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# DUAL FORAGING IN A LONG-LIVED SEABIRD: PUTTING YOURSELF FIRST WHILE KEEPING AN EYE ON YOUR PARTNER?

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## 1. INTRODUCTION

In many animal species, parents make substantial efforts to increase the chances of survival of their offspring (Trivers 1972 & Royle et al. 2012). These parental investments are defined by Trivers (1972) as “any investment by the parent in an individual offspring that increases the offspring’s chance of surviving (and hence reproductive success) at the cost of the parent’s ability to invest in other offspring”, such as providing food or safeguarding the offspring from predators (Royle et al. 2012). Yet, parental care is costly, as the time and energy devoted to tending to the needs of the offspring cannot be spent on self-maintenance, which may even result in an increased mortality (Owens & Bennett 1994, Liker & Szekely 2005, Santos & Nakagawa 2012), infection (Knowles et al. 2009) or predation risk (Reguera & Gomendio 1999, Li & Jackson 2003). How much care each parent should provide should thus be decided by balancing each parent’s immediate benefits of investing in current offspring against the losses in terms of future fecundity, such as lost mating chances (Maynard Smith 1977). However, through parental care individuals may not only yield the direct benefits of their own investment, but also the indirect benefits of the care provided by the partner, and hence the efforts of the partner also influence an individual’s reproductive success. When the amount of care that one parent intends to give does not correspond with what would be optimal for its partner, a conflict between the parents arises (Trivers 1972, Westneat & Sargent 1996).

This parental, or sexual, conflict is thus dual: 1) which sex should provide care and 2) how much care should each sex provide? In part, this conflict arises due to inherent differences in interest between males and females (Westneat & Sargent 1996). A male’s reproductive success is limited not by his production of gametes, but by the number of eggs he can fertilise, whereas a female’s reproductive success is limited by her ability to produce eggs, not by her ability to have them fertilised (Bateman 1948). Optimal reproductive strategies hence differ between males and females in the amount of energy and time they should invest in caring for the current offspring (Trivers 1972, Ketterson & Nolan 1994). For instance, in a population with distinct breeding seasons, the cost of egg production might prevent females from remating in time after producing a first clutch. For males however, the chance of finding another mate after fertilising a first set of eggs could be high. In this situation, the optimal strategy for females would be to stay with the offspring, but for males, it would be better to desert (Maynard Smith 1977), resulting in monoparental care by the female. Even in species with full biparental care, there remains a sexual conflict about how much care each parent should provide, as it would be best for every individual to limit their own investments to the minimum and shift most of the care to the partner, in order to allocate more resources to self-maintenance (and hence future offspring) (Trivers 1972, Westneat & Sargent 1996, Royle et al. 2002). A variety of theoretical models has been developed to explore the evolution of biparental care, and clarify how parents could resolve this conflict by adjusting their own investment to that of their partner. These models show that parental care could evolve in multiple ways, depending on the timescale on which parents react and the completeness of information they have on the investment of their partner. For instance, Houston & Davies (1985) and Jones et al. (2002) assumed that parents show a fixed level of parental care, independently of the investments of their partner, and that this level is identical for all members of a given sex. Under these assumptions, these models predict that biparental care can be an evolutionary stable strategy if a decrease in investment by one sex is compensated by an increase in effort of smaller magnitude (Houston & Davies 1985) or of equal magnitude (Jones et al. 2002) by the other sex over the next generations. The outcome of this compensation over evolutionary time is a fixed optimal effort for males and females, considering the investment of the other sex. Since fixed levels of care were assumed, these models do not allow for negotiation and adjustments between partners during their own lifetime, showing that such negotiation is not a prerequisite for the evolution of biparental care. Several other models, such as

the ones by McNamara et al. (1999, 2003) and Lessels & McNamara (2012) relaxed the assumption of fixed efforts and allowed individuals to react to the efforts of the partner in real time, introducing negotiation. They too found that for biparental care to evolve, decreases in investment of one parent should be, at least partially, compensated by the other parent. This prediction, however, differs from the prediction by Houston & Davies (1985) and Jones et al. (2002) in the timescale over which such compensation can occur. Indeed, the compensation predicted by Houston & Davies (1985) and Jones et al. (2002) occurs over generations, whereas the models by McNamara et al. (1999, 2003) and Lessels & McNamara (2012) predict partial compensation over the behavioural timescale, i.e. during the own lifetime of the parents. Thus, the ability of partners to negotiate and adjust the amount of care provided increases the likelihood of the evolution and the stability of biparental care. The models described above (Houston & Davies 1985, McNamara et al. 1999 and 2003, Jones et al. 2002, Lessels & McNamara 2012) all predict a compensating response, when individuals have full knowledge on the investment of their partner and on the fitness of their offspring. In contrast, Johnstone & Hinde (2006) predicted that, when parents have only incomplete information on the needs of their offspring, natural selection should favour a matching response, where changes in the care provided by one parent lead to changes in the efforts of the other parent in the same direction, rather than the opposite direction (i.e. compensation). These models thus show great diversity in predictions depending on the ability to negotiate and the completeness of information on the partner's investment, which is matched by the variety of responses that have been shown to occur in reality with experimental studies, including partial compensation, full compensation, a matching response or no response at all (Houston et al. 2005, Hinde 2006, Hinde & Kilner 2007, Harrison et al. 2009, Meade et al. 2011, Johnstone et al. 2014). This variation in predictions and observations leads to uncertainty about the interactions between partners at play. It might indicate that different species or perhaps even different populations or individuals adopt different strategies (Westneat & Sargent 1996). Moreover, there is a heavy bias in observational studies towards species that are able to closely monitor their partner (Harrison et al. 2009). In some species however, parents spend the majority of the time away from each other, so they cannot directly assess how much parental care is provided by their partner. This is particularly the case for pelagic seabirds, which often have to travel large distances to collect food (Weimerskirch et al. 1988, Weimerskirch et al. 1994), during which they usually cannot track the actions of their partner. Several of these species have been found to adopt a dual foraging strategy, where long and short foraging trips are alternated (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, Weimerskirch & Cherel 1998, Magalhães et al. 2008, Tyson et al. 2017). Long trips are likely intended for self-maintenance, as adults gain more weight during these trips, whereas short trips result in a higher amount of food provisioned to the offspring (Weimerskirch et al. 1994, Weimerskirch & Cherel 1998, Chaurand & Weimerskirch 1994). This suggests that the dual foraging strategy is a way to balance and moderate parental care. However, dual foraging could also lead to prolonged bouts of starvation for the chicks when the long trips of both parents coincide, and thus coordination between parents seems crucial. Whether there is coordination between partners that spend such long periods away from each other has only been studied in a few examples, and these studies show contrasting results, with coordination occurring in some species but not in others (Chaurand & Weimerskirch 1994, Booth et al. 2000, Congdon et al. 2005, Magalhães et al. 2008, Tyson et al. 2017). Furthermore, most of these studies relied on observing the arrival of the birds at their nest, and the exact trajectory of their foraging trips is unknown. This makes it unclear if and how these birds that cannot monitor their partner adjust their foraging strategy to each other in an attempt to solve sexual conflicts.

The advent of high-resolution tracking devices now enables studying individual decisions at unprecedented resolutions (Kays et al. 2015, Hussey et al. 2015). In this thesis, I will study foraging behaviour of 24 pairs of GPS-tagged Lesser Black-backed Gulls (*Larus fuscus*) to assess how this

species with biparental care deals with the sexual conflicts during the breeding season. Lesser Black-backed Gulls use both marine and terrestrial food sources during the breeding season, making intensive use of anthropogenic landscape and seascape (Götmark 1984, Garthe et al. 2016). Their foraging trips usually last for several hours, sometimes even more than a day (Shamoun-Baranes et al. 2011, Garthe et al. 2016), during which they cannot track the actions of their partner. These long foraging trips also entail long periods away from their offspring and result in a high starvation and predation risk for the nestlings, which are the main causes of nestling mortality (Bukacinski et al. 1998). Predation risk is highest in the first couple of days post-hatching, when the chicks are still very small and vulnerable (Bukacinski et al. 1998). Due to the colonial breeding, predation by conspecifics or other *Larus* species (in mixed-breeding colonies) is especially frequent (Tinbergen 1960, Parsons 1971, Hunt & McLoon 1975, Pierotti & Murphy 1987, Bukacinski et al. 1998). It has been found that when parental care is low, chicks start wandering off into the colony, increasing their predation risk (Hunt & McLoon 1975, Pierotti & Murphy 1987). Furthermore, experiments suggest that when food is not a limiting factor, parents spend more time in the colony, guarding their chicks and this effectively leads to a lower nestling mortality (Morris 1987, Bukacinski et al. 1998). This further emphasises the threat of predation when the nestlings are left alone for too long. However, it is not clearly known how this species deals with these challenges.

Considering the severity of the consequences of inadequate parental care, as illustrated above, negotiation between partners seems imperative to ascertain successful reproduction, especially since they stay away from the nest for long periods of time and cannot constantly keep track of their partner. In addition, it seems crucial that Lesser Black-backed Gulls coordinate their foraging trips, to maximise the total nest attendance and ascertain regular food provisioning, thereby increasing the survival chances of their offspring. One way to deal with this challenge is to adopt a dual foraging strategy, similar to that of purely pelagic birds, to which its ecology borders. However, Lesser Black-backed Gulls can make use of a variety of food sources in the surroundings of the colony. Hence, they may be more flexible in the ways by which they can adjust their parental care, for instance by using closer or different food sources.

