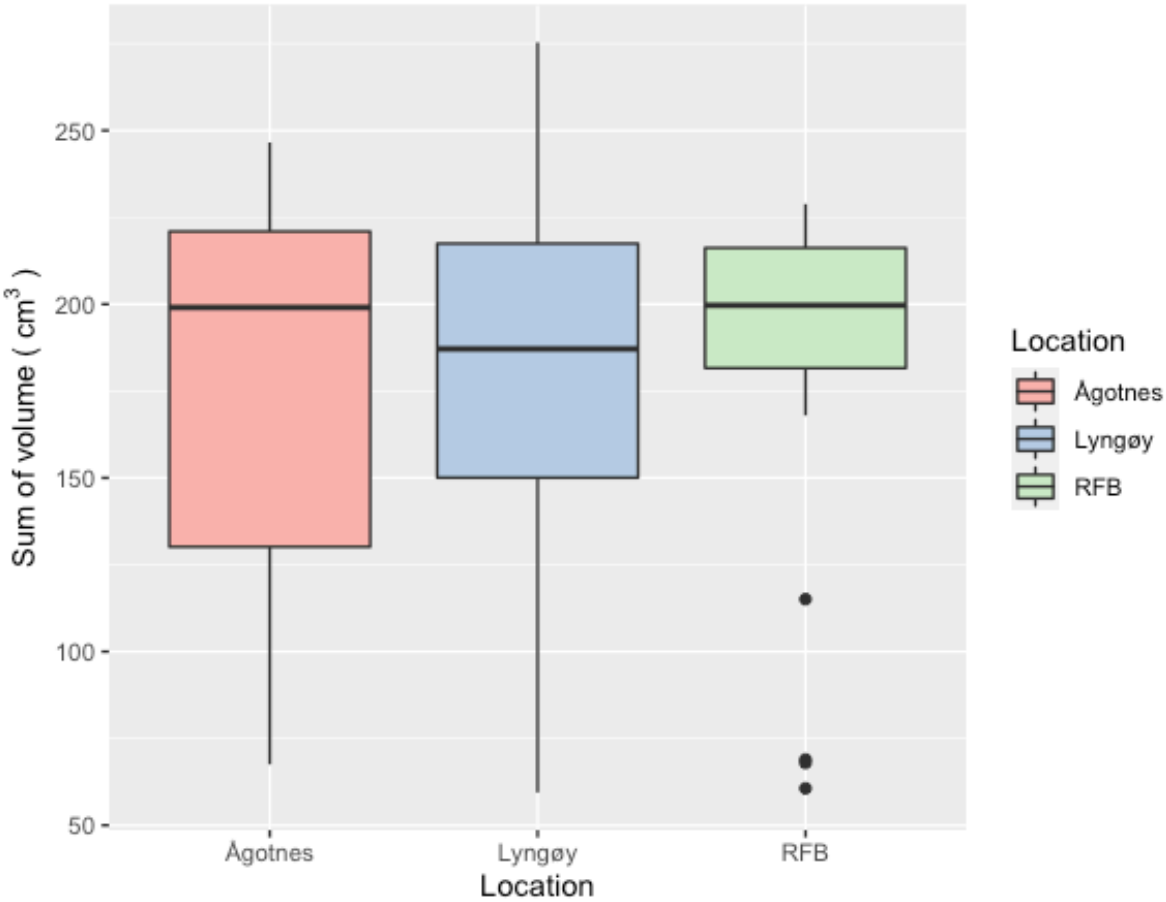

Figure 4: Sum of volume per brood of lesser black-backed gull eggs from three colonies; Lyngøy, RFB and Ågotnes.

The egg rate showed no significant difference between Lyngøy (mean±SD, 1,33±0.06 g/cm^3) and RFB (1,33±0,04 g/cm^3) when the time difference in measurements was accounted for ($p>0.05$), indicating no difference in the timing of egg-laying.

Discussion

This study presents an assessment of egg investment from three lesser black-backed gull colonies experiencing different predation pressures. The results showed that gulls from the urban colony laid significantly more eggs on average, but the birds in the rural colony laid significantly larger eggs regardless of clutch sizes. The control colony generally showed intermediate levels relative to the other colonies, strengthening the basis of predation. No significant differences in either the timing of egg-laying or variance of egg volume between the colonies was found. The results, therefore, indicate a difference in external selection pressure, most likely resulting from a divergence in predation risk. This observed variation can result from of several factors, but it is important to note that the two strategies represent a trade-off that is not equal in investment. An Increase in egg number most often results in a higher amount of reproductive output relative to an increase in size. It also represents a clear continuous increase in investment that requires an incremental increase throughout the nesting cycle (i.e., more offspring to heat, feed & protect). Larger eggs, however, require no such clear increase but rather an energetic increase relative to the size change. Expanding the brood size, therefore, represents a higher amount of investment than an increase in egg size. As the lesser black-backed gulls from the RFB colony laid more eggs on average and produced a higher sum of egg volume per clutch, they displayed the highest amount of investment.

