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Title

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

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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.

Keywords

Competition, seabirds, activity time-budgets, GPS-tracking, reproductive success

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.

2. Materials and methods

2.1 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.

2.2 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 ∗ height ∗ width2 / 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).

2.3 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.

2.4 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.

2.5 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 0), 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.

3. Results

3.1 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).

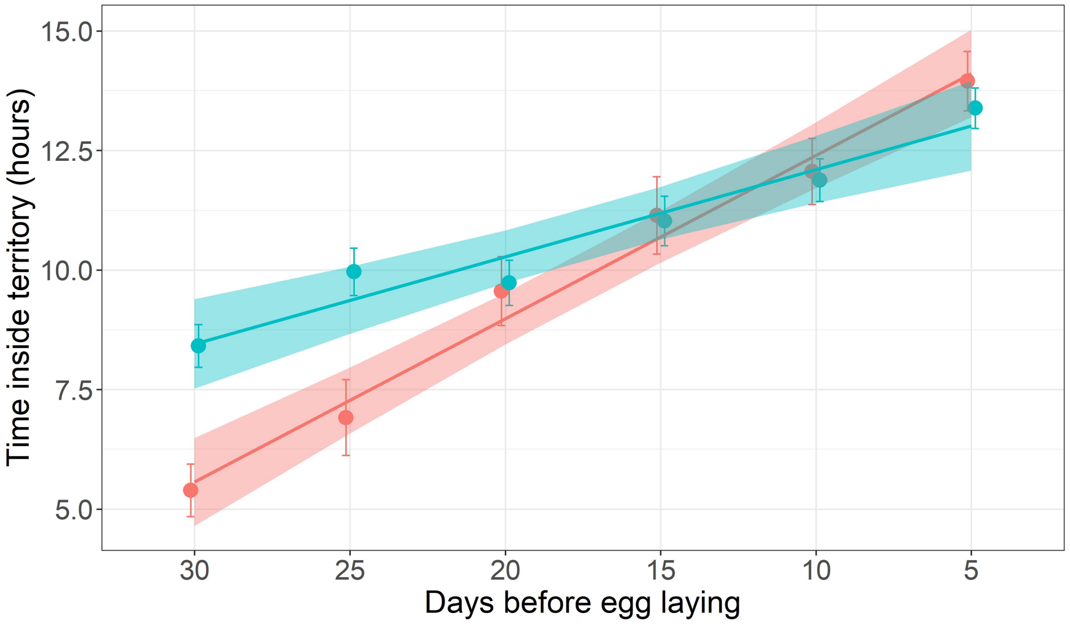
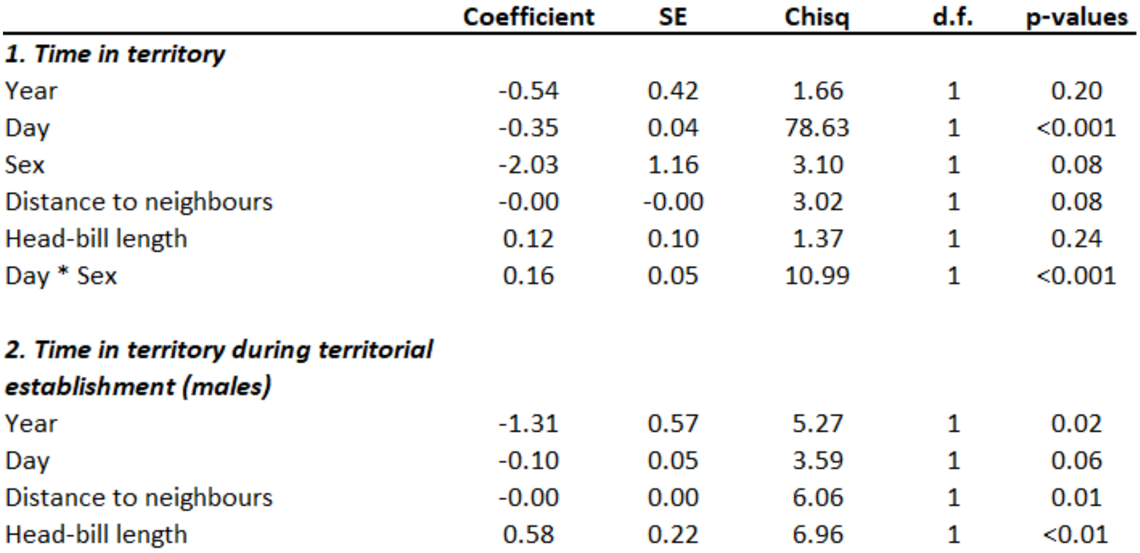


Figure 1. Time spent inside the territory across the 30 days prior to egg laying (binned in 5-day interval) for males (blue) and females (red). Dots represent the mean values, whiskers the standard error, and bands represent the 95% confidence interval.

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

3.2 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).