## 2. OBJECTIVES

The aim of this thesis is to provide clarity in how the parental conflict is solved in the Lesser Black-backed Gull during chick-rearing. During chick-rearing, the nestlings are supposed to be less relying on the continuous presence of their parents, allowing for more flexibility in negotiation. Specifically, four main questions are addressed throughout the study:

- 1) Do Lesser Black-backed Gulls adopt a dual foraging strategy?
- 2) Do partners coordinate their foraging trips to minimise the time that the nestlings are left alone, and does the amount of coordination decrease as chicks grow?
- 3) Does the amount of coordination depend on the similarity in foraging strategies between partners, or vary between foraging strategies?
- 4) Do partners negotiate their efforts and consequently adjust their own investments to those of their partner?

### 3. MATERIAL AND METHODS

#### 3.1 Data collection

A total of 30 pairs of Lesser Black-backed Gulls were equipped with UvA-BITS GPS tracking devices (Bouten et al. 2013) during the 2015-2018 breeding seasons. Pairs originated from two nearby mixed-breeding colonies, where they breed alongside Herring Gulls (*Larus argentatus*): Zeebrugge in Belgium (13 pairs) and Vlissingen in the Netherlands (15 pairs) (see Figure 1 for the location of these colonies, see Table A.1 (appendix) for the colony boundary coordinates). Birds were caught on their nests using walk-in traps. The tracking devices were attached to the back of the birds using a body harness of Teflon ribbon (Stienen et al. 2016). The sex of each bird was molecularly determined or based on biometrics. To avoid any influence of maternal or paternal effects on the experiments and to ensure all tracked couples had an equal number of offspring to care for and consequently were subjected to comparable offspring demands, clutches of the tagged pairs were replaced with two unrelated eggs from non-tagged couples. Replacement was done when pipping occurred, to assure that couples received hatching nestlings at the time they were expecting their own offspring.

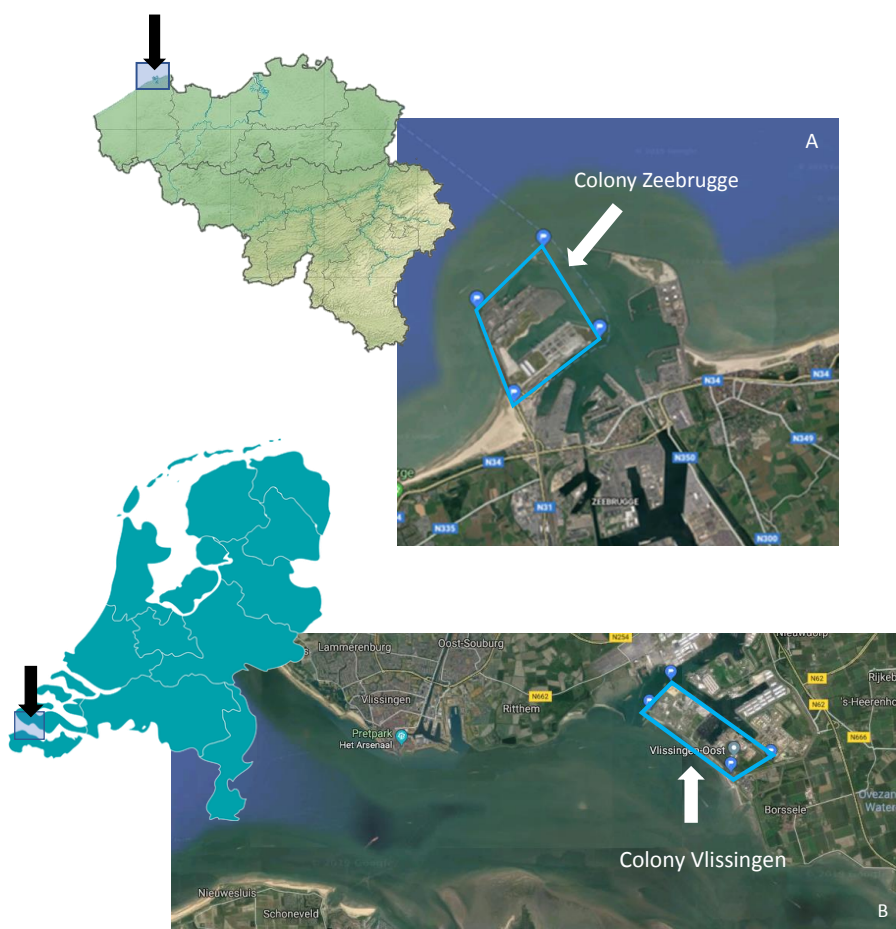


Figure 1: Map of the colony locations. A: colony of Zeebrugge. B: colony of Vlissingen

## 3.2 Data treatment

The UvA-BiTS GPS tracking devices used here allow not only to acquire the birds' positions at regular time intervals, but also to infer the behaviour of the birds at that time, by combining GPS receivers with tri-axial accelerometers. The accelerometer integrated in the device measures the body movement in 3 directions. Behaviour was identified by an artificial neural network with a 3-point moving input window (Baert et al. 2019, under revision). The network was trained based on an expert-annotated dataset to identify foraging, commuting flights and resting behaviour based on path geometry (step length and turning angle between the current and previous position), habitat type (derived from the 2006 CORINE land cover dataset) and body movement (based on accelerometer data) information. To avoid bias due to differences in tracking resolution, all GPS data were subsampled to a 5-min resolution.

Next, trajectories of each individual were spliced into foraging trips. The starting point of each foraging trip was defined as the last data point inside the boundaries of the colony (defined as a polygon, Figure 1), before leaving the colony. The first data point after being away with GPS locations inside the colony boundaries was taken as the end point of the trip. The duration of each trip was calculated, as well as the time spent in the colony in between trips. Periods in the colony or foraging trips with 1h data gaps, due to low battery levels, were omitted from the analysis. No such gaps were found during foraging trips, but there were 38 periods of nest attendance which had to be omitted. Next, the habitat use during foraging trips was calculated as the percentage of GPS points associated with foraging behaviour on marine, urban and agricultural resources respectively. Habitat types were derived from the 2006 CORINE land cover dataset. 'Marine areas' included coastal lagoons, estuaries and the sea and ocean. 'Urban areas' consisted of continuous and discontinuous urban fabric, industrial or commercial units, road and rail networks and associated structures, port areas, airports, mineral extraction sites, dump sites, construction sites, green urban areas and sport and leisure facilities. The 'agricultural areas' comprised non-irrigated arable land, permanently irrigated land, rice fields, vineyards, fruit trees and berry plantations, olive groves, pastures, annual crops associated with permanent crops, areas with complex cultivation patterns, land principally occupied by agriculture and agro-forestry areas. Pairs in which there was data on 10 or less foraging trips during the chick-rearing period for either one of the partners were omitted from further analyses. This resulted in a sample size of 24 couples.

## 3.3 Data analysis

All analyses were performed in R version 3.4.4 (R Core Team 2018). Models were fitted using the lme4 and glmmTMB packages (Bates et al. 2015, Brooks et al. 2017). Calculating marginal means for categorical variables was done using the lsmeans package (Lenth 2016). The significance of random effects was determined using the Akaike Information Criterion (AIC) (Zuur et al. 2009). In all models, all mentioned random effects were retained, since this was either the most optimal model or the difference in AIC-values was so small that there was strong support for the model with all random effects included (Burnham & Anderson 2004). Non-significant interaction terms between fixed effects were always removed from the models, but non-significant main effects were retained, to avoid biases in parameter estimation (Whittingham et al. 2006). Statistical significance was

assessed at the 95% confidence level. Normality, homoscedasticity and independence of model residuals was inferred from graphical inspection (Figures A.3 – A.13 in appendix).

### 3.3.1 Do Lesser Black-backed Gulls adopt a dual foraging strategy?

Dual foraging is defined by the occurrence of two distinct types of foraging trips: short trips and long trips, with a clear separation between the two instead of a continuous transition (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, Weimerskirch & Cherel 1998, Magalhães et al. 2008, Tyson et al. 2017). To assess if Lesser Black-backed Gulls adopt this strategy to meet the needs of both themselves and their offspring, it was tested if the distribution of the durations of their foraging trips deviated from a unimodal distribution, using Hartigan's dip test for unimodality from the diptest package (Maechler 2016).

### 3.3.2 Do partners coordinate their foraging trips to minimise the time that the nestlings are left alone, and does the amount of coordination decrease as chicks grow?

To assess if partners coordinate their foraging trips during the chick-rearing stage, it was tested if the proportion of time that at least one of the parents was present in the colony (i.e. total nest attendance), the proportion of trips started by the male when the female was present in the colony and the proportion of trips started by the female when the male was present in the colony was higher than expected by chance for each breeding pair. The time that the nestlings are guarded is a frequently used index for coordination in gulls (Nur 1984, Reid 1988) and the proportion of trips started with the partner present in the colony could be a way to obtain this coordination.

Randomising trip duration is commonly used as a null model of uncoordinated parental care (Johnstone et al. 2014, Bebbington & Hatchwell 2015, Savage et al. 2017). Here, the expected values for the proportion of total nest attendance and the proportion of trips started when the partner was in the colony when there is no coordination were calculated by randomising foraging trips for each breeding pair. For each bird, sequences of foraging trips and colony visits were generated by randomising both and rearranging them so that a foraging trip was always followed by a period spent in the colony and vice versa (Figure 2). Whether the randomised sequence started with a foraging trip or period of nest attendance was also decided at random. This way, a randomised sequence of foraging trips and nest attendance was obtained for both partners. Next, the length of the new sequences was made equal, by shortening the sequence with the longest cumulative duration (as indicated by the vertical black bar in Figure 2). Based on these newly obtained, randomised sequences, the proportion of total nest attendance, the proportion of trips started by the male when the female was present in the colony and the proportion of trips started by the female when the male was present in the colony was calculated. This process was repeated a hundred times for each pair, to obtain a distribution of the expected values for the parameters.