Due to the difference in predation pressure in the colonies, there is a divergence in factors affecting their reproductive strategies. In the non-urban colony, a higher amount of predation and associated offspring mortality have most likely increased the need for more viable and competitive offspring. In harsher environments like these, it is assumed a larger dependence of offspring fitness on parental investment, leading to the selection of larger eggs that provide the offspring with traits that increase their opportunities for survival (i.e., heavier and or larger fledglings) ((Bolton, 1991; Krist, 2011). However, as laying more eggs represents a bigger investment relative to larger eggs, choosing to invest in larger eggs could also be a form of bet hedging in case the female makes mistakes when assessing the predation risks and produces an unsustainable clutch relative to the environment (Fontaine & Martin, 2006). In the urban colony, offspring mortality due to predation is presumably minimal, and an initial increase in size probably would have little effect on offspring survival. In these environments, given relatively stable food resources, laying an extra egg provides no added risk for the parent individual. The priority would her lie instead in enhancing reproductive success through more eggs and or future reproductive opportunities. Larger eggs would then have been exchanged in favor of the ability to lay more eggs, causing a trade-off. This follows theory that suggests females should increase investment in themselves, and therefore in future reproductive opportunities, when current cost to offspring is minimal, which is the case in low predation systems (Fontaine & Martin, 2006; Roff, 1992).

In this study, indicators of investment and predation were the main focus, and other factors were assumed to be relatively equal between the locations (i.e., environmental conditions, diet & condition). A couple of points are, therefore, important to acknowledge. First is the composition of the colonies. This study was conducted based on the assumption that the colonies had comparable populations, and variations were not controlled for. However, studies show that older and more established colonies, like Lyngøy, have fewer immigrating pairs as the colony reaches an asymptote (Coulson & Coulson, 2008). Younger or newly established colonies like RFB however, have high rates of immigrating pairs and often considerably lower recruitment ages than older colonies (Coulson et al., 1982). It could therefore be that a notable proportion of the Lyngøy population consists of older or more experienced breeders, while the RFB has a higher proportion of younger gulls. As long-lived animals, gulls have many reproductive opportunities, but how they can best maximize their lifetime reproductive success varies with age. Studies show that older gulls tend to increase their reproductive effort relative to younger gulls, laying either larger, more eggs, or both (Pugesek, 1981, 1987; Sydeman et al., 1991; Sydeman & Emslie, 1992). It is, therefore, possible that some of the variation seen in this study could be explained by age-related factors. However, it is likely that any significant difference in the ages between colonies would also have resulted in a difference in laying dates as older gulls tend to lay their eggs earlier (Haymes & Blokpoel, 1980) which was not found in this study. Further research on this topic should take age related factors into account and seek to control for any potential differences by attaining an overview of colony composition.

Secondly, in this research, the availability and quality of food resources was assumed to be, and therefore treated, as equal between the colonies. This was mainly due to the close proximity and, therefore, equal foraging opportunities between the colonies. However, this might not be the reality. The colonies all have different sources of food more readily available: Lyngøy is located inshore with close marine food opportunities, RFB in the city with anthropogenic refuse as the closest food source, and Ågotnes in close proximity to both a landfill site as well as marine feeding areas. While they all inhabit areas within range of each other's closest resources, the time and energy required to make use of them might cause a divergence in preference where birds choose the closest source as long as it is sufficient. Previous research comparing diet between urban and non-urban gulls found that urban gulls rely heavier on anthropogenic refuse as food, while non-urban gulls consumed considerably more marine prey (de Faria et al., 2021; Pierotti & Annett, 2001). Depending on which source proves more lucrative, a potential difference in diet could affect the parental body condition within the colonies which in turn has been shown to affect egg investment (Bolton et al., 1992). Anthropogenic refuse have also been shown to negatively affect hatchling success compared to marine resources (Pierotti & Annett, 2001). Getting a measure of parental body condition and estimates of realized hatchling success would, therefore, be a useful addition to further research. Getting a measure of body condition was attempted during this study through the capture of parent individuals, but the resulting sample size was too small to make use of.

While the results correlate with the hypothesis in terms of investment, they surprisingly differ from similar studies comparing breeding between urban and non-urban colonies. No previous studies (that I was able to locate) have found larger clutch sizes in urban colonies, but both smaller (Kroc, 2018; Perlut et al., 2016) no difference has been found (Hooper, 1988; P Monaghan, 1979; Pierotti & Annett, 2001). Similarly, no studies have found smaller egg volume in urban colonies, but one previous study found larger egg volume (Belant, 1993), and many have found higher fledglings success (Kroc, 2018; Perlut et al., 2016; Sellers & Shackleton, 2011). This study, therefore, demonstrates novel results in its field.

Conclusion

The results demonstrate clear differences in reproductive strategies between urban and non-urban colonies experiencing different predation pressures. This observed divergence suggests that urban areas provide advantageous conditions, enabling parents to invest more in their offspring. While no definite cause can be concluded in this study, the effect of decreased predation is likely a major component of their success in these systems. The novelty of the results also emphasizes the importance of studies surrounding the urbanization of gulls. Lesser black-backed gull numbers are declining in many natural populations within its range at the same time as urban populations are increasing (Balmer et al., 2007; Ross-Smith et al., 2015; Spelt et al., 2019). Gaining a thorough insight into the species breeding biology is, therefore, necessary to facilitate effective conservation management. It is especially vital since these trends have been associated with increasing public nuisance leading to heated debates and calls for stricter control measures (Rock, 2005).

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