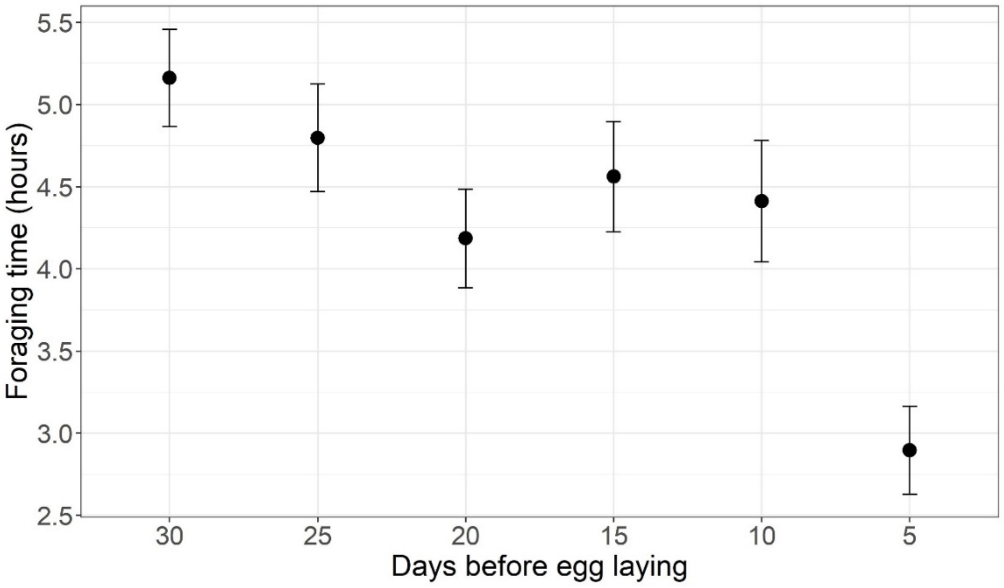


Figure 2. Daily time spent actively foraging across the 30 days prior to egg laying, for visualisation binned in 5-day intervals. Dots represent the mean values, and whiskers the standard error.

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.

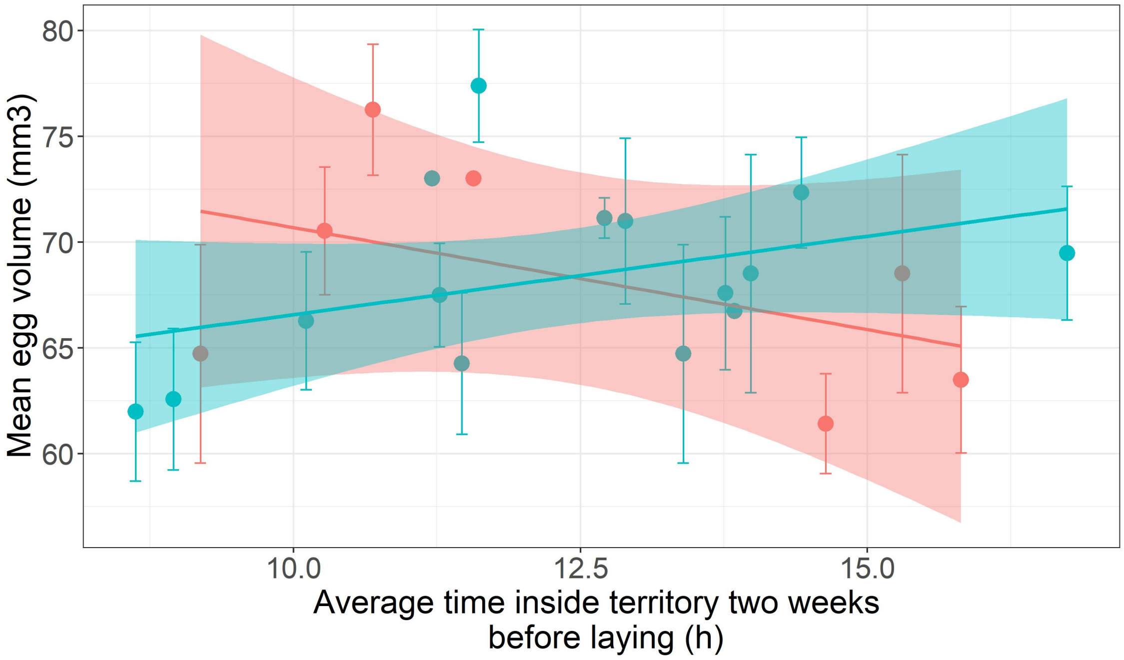


Figure 3. Effect of average time spent in the territories on mean egg volume for males (blue circles, standard error and regression line) and females (red circles, standard error and regression line). Bands represent the 95% confidence interval.

4. 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.

4.1 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.

4.2 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 preferentiallychoose 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.

5. 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.

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Statements and declarations

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Competing interests

The authors declare that they have no competing interests.

Authors’ contribution

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.

Availability of data and materials

GPS tracking data used in this study are publicly available in Movebank and Zenodo (https://doi.org/10.5281/zenodo.3540799). Dataset supporting the conclusions of this article will be made available upon acceptance.

Ethical Note

For this study, no lesser black-backed gulls were specifically fitted with GPS trackers, as we could make use of individuals that were part of a different project. All procedures performed in this project have been approved by the ethical committee of the University of Groningen (file number 6986/6986A). Furthermore, the application of GPS trackers has been evaluated in a previous study for this species (Kavelaars et al. 2018). Our experiment itself was non-invasive and for nest checking we followed strict rules, i.e., we did not enter a colony when weather conditions were not suitable (rain or high sun radiation) and limited the colony visits to max. 20

min. This study complied with Dutch law and meets the latest ASAB/ABS ethical guidelines (www.sciencedirect.com/science/article/pii/S0003347215004613).