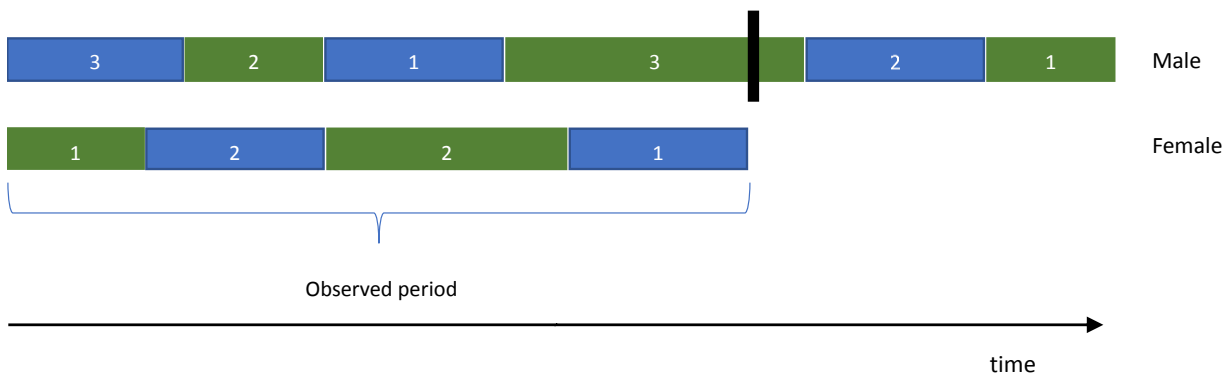


Figure 2: Visualisation of the randomisation process. The blue bars represent nest attendance periods and the green bars represent foraging trips. The length of the bars corresponds to the duration of the periods. The numbers on each bar indicate the original order, before randomisation. The vertical black bar shows the shortening of the longest sequence.

Next, the actual values for these parameters were calculated for each pair, based on the real, non-randomised vectors of foraging trips and nest attendance alternations. The starting point and end point of the observation period was set equal for both partners, so that the time interval on which the metrics were calculated was the same for the male and female (Figure 3).

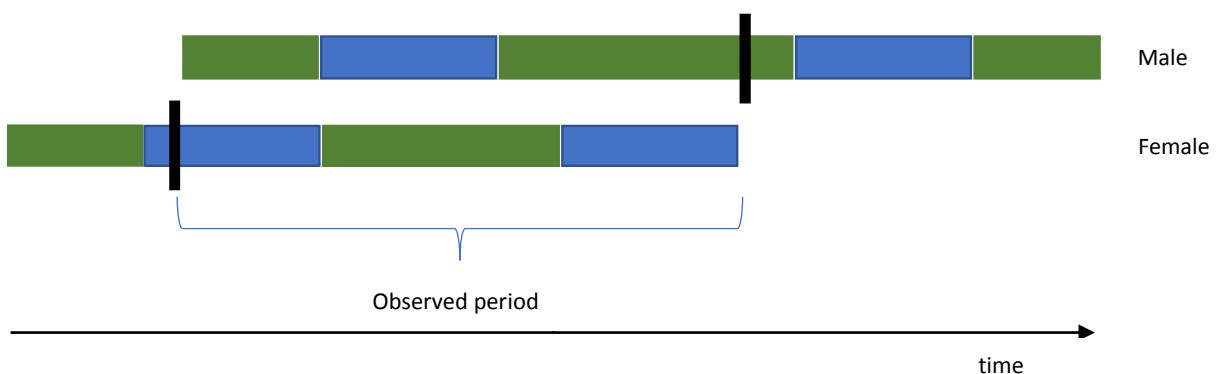


Figure 3: Calculation of the metrics based on actual alternations of nest attendance periods and foraging trips. The blue bars represent nest attendance periods and the green bars represent foraging trips. The length of the bars corresponds to the duration of the periods. The vertical black bars show the shortening of the sequences, to obtain equal starting and end points for both partners.

The observed values of the metrics were then compared to the distribution of expected values, as obtained by the randomisation process. Since coordination between partners is expected to result in a higher total nest attendance and proportion of trips started with the partner in the colony, it was tested if the observed value was higher than expected based on uncoordinated foraging trips. An observed value larger than the 95<sup>th</sup> percentile of the distribution of the expected values was taken as significantly larger than expected when parents don't coordinate (Figure 4).

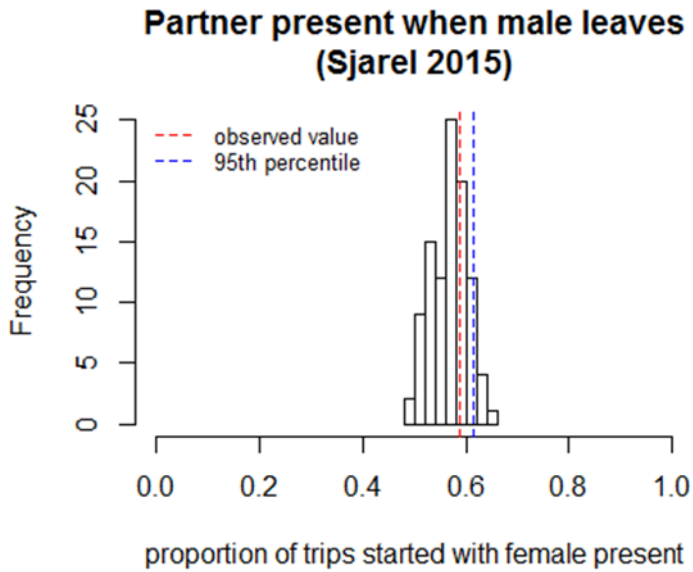


Figure 4: Comparing observed and expected values of the parameters. The Gaussian distribution is the distribution of the expected values of the parameter (here proportion of trips started by the male with the female present in the colony) as calculated during the randomisation process. In this case, the observed value was smaller than the 95<sup>th</sup> percentile, so it was not significantly higher than expected based on uncoordinated foraging trips.

Since coordination between partners is expected to decrease with increasing age of the offspring, due to a relaxed predation rate and a higher need for frequent food provisioning as the nestlings grow older (Bukacinski et al. 1998), it was examined if 1) the time spent in the colony in between foraging trips and 2) the proportion of time that at least one parent was present in the colony differed with the age of the nestlings (in days). This was done by fitting mixed effects models. The effect of nestling age on the time spent in the colony in between foraging trips was modelled using a gamma distribution with log link function, since the duration of the nest attendance periods can only take positive values. In addition to nestling age, the sex of the parent was also incorporated as a fixed effect, to account for differences between males and females. Bird.year was included as a random effect. Secondly, the effect of chick age on the time that at least one of the parents was present in the colony was modelled using a beta regression, since the total nest attendance was expressed as proportions of total time. To avoid problems when using the logit link function used by the beta regression on values of 0 and 1, a value  $10^{-9}$  was added or subtracted, respectively. In this model, colony and couple.year were incorporated as random effects.

### 3.3.3 Does the amount of coordination depend on the similarity in foraging strategies between partners, or vary between foraging strategies?

The similarity in foraging strategies was defined as the similarity in resource use between partners and the proportion of overlap in their foraging sites. The similarity in resource use was calculated as the Bray-Curtis similarity based on habitat use:

$$1 - \frac{\sum_i |p.m_i - p.f_i|}{2}$$

where  $p.m_i$  and  $p.f_i$  correspond to the proportion of foraging by the male and female respectively, in a particular habitat type  $i$  ( $i \in \{\text{marine, agricultural, urban}\}$ ). A similarity coefficient of 0 indicates that the male and female forage on completely different habitat types, whereas a coefficient of 1 signifies that they use the same resources with the same intensity. Overlap in foraging sites was calculated using the autocorrelated-kernel density estimation (AKDE) of the `ctmm` package in R (Calabrese et al. 2016, Winner et al. 2018, Fleming & Calabrese 2019). AKDE was used for the estimation of overlap because this method corrects for bias due to spatial and temporal autocorrelation, resulting in more accurate estimations of home range compared to classic kernel density estimates that are susceptible to overestimation (Winner et al. 2018). For these calculations, only the data points with locations outside the colony boundaries were used, as otherwise a high overlap would be found for all pairs, since partners share the same colony. A high value for overlap means that both partners tend to frequent the same foraging areas, whereas a low value means they forage at different locations.

Mixed effects models were fitted to test for the effect of foraging strategies on coordination and nest attendance. Firstly, to assess if the similarity in foraging strategies between partners had an influence on the degree of coordination between partners, the proportion of time that at least one of both parents was present in the colony, the proportion of nest attendance by an individual, the proportion of time that both partners were present in the colony simultaneously and the proportion of trips started by an individual with the partner present in the colony were used as proxies for coordination and hence included as response variables. Similarity in resource use, overlap in foraging sites and the sex of the parent were included as fixed effects, as well as all possible interactions between them. Secondly, to test the effect of individual foraging strategies on the decisions of parents and their coordination, the proportion of nest attendance of each bird, the proportion of trips started with the partner present in the colony, the proportion of time that at least one parent was present in the colony and the proportion of time that they were in the colony simultaneously were used as response variables. The foraging strategy of the individual, the foraging strategy of its partner and the sex of the bird were included in these models as explanatory variables, as well as all possible interactions between them. Here, the individual foraging strategy was defined rather broadly as either marine or terrestrial foraging. All models included colony and year as random effects. A beta regression was used for these analyses, since all of the proxies for coordination were expressed as proportions. Because the logit link function used in a beta regression doesn't allow values of 0 and 1, a value  $10^{-9}$  was added or subtracted, respectively.

### 3.3.4 Do parents adjust their efforts to those of their partner?

Negotiation and adjustment of parental efforts was tested by investigating if partners adjust the duration of their foraging trips to the duration of the last foraging trip made by the partner. The last foraging trip by the partner was defined as the last completed trip by the partner, i.e. the last trip performed by the partner with time of returning to the colony prior to the start time of the foraging trip of the focal bird. The sequences were cut off to equal length to avoid biases in the analysis (Figure 5). A mixed effects model was then fitted, using a gamma distribution with log link function, since the trip durations are strictly positive. Duration of the foraging trip was included as the response variable, and the duration of the last foraging trip of the partner, as well as sex and the

interaction between these variables, were included as explanatory variables. Bird.year was included as a random effect.

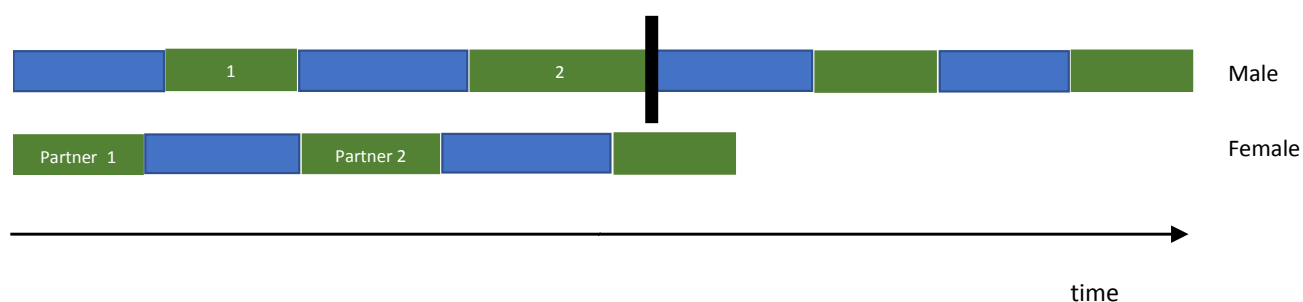


Figure 5: This figure is meant to clarify how the durations of the foraging trips of the partner were defined, as used in the model to test for negotiation. The blue bars represent nest attendance periods and the green bars represent foraging trips. The length of the bars corresponds to the duration of the periods. In this example, the male is the focal bird. The numbered green bars (1 and 2) are the durations of the foraging trips that will be used in the model. The foraging trips of its partner indicated with 'Partner 1' and 'Partner 2' are the last completed foraging trips of the partner that correspond to the focal birds' own trip 1 and 2 respectively. The vertical black bar shows the shortening of the longest sequence. Note that if this shortening had not been performed, the last two foraging trips of the male would have both been linked to the same foraging trip of the partner (the last green bar of the female). This shortening was thus necessary to deal with missing data.

## 4. RESULTS

### 4.1 Do Lesser Black-backed Gulls adopt a dual foraging strategy?

The distribution of foraging trip durations did not significantly differ from unimodality for most individuals based on Hartigan's dip tests for unimodality. Only 1 individual showed a significant deviation from unimodality, with a p-value obtained by the Hartigan's dip test of  $< 0.05$  (Figure 6). However, even for this individual, the multimodal pattern was not very clear, as the peaks were positioned very closely together (Figure A.1 in appendix). The overall mean of the trip durations ( $\pm$  standard error) was  $3.76 \pm 0.09$  h.

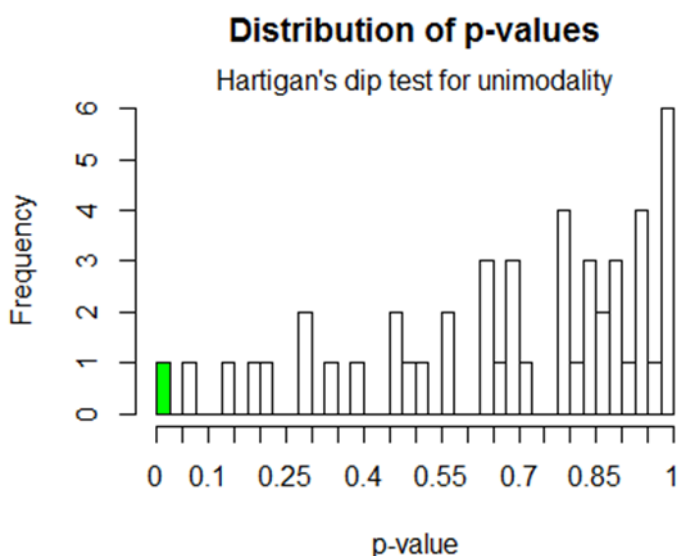


Figure 6: Distribution of the p-values obtained by the Hartigan's dip test for unimodality. 1 of the 48 tests resulted in a p-value of  $< 0.05$  and hence a significant deviation from unimodality (indicated in green).

### 4.2 Do partners coordinate their foraging trips to minimise the time that the nestlings are left alone, and does the amount of coordination decrease as chicks grow?

In total, 18 out of the 24 males showed a significantly higher proportion of trips started when the female was present in the colony than expected for uncoordinated trips (Table 1). The observed values were on average 25.7% higher than the mean expected value under the null model. Similarly, the number of trips started by the female when the male was present in the colony was significantly higher (on average 39.7% higher) for 21 out of 24 individuals (Table 1). The fraction of total nest attendance was also significantly higher (on average 8.9% higher) than expected from uncoordinated trips for 23 couples (Table 1).

	No. of tests with observed value > the 95 <sup>th</sup> percentile of the expected values	Total no. of tests	% higher than the mean expected value
Proportion of trips started by the male with female present	18	24	25.7
Proportion of trips started by female with male present	21	24	39.7
Proportion of total nest attendance	23	24	8.9

Table 1: Overview of the number of significant tests per metric. When the observed value was larger than the 95<sup>th</sup> percentile of the expected values, the observed value for the metric was significantly larger than expected based on uncoordinated trips.

When testing for the effect of the age of the nestlings on coordination, the models showed that the age of the offspring had a significant effect on the time the parents spent at the nest in between foraging trips, with a shorter period of time spent in the colony as the nestlings grew older (Table 2, Figure 7). Males and females did not differ significantly in the time spent in the colony in between foraging trips (Table 2). Furthermore, the proportion of time that at least one of the parents was present in the colony also decreased significantly with increasing nestling age (Table 2, Figure 8).

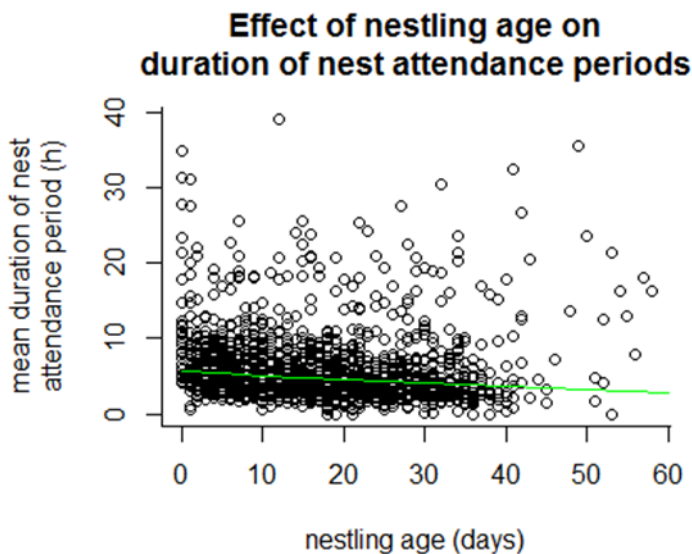


Figure 7: Estimated effect of the age of the nestlings on the duration of the nest attendance periods of the parents from the mixed effects model. Nest attendance periods became shorter with increasing age of the nestlings. For clarity, only the mean duration of nest attendance periods per day per bird was plotted.

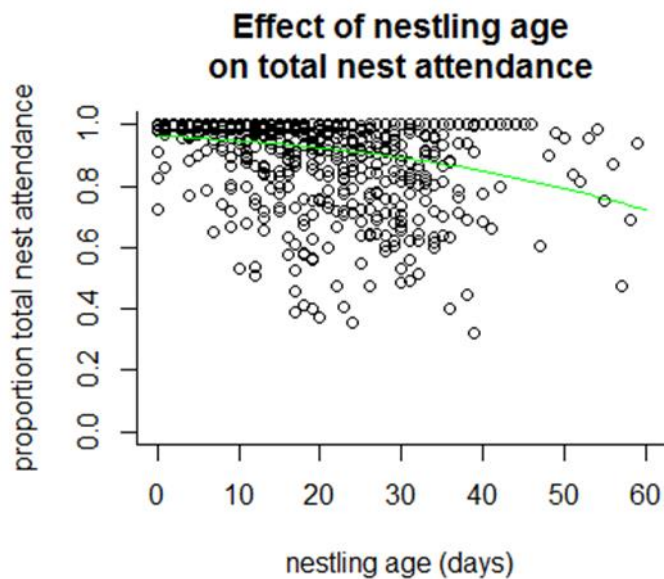


Figure 8: Estimated effect of nestling age on the proportion of time that at least one of the parents was present in the colony, from the mixed effects model. With increasing nestling age, the proportion of total nest attendance decreased.

	F-statistic	d.f.	p-value	Estimated marginal mean/ coefficient $\pm$ s.e.	Back-transformed estimated marginal mean $\pm$ s.e.
<b>Time in colony in between foraging trips (h)</b>					
Nestling age	60.0169	1	4.52e-05	-0.0116 $\pm$ 0.0029	
Sex	3.5719	1	0.0920		
Male				1.7476 $\pm$ 0.0862	5.7408 $\pm$ 0.4951
Female				1.5378 $\pm$ 0.0900	4.6546 $\pm$ 0.4189
	$\chi^2$	d.f.	p-value	Estimated marginal mean/ coefficient $\pm$ s.e.	
<b>Proportion of total nest attendance</b>					
Nestling age	115.70	1	< 2.2e-16	-0.0387 $\pm$ 0.0036	

Table 2: Mixed effects models of 1) individual nest attendance in relation to nestling age and sex and 2) the proportion of total nest attendance in relation to nestling age. In the first model, a gamma distribution with log link function was used, with bird.year included as a random effect, whereas in the second model, a beta regression with logit link function was fitted, with colony and couple.year included as random effects. Estimated coefficients are to be back-transformed for interpretation. Non-significant interaction terms were removed.  $N = 24$  pairs.

### 4.3 Does the amount of coordination depend on the similarity in foraging strategies between partners, or vary between foraging strategies?

Neither similarity in resource use, nor overlap in foraging sites significantly affected the proportion of time that at least one of both parents was present in the colony during the chick-rearing period (Table 3). There was also no significant effect of similarity in resource use or overlap in foraging sites on the proportion of individual nest attendance during chick-rearing (Table 3). Furthermore,

males and females did not differ significantly in the proportion of time they spent in the colony (Table 3). Similarly, no significant effects were found of similarity in resource use and overlap in foraging sites on the proportion of overlap in nest attendance during the chick-rearing stage (Table 3). Lastly, the proportion of trips started with the partner present in the colony was also independent of the similarity in resource use and the overlap in foraging sites (Table 3). The proportion of trips started with the partner present in the colony also did not differ significantly between males and females (Table 3).

	$\chi^2$	d.f.	p-value	Estimated marginal mean/ coefficient $\pm$ s.e.	Back-transformed estimated marginal mean [mean - s.e., mean + s.e.]
<b>Proportion of total nest attendance</b>					
Resource similarity	3.6904	1	0.0547	-1.5007 $\pm$ 0.7812	
Overlap in foraging sites	0.0027	1	0.9585	-0.0410 $\pm$ 0.7871	
<b>Proportion of individual nest attendance</b>					
Resource similarity	3.5050	1	0.0612	-0.8007 $\pm$ 0.4277	
Overlap in foraging sites	0.0335	1	0.8547	0.0834 $\pm$ 0.4554	
Sex	1.7603	1	0.1846		
Male				0.4724 $\pm$ 0.1326	[0.5841, 0.6468]
Female				0.2279 $\pm$ 0.1282	[0.5249, 0.5881]
<b>Proportion of overlap in nest attendance</b>					
Resource similarity	1.1592	1	0.2816	-0.3079 $\pm$ 0.2859	
Overlap in foraging sites	0.2979	1	0.5851	-0.1599 $\pm$ 0.2929	
<b>Proportion of trips started with partner present</b>					
Resource similarity	2.4433	1	0.1180	-1.0971 $\pm$ 0.7019	
Overlap in foraging sites	1.2161	1	0.2701	-0.8128 $\pm$ 0.7371	
Sex	0.4285	1	0.5127		
Male				1.0193 $\pm$ 0.2908	[0.6745, 0.7875]
Female				0.8173 $\pm$ 0.3044	[0.6255, 0.7543]

Table 3: Mixed effects beta regression models of the amount of coordination in relation to resource use similarity, overlap in foraging sites and sex (where appropriate). Non-significant interaction terms were removed from the models. All models included colony and year as random effects. Coefficients ought to be back-transformed for interpretation.  $N = 24$  pairs.

There was a significant interaction effect between the proportion of marine foraging by the partner and sex on the proportion of nest attendance during the chick-rearing period (Table 4), meaning that the effect of the proportion of marine foraging by the partner on an individual's nest attendance was different for males and females. Males spent significantly less time in the colony when their partner foraged more on marine resources, whereas the nest attendance of females did not differ significantly with the proportion of marine foraging by their partner (Table 4 and Figure 9). The proportion of trips started with the partner present in the colony was independent on both the foraging strategy of the individual and that of its partner (Table 4). Furthermore, males and females



did not differ significantly in the proportion of trips they started when their partner was present in the colony (Table 4). Similarly, the proportion of time that at least one parent was present in the colony and the proportion of time that both parents were present simultaneously did not vary with the foraging strategies of the male and female (Table 4).

	$\chi^2$	d.f.	p-value	Estimated marginal mean/ coefficient $\pm$ s.e.	Back-transformed marginal mean [mean - s.e., mean + s.e.]
<b>Proportion of individual nest attendance</b>					
Marine foraging	0.2058	1	0.6501	-0.1381 $\pm$ 0.3044	
Marine foraging partner	0.1179	1	0.7313		
Sex	19.3756	1	1.074e-05		
Male				0.8688 $\pm$ 0.1554	
Female				0.1847 $\pm$ 0.1052	
Marine foraging partner : Sex	6.5358	1	0.0106		
Male				-3.5194 $\pm$ 1.4176	
Female				0.1047 $\pm$ 0.3049	
<b>Proportion of trips started with partner present</b>					
Marine foraging	0.0984	1	0.7538	0.2084 $\pm$ 0.6646	
Marine foraging partner	0.1976	1	0.6567	0.3072 $\pm$ 0.6911	
Sex	1.5681	1	0.2105		
Male				1.3148 $\pm$ 0.5818	[0.6755, 0.8695]
Female				1.6174 $\pm$ 0.5716	[0.7400, 0.8993]
<b>Proportion of total nest attendance</b>					
Marine foraging male	0.3307	1	0.5652	0.4132 $\pm$ 0.7186	
Marine foraging female	1.8103	1	0.1785	-3.9340 $\pm$ 2.9239	
<b>Proportion of overlap in nest attendance</b>					
Marine foraging male	0.0061	1	0.9378	-0.0191 $\pm$ 0.2443	
Marine foraging female	0.0461	1	0.8301	0.2244 $\pm$ 1.0455	

*Table 4: Mixed effects beta regression models of the amount of coordination in relation to the proportion of marine foraging by the individual, the proportion of marine foraging by the partner and sex (where appropriate). Non-significant interactions were removed from the models. All models included colony and year as random effects. Coefficients ought to be back-transformed for interpretation. N = 24 pairs.*

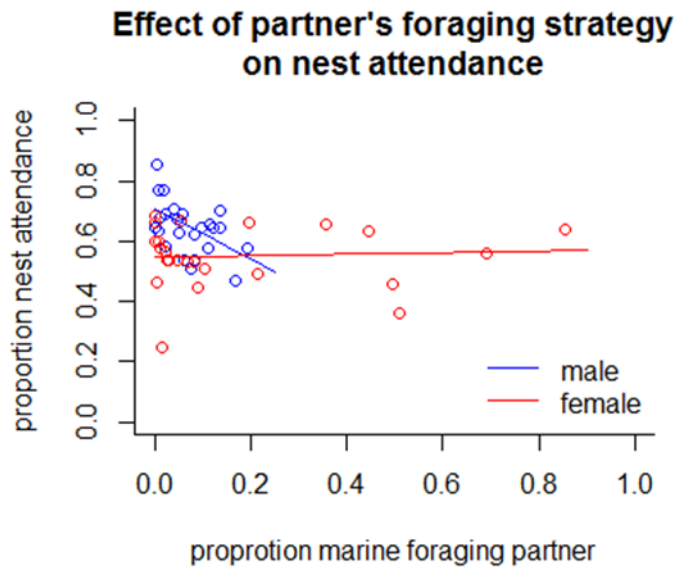


Figure 9: Estimated effect of the proportion of marine foraging by the partner on the nest attendance of an individual, from the mixed effects model. The effect was different for males and females. Males whose partner used more marine resources spent less time in the colony, whereas females whose partners foraged more on marine resources did not show a significant response in their nest attendance.

#### 4.4 Do parents adjust their efforts to those of their partner?

The duration of the foraging trips during the chick-rearing period was not significantly affected by the duration of the last completed foraging trip of the partner (Table 5, Figure A.2 in appendix). No differences between sexes in the duration of the foraging trips were found either (Table 5).

	F-statistic	d.f.	p-value	Estimated marginal mean/coefficient $\pm$ s.e.	Back-transformed marginal mean $\pm$ s.e.
<b>Trip duration (h)</b>					
Trip duration partner	0.8469	1	0.3570	-0.0031 $\pm$ 0.0034	
Sex	2.6357	1	0.1240		
Male				1.2155 $\pm$ 0.0718	3.3720 $\pm$ 0.2421
Female				1.3713 $\pm$ 0.0713	3.9404 $\pm$ 0.2811

Table 5: Mixed effects model of trip duration in relation to the trip duration of the partner, using a gamma distribution with log transformation. Bird.year was included as a random effect. The non-significant interaction term was removed from the model. N = 48 individuals. Coefficients are to be back-transformed for interpretation.

## 5. DISCUSSION

### 5.1 Do Lesser Black-backed Gulls adopt a dual foraging strategy?

Among pelagic seabirds, dual foraging has been identified to be a rather common strategy to balance parental care with their own needs (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994, Weimerskirch & Cherel 1998, Magalhães et al. 2008, Tyson et al. 2017). GPS tracking, however, does not suggest the occurrence of such strategy in Lesser Black-backed Gulls. Indeed, the vast majority of the birds did not perform distinct long and short foraging trips. Even for the single individual for which a significant deviation from unimodality in the trip durations was found, the histogram of its trip durations show that these peaks are not very pronounced, as they lie very closely together (Figure A.1 in appendix). Moreover, the histograms show that Lesser Black-backed Gulls undertake mainly foraging trips of a couple of hours, and only occasionally stay away longer than one day, the mean of all trip durations being 3.76 h. Only 0.45% of all trips lasted longer than a day. These trip durations are similar to what was found by Garthe et al. (2016) (trips lasting 0.5-26.4 h, with a mean of  $8.7 \pm 0.9$  h) and Shamoun-Baranes et al. (2011) (mean trip duration of  $7.9 \pm 9.0$  h), and are in sharp contrast with the much longer trips undertaken by Procellariiform seabirds, which usually last for several days (Weimerskirch et al. 1994, Phillips et al. 2009, Tyson et al. 2017).

Thus, foraging strategies exhibited by Lesser Black-backed Gulls breeding along the Belgian and Dutch coast do not seem to impose the need for a dual foraging strategy. Even in Procellariiform seabirds, where dual foraging seems to be common, the strategy is sometimes absent or facultative, with variation between populations and years. This variation seems to be dependent on the resource distribution, with dual foraging only occurring when the resources in proximity of the colony are poor (Granadeiro et al. 1998, Gray & Hamer 2001, Baduini & Hyrenbach 2003, Peck & Congdon 2005, Phillips et al. 2009). Furthermore, it has been found that birds sometimes first visit nearby foraging areas and only follow this up with a visit to more distant regions when there was little food available in the nearby waters (Xavier et al. 2003, Catry et al. 2004). This suggests that dual foraging is a strategy to compensate for low or unpredictable resource levels close to the colony. So, when resources are patchy or unpredictable, adults need to undertake longer foraging trips to more rich feeding grounds in order to acquire enough food and maintain their own body mass (Buidini & Hyrenbach 2003). Marine resources typically show a very patchy distribution and are rather unpredictable (Platt 1972, Mackas et al. 1985, Weimerskirch 2007). Lesser Black-backed Gulls have been shown to intensively use a variety of terrestrial resources (Götmark 1984, Garthe et al. 2016, Gyimesi et al. 2016, Coulson & Coulson 2008), and hence they might experience a higher availability and predictability and lower patchiness of their resources in the foraging sites close to the colony (Corman et al. 2016, Palm et al. 2013, Hackenberger & Hackenberger 2014). The variety of available resources that can be found in the surroundings of the colonies along the Belgian and Dutch coast is indeed high, including fishery discards, refuse dumps and several crop types and invertebrate species that can be found on agricultural fields, all known to be preferred food sources of Lesser Black-backed Gulls (Garthe et al. 2016, Gyimesi et al. 2016). As a result, the need of visiting faraway foraging grounds is avoided, and all foraging trips can be completed successfully in only a few hours. Furthermore, a dual foraging strategy is likely to be costly, as demonstrated by the absence of the strategy in Procellariiformes when resource levels in the surroundings of the colony are high (Granadeiro et al. 1998, Gray & Hamer 2001, Baduini &

Hyrenback 2003, Peck & Congdon 2005, Phillips et al. 2009). Hence, due to the high availability and diversity of resources in the vicinity of the colony, Lesser Black-backed Gulls might not need to adopt a dual foraging strategy to balance the needs of their offspring with their own, thereby avoiding the cost of having to explore unknown, faraway foraging sites.

## 5.2 Do partners coordinate their foraging trips to minimise the time that the nestlings are left alone, and does the amount of coordination decrease as chicks grow?

Lesser Black-backed Gulls engage in relatively long foraging trips, and hence if these trips are not coordinated between partners, the nestlings could be left alone in the colony for long periods at a time, resulting in high starvation and predation risks. When parental care is low and parents stay away from the nest for too long, nestlings start wandering around in the colony (Hunt & McLoon 1975, Pierotti & Murphy 1987, Bukacinski et al. 1998). Lesser Black-backed Gull parents and other *Larus* species oftentimes attack these wandering chicks when they come too close to their nests (Tinbergen 1960, Parsons 1971, Hunt & McLoon 1975, Pierotti & Murphy 1987, Bukacinski et al. 1998). Coordination of the foraging trips could reduce the starvation and predation risk by ensuring a more regular food provisioning and preventing the nestlings from wandering away from the nest, or actively defending them against predators. Morris (1987) and Bukacinska et al. (1996) showed that in Herring Gulls (*Larus argentatus*), a closely related species, parents which had a higher total nest attendance due to coordinated foraging trips had a higher number of successfully fledging offspring than parents that did not coordinate their foraging trips. Hence, coordination between parents seems crucial to ensure a successful reproduction. The results of this study show that Lesser Black-backed Gull parents indeed seem to coordinate their foraging trips during the chick-rearing stage. In all breeding pairs but one, the proportion of time that the nestlings were guarded was significantly higher than would be expected when the parents do not coordinate their foraging trips. In most of the couples, the proportion of time that there was at least one parent present in the colony was close to 1. This clearly indicates that Lesser Black-backed Gulls actively coordinate their trips to minimise the time that the nestlings are left alone, thereby minimising their predation risk. In order to achieve such a high proportion of total nest attendance, it is expected that parents wait for each other in the colony before one of them leaves on a foraging trip. Indeed, the proportion of trips started by the male when the female was present in the colony was higher than expected for most of the breeding pairs, and so was the proportion of trips started by the female when the male was present in the colony. The period of time spent together in the colony before leaving on a trip could also be used to negotiate which of the two parents should leave on a foraging trip and which should stay with the nestlings (Niebuhr & McFarland 1983).

Furthermore, our results show that the time the chicks are guarded decreases with increasing nestling age, indicating that coordination is highest in the early chick-rearing period and decreases throughout the breeding season. These results are consistent with what was found for Slaty-backed Gulls (*Larus schistisagus*) by Watanuki (1992). In addition, we found that the time Lesser Black-backed Gull parents spent in the colony in between foraging trips did not differ between males and females, and also decreased as the nestlings grew older. Hence, males and females invest equally in guarding the nestlings and the territory, and this investment decreases throughout the breeding season. The latter observation is consistent with the findings of Camphuysen et al. (2015) and

indicates that, as the nestlings age, the succession of the foraging trips occurs more rapidly. Lesser Black-backed Gull nestlings are most susceptible to predation in the first days after hatching, and the predation risk decreases with the age of the nestlings, as they grow stronger and bigger (Bukacinski et al. 1998). Especially predation by other gulls in the colony poses a threat to the young nestlings, as they cannot yet defend themselves, and are still small enough to be preyed on by the gulls. Therefore, coordination of foraging trips between partners is most important during the early chick-rearing period, to ensure that there is always at least one parent present in the colony to guard and defend the vulnerable nestlings. In contrast to the predation risk, the starvation risk becomes higher as the nestlings grow older (Bukacinski et al. 1998), because they require more food (Dunn 1975, Drent & Daan 1980). Generally, nestlings provided with more food in the late chick-rearing stage not only suffer a lower starvation risk, but also experience a higher growth rate and reach a higher mass at fledging, further increasing their survival chances (Harris 1978, Quinney et al. 1986, Bukacinski et al. 1998). Coordination probably results in a lower amount of food that can be provided to the offspring, since only one parent at a time is foraging. The combination of the decreasing need to protect the offspring from neighbouring gulls and the higher requirements of the nestlings with increasing age hence results in a decreasing coordination between the parents and consequently less guarding of the nestlings as they grow older.

### 5.3 Does the amount of coordination depend on the similarity in foraging strategies between partners, or vary between foraging strategies?

*Larus* gulls are generalists at species level, but show individual diet specialisation (Harris 1965, McCleery & Sibly 1986, Tyson et al. 2015, Corman et al. 2016). Similarity in diet between partners may affect the reproductive success through the compatibility between them, i.e. the tendency of the partners to coordinate their foraging trips and maximise the time of guarding the nestlings (Niebuhr & McFarland 1983, Watanuki 1992). The similarity in resource use in the pairs studied here was on average 0.68, with values ranging from 0.16 to 0.99. The average overlap in foraging sites was 0.63, with values ranging from 0.36 to 0.99. These values indicate that there is a substantial overlap in diet for some couples, which may have consequences for the coordination in these pairs. Niebuhr & McFarland (1983) and Niebuhr (1983) found that when partners forage on the same resources, they experience a conflict of interest in terms of nest relief during incubation. This conflict is caused by the availability of the resources, which is variable in time. If both partners forage on the same resources, they intend to leave the nest at the same time, coinciding with the peak abundance of the preferred resource. In such incompatible pairs, nest relief was less smooth and the period of exposure of the eggs was longer, resulting in a higher risk of egg loss (Niebuhr & McFarland 1983, Niebuhr 1983). Even though in this study we analysed the period of chick rearing instead of the incubation period, we would expect similar results, since coordination is also of great importance in the chick-rearing stage, as established before. Following this reasoning, we would have expected the time that at least one parent is present in the colony to decrease with increasing similarity in resource use and increasing overlap in foraging sites, and the overlap in nest attendance to increase with increasing similarity in resource use and overlap in foraging sites. However, we found no effect of similarity in resource use and overlap in foraging sites between partners on the time that the nestlings were guarded and the time that the parents were present in the colony simultaneously. Furthermore, neither the proportion of nest attendance of an individual,

nor the number of trips started by a parent with the partner present in the colony varied with increasing similarity in resource use or overlap in foraging sites. These results hence do not show the occurrence of a conflict of interest with increasing similarity in diet between partners, in contrast to the observations of Niebuhr & McFarland (1983) and Niebuhr (1983) that nest relief was less smooth with increasing overlap in diet between partners. Thus, our results suggest that the amount of coordination between partners is independent of the overlap in their diet, which is consistent with observations of a study on Slaty-backed Gulls (Watanuki 1992). There are several possible explanations for these contradictory results about whether or not there is a conflict between parents foraging on the same resources. The availability of the preferred resources of our Lesser Black-backed Gull populations might not be as variable in time, or might be available for a longer period of time than assumed by Niebuhr & McFarland (1983) and Niebuhr (1983), and as a result the parents might not be restricted to a certain time of day for optimal foraging. In this case, the foraging trips do not necessarily coincide when both partners exploit the same resource during peak abundance. Furthermore, it has to be noted that Niebuhr & McFarland (1983) and Niebuhr (1983) based their study on a more detailed description of resource use than was done here. In our study, we defined resource use as foraging on either marine, agricultural or urban resources. It is hence possible that both partners forage most frequently on agricultural resources, which we defined as a high similarity in resource use, but that they exploit completely different types of agricultural resources.

Apart from similarity in foraging strategies between partners, individual diet specialisation might also affect the amount of parental care individuals are able to give, due to differences in the time and distance travelled during foraging trips (Hunt 1972, van den Bosch et al. 2019), or due to differences in nutritional value between resources (Bukacinska et al. 1996, van Donk et al. 2017, Watanuki 1992). The time a parent can be present in the nest to guard the chicks might hence depend on the chosen foraging strategy (Watanuki 1992), and as a result, the individual foraging strategies might affect the coordination between parents. It has been shown that marine resources, especially fish, result in a higher reproductive success than other resources, probably due to the high energetic value (Bukacinska et al. 1996, van Donk et al. 2017). However, foraging on marine resources entails high levels of competition (Hudson 1989, Camphuysen et al. 2015). This competition prevents the smallest individuals from successfully foraging on marine resources and hence these individuals are found to forage more on terrestrial resources, which involves less competition (Camphuysen et al. 2015). This exclusion from marine resources might affect the amount of parental care these individuals are able to give. It is expected that a higher proportion of foraging on the profitable marine resources would result in a higher amount of time spent in the colony, since less time is needed to search for other, less profitable resources, and this might also benefit the coordination between partners. However, our results show that the time the parents spend in the colony does not depend on their own foraging strategy, indicating that exclusion from the most profitable resources does not negatively affect parental care. Even though marine foraging trips are generally shorter than terrestrial ones, and marine resources are more profitable, foraging on these resources is energetically more demanding (Camphuysen et al. 2015), which might explain our observation that the time devoted to guarding the nestlings does not depend on the foraging strategy of the parents. Furthermore, the time that the nestlings were guarded, and the time that both parents were present in the colony simultaneously did not depend on the foraging strategy of the parents, indicating that the ability of the parents to coordinate their foraging trips is not affected by which resources they prefer. However, our results show a sexual difference in the

effect of the foraging strategy of the partner on an individual's nest attendance. Males seemed to decrease the time they spent guarding the nestlings when the female used more marine resources, whereas the nest attendance of the females was not affected by the foraging strategy of their partner. Though, it has to be remarked that the proportion of foraging on marine resources by the females only ranged from 0 to 0.19 (Figure 9), which is a very limited range. As a result, this observation is likely an artefact caused by small sample size, rather than an actual trend.

#### 5.4 Do parents adjust their efforts to those of their partner?

Parental care is costly, and hence every parent benefits from shifting more of the workload to the partner (Trivers 1972, Westneat & Sargent 1996, Royle et al. 2002). Therefore, parents are expected to negotiate their efforts, and adjust them to those of their partner. However, the outcome of such negotiation is variable, depending on the completeness of the information parents have on the investment of their partner and the fitness of their offspring, and ranges from a compensating response to a matching response. Some studies on passerines show that parents alternate their feedings of the nestlings, delaying their own efforts until the partner had provisioned (Johnstone et al. 2014, Bebbington & Hatchwell 2015, Savage et al. 2017). Hence these birds closely monitor their partner to be able to immediately adjust their own efforts to momentary changes in the investment of their partner. Our results show that the duration of the trips undertaken by Lesser Black-backed Gulls does not depend on the duration of the last trip undertaken by the partner, suggesting that Lesser Black-backed Gulls do not directly adjust their own efforts to those of their partner. This contrast with the response found in passerines is possibly because of the inability of Lesser Black-backed Gulls to closely monitor their partner. Lesser Black-backed Gulls spend relatively long periods away from the colony when they go on a foraging trip, and as a result they cannot directly assess the efforts of their partner during this period, making it hard to react to momentary changes in the effort of their partner. This could imply that parental care is a fixed property in Lesser Black-backed Gulls, rather than a flexible one subjected to negotiation. However, apart from directly observing the efforts of their partner, parents might also be able to infer the investments of their partner from the state of the offspring. This might provide information on the overall investment of their partner. Taking this into account, it is possible that Lesser Black-backed Gulls don't adjust their efforts to momentary changes in their partner's efforts (i.e. the last foraging trip of the partner), but rather to the total investments of the partner up to that point. However, this response has yet to be investigated. Alternatively, it is possible that negotiation occurs earlier in the breeding season and that at the time the eggs hatch, the parents have fixed the amount of care they will provide.

## 6. CONCLUSION

Lesser Black-backed Gull parents engage in relatively long foraging trips, and hence spend long periods away from their partner and their offspring. This could have disastrous consequences for the nestlings if both parents were to undertake foraging trips at the same time, since nestlings that are left alone in the colony for too long are often predated by neighbouring adult gulls. With this study, we showed that parents coordinate their foraging trips, which serves to both increase the chances of survival of the nestlings and balance parental care between partners. By coordinating their foraging trips, the time that the nestlings are left alone in the colony is minimised, and a regular food provisioning is ensured. Coordination between partners decreased throughout the breeding period, as there is a reduced predation risk for the nestlings when they grow older and bigger. Hence, as the nestlings age, maximising the amount of food provided becomes more important than constant guarding.

To achieve such coordination, we showed that parents seem to wait for each other in the colony, before they leave on a foraging trip. The ability of the parents to coordinate their foraging trips is unaffected by which resources they prefer, even though marine foraging trips are generally much shorter than terrestrial foraging trips. In addition, we did not find evidence that gulls alternated different food sources or foraging locations, suggesting that Lesser Black-backed Gulls do not need to adopt a dual foraging strategy to coordinate parental care. High levels of coordination were thus achieved independently of the foraging strategies or the similarity in foraging strategies within a pair. Moreover, we did not find evidence that individuals adjusted their foraging trip durations to the duration of the foraging trips, and thus the parental investment, of their partner.

Our results thus show that Lesser Black-backed Gulls indeed seem to coordinate their parental care by keeping an eye on their partner, even though they are apart for most of the day. Yet, in contrast to most studies on passerines, we could not find conclusive evidence that individuals make short-term adjustments in their parental investment based on that of their partner. Whether this is due to parents using more direct cues for the net investment of their partner, such as nestling condition, or because parental investment and coordination are rather fixed properties will require additional studies.



## 7. SUMMARY

Parental care is a common behaviour among animals, by which parents aim to increase the chances of survival of their offspring. Yet, providing parental care is costly, since the time and energy that is spent on caring for the offspring cannot be spent on self-maintenance, and hence might decrease the future reproductive success of the parents. Thus, how much a parent should invest in the current offspring is decided by balancing the immediate benefits of investing in current offspring against the losses caused by the investment in terms of future fecundity. Through parental care, individuals benefit not only from their own investment in the offspring, but they also yield the indirect benefits from the parental care provided by the partner. Hence, each parent would prefer their partner to work harder and bear the majority of the cost. This results in a conflict between parents about how much each should invest in the offspring. Several theoretical models have been developed to clarify how parents could resolve this conflict by adjusting their own effort to that of the partner. These models show that parental care could evolve in multiple ways, depending on the timescale on which parents react and the completeness of information they have on the investment of their partner. The most simple evolutionary models show that even when individuals are unable to adjust the amount of care they provide during their own lifetime, biparental care can still be an evolutionary stable strategy, on the condition that changes in the investment of one sex are compensated by the other sex over the next generations. This implies that negotiation, i.e. adjustment of efforts during the own lifetime of the parents, is not a prerequisite for biparental care to evolve. However, more complex models show that the ability of partners to negotiate and adjust the amount of care provided increases the likelihood of the evolution and the stability of biparental care. Furthermore, such negotiation allows for more flexible responses to changes in effort, including both a compensating and a matching response, depending on the completeness of information the parents have on the investment of their partner. This great diversity in predictions by theoretical models is matched by the variety of responses that have been shown to occur in reality with experimental studies, including partial compensation, full compensation, a matching response or no response at all. Hence, an important prediction made by these models is that the extent to which individuals compensate for changes in the investment of their partner depends on their ability to monitor their partner. In some species, parents stay away from their partner and the offspring for very long periods at a time, and it is not clearly known how these species solve the conflicts surrounding parental care. Hence, the aim of this study was to provide more insight into how parental care is balanced between partners that cannot monitor each other during the period of chick-rearing, using the Lesser Black-backed Gull (*Larus fuscus*) as a study species. This species is an ideal study organism for testing how conflicts surrounding parental care are resolved because, due to the relatively long foraging trips of the parents, the nestlings are subjected to high predation and starvation risks. In order to protect their offspring, it seems crucial that Lesser Black-backed Gull parents negotiate and coordinate their efforts, even when they spend long periods of time away from each other. Using GPS data of 24 breeding pairs from the years 2015 to 2018, the timing and duration of their foraging trips and periods of nest attendance during the chick-rearing period was analysed, and their individual resource use was inferred from their foraging grounds.

The first part of the thesis consisted of testing if Lesser Black-backed Gulls adopt a dual foraging strategy. Dual foraging is a strategy in which parents make distinct long and short foraging trips to balance parental care with the needs of the parents. The long foraging trips are meant for self-

maintenance of the adults, as they gain more weight during these trips than during short trips. The short foraging trips result in a higher rate of food provisioning to the offspring and are hence meant to improve the condition of the nestlings. Such a strategy has been found to occur in many pelagic seabirds. Lesser Black-backed Gulls, of which the ecology borders to that of pelagic seabirds, could potentially also benefit from a dual foraging strategy, to balance and moderate parental care. However, our results do not suggest the occurrence of such strategy in Lesser Black-backed Gulls. Indeed, 47 out of the 48 tested birds showed no distinct long and short foraging trips. This is probably due to the high diversity and availability of resources in the vicinity of the colonies, including several types of marine and terrestrial food sources known to be preferred by Lesser Black-backed Gulls. As a result, the need of visiting faraway foraging grounds is avoided, and all foraging trips can be completed successfully in only a few hours. Thus, foraging strategies exhibited by Lesser Black-backed Gulls breeding along the Belgian and Dutch coast do not seem to impose the need for a dual foraging strategy.

In the second part of the study, it was tested if Lesser Black-backed Gull parents coordinate their foraging trips. Since the foraging trips of Lesser Black-backed Gulls last for several hours, sometimes even more than a day, the nestlings would be left alone in the colony for a very long time if the foraging trips of the parents were to coincide. During this time, nestlings could start wandering off into the colony, approaching the nests of neighbouring gulls. Such wandering gull chicks risk being predated by the other gulls in the colony. The results of this study show that Lesser Black-backed Gull parents actively coordinate their foraging trips to maximise the time the nestlings are guarded, thereby increasing the chances of survival of the nestlings. They seem to do this by waiting for each other in the colony, before one of them leaves on a foraging trip. Furthermore, our results support the hypothesis that coordination is most important during the early chick-rearing stage, and the importance decreases throughout the breeding season. The proportion of time the nestlings were guarded was indeed highest in the first days after hatching, and declined as the nestlings grew older. In addition, the time that the parents spent in the colony in between foraging trips also decreased throughout the breeding season, indicating that the succession of the foraging trips occurs more rapidly as the nestlings age. These observations can be explained by a higher predation risk for young nestlings, since they are still small and unable to defend themselves, and a higher starvation risk as the nestlings grow older, due to higher requirements. Hence, as the nestlings grow older, maximising the amount of food provided becomes more important than constant guarding against predators.

Lesser Black-backed Gulls are generalists at species level, but show individual diet specialisation. Therefore, the third part of the study consisted of analysing the effect of the foraging strategies of the parents on the amount of coordination between them and on the time they each spent guarding the nestlings. First, it was tested if the similarity in foraging strategies between partners had an influence on the coordination of their foraging trips. Partners foraging on the same resources could be expected to be in conflict with each other, because they both want to leave on foraging trips at the same time, i.e. when their preferred resource is in peak abundance. This could have negative consequences on their coordination. However, our results show no evidence for such a conflict of interest. Indeed, the coordination between partners was not affected by their diet overlap. Aside from the effect of similarity in foraging strategies, the effect of the individual foraging strategies of the parents on their nest attendance and coordination was also analysed. Marine resources are generally more profitable than terrestrial resources, and hence it is expected that the time a parent

can spend guarding the nestlings would increase when foraging more on these profitable marine resources, possibly also affecting the amount of coordination between partners. However, our results show that the time that the parents spend in the colony does not depend on their own foraging strategy. Furthermore, the time that the nestlings were guarded, and the time that both parents were present in the colony simultaneously did not depend on the foraging strategy of the parents, indicating that the ability of the parents to coordinate their foraging trips is not affected by which resources they prefer. However, we found that males spend less time guarding the nestlings when their partner forages more on marine resources, but this is likely an artefact caused by small sample size, rather than an actual trend.

In the final part of the thesis, the adjustment of an individual's efforts to changes in the efforts of its partner was studied. Our results show that the duration of the trips undertaken by Lesser Black-backed Gulls does not depend on the duration of the last trip undertaken by the partner, suggesting that Lesser Black-backed Gulls do not adjust their own efforts to changes in those of their partner in the short term. This might be due to the inability of Lesser Black-backed Gull parents to closely monitor their partner at all times. Since their foraging trips last for hours at a time, they cannot track the investment of their partner during this period, making it hard to react to momentary changes in the effort of their partner. Possibly, they adjust their investment to the overall effort of the partner, rather than to momentary changes in effort. Alternatively, parental care might be a fixed property in Lesser Black-backed Gulls, or negotiation might occur earlier in the breeding season.

In conclusion, we showed that Lesser Black-backed Gulls coordinate their foraging trips by keeping an eye on their partner, even though they are apart for most of the day. Negotiation over parental care does not seem to be necessary to obtain such coordination, since we did not find evidence that individuals make short-term adjustments in their parental investment based on that of their partner. Further research could clarify if this is due to parents using more direct cues for the net investment of their partner, or because parental investment and coordination are rather fixed properties in the Lesser Black-backed Gull.

## 8. SAMENVATTING

Heel wat dieren investeren in ouderzorg om de overlevingskansen van hun jongen te verhogen. Dit brengt echter kosten met zich mee, aangezien de tijd en energie geïnvesteerd in de jongen niet gebruikt kan worden voor het voorzien in de eigen behoeften van de ouders, waardoor hun toekomstige reproductief succes beïnvloed wordt. Hoeveel zorg een ouder moet investeren in de huidige jongen wordt dus bepaald door de directe voordelen van zorg af te wegen tegen het verlies in toekomstig reproductief succes. Ouders halen niet alleen voordelen uit hun eigen investeringen in de jongen, maar ook uit de zorg die de partner voorziet. Voor iedere ouder zou het dus beter zijn als de partner meer investeerde en een groter deel van de kost droeg. Als gevolg hiervan ontstaat er een conflict tussen de ouders over hoeveel zorg ieder moet voorzien. Verschillende theoretische modellen werden reeds ontwikkeld om na te gaan hoe ouders dit conflict zouden kunnen oplossen door hun eigen investeringen aan te passen aan veranderingen in de inspanningen van de partner. Deze modellen tonen aan dat ouderzorg op veel manieren kan evolueren, afhankelijk van de snelheid waarmee individuen reageren en de informatie die ze hebben over de investering van hun partner. De meest eenvoudige evolutionaire modellen tonen aan dat zelfs wanneer individuen hun ouderzorg niet kunnen aanpassen gedurende hun leven, ouderzorg door beide ouders nog steeds een evolutionair stabiele strategie kan zijn. Een voorwaarde hiervoor is dat veranderingen in de investering van één geslacht over generaties heen steeds weer gecompenseerd worden door het andere geslacht. Dit toont aan dat onderhandeling, i.e. aanpassing van inspanningen gedurende het eigen leven van de ouders, geen voorwaarde is voor het ontstaan van ouderlijke zorg door beide ouders. Meer complexe modellen tonen echter aan dat het vermogen van ouders om te onderhandelen over hun investeringen en hun inspanningen aan te passen aan die van hun partner het ontstaan van ouderzorg door beide ouders vergemakkelijkt en de evolutionaire stabiliteit ervan sterk verhoogt. Dit onderhandelen laat ook meer flexibiliteit toe in de mogelijke reacties op veranderingen in inspanningen. Modellen voorspellen zowel compenserende als kopiërende reacties, afhankelijk van hoe volledig de informatie is die ouders hebben over de investering van hun partner. Deze grote diversiteit aan mogelijke reacties vinden we ook terug in observationele studies, inclusief gedeeltelijke compensatie, volledige compensatie, een kopiërende reactie of helemaal geen aanpassing. Een belangrijke voorspelling van deze modellen is dus dat de mate waarin partners compenseren sterk afhankelijk is van de mate waarin ze hun partner kunnen controleren. In sommige soorten brengen de ouders veel tijd alleen door, weg van de partner en de jongen, en het is onduidelijk hoe deze soorten de conflicten rond ouderlijke zorg oplossen. Het doel van deze studie was daarom om meer duidelijkheid te scheppen in hoe ouderlijke zorg gebalanceerd wordt tussen partners die elkaar niet voortdurend in het oog kunnen houden tijdens het grootbrengen van de jongen. De Kleine Mantelmeeuw (*Larus fuscus*) werd hiervoor als studie-organisme gebruikt. Deze soort is uiterst geschikt voor onderzoek rond conflicten over ouderlijke zorg en hoe deze opgelost worden, aangezien de jongen onderworpen worden aan een hoog predatie- en verhongeringsrisico door de lange foerageertrips van de ouders. Om hun jongen hiertegen te beschermen lijkt het dus van groot belang dat de ouders onderhandelen over hun inspanningen en hun investeringen coördineren, zelfs al brengen ze lange periodes zonder hun partner door. GPS-data van 24 koppels, verzameld tijdens de jaren 2015 tot 2018, werd geanalyseerd. De timing en de duur van hun foerageertrips en periodes van aanwezigheid bij het nest tijdens het grootbrengen van de jongen werd bestudeerd, en ook het habitatgebruik van de ouders werd onderzocht.

Het eerste deel van de thesis bestond erin te testen of de Kleine Mantelmeeuw een dubbele foerageerstrategie aanneemt. Dit is een strategie waarbij de ouders duidelijk korte en lange foerageertrips maken, om zo ouderzorg te balanceren met hun eigen behoeften. De lange foerageertrips zijn bedoeld om tegemoet te komen aan de behoeften van de ouders, aangezien ze een grotere gewichtstoename vertonen tijdens deze foerageertrips dan gedurende korte trips. De korte foerageertrips bevorderen het welzijn van de jongen, aangezien meer voedsel wordt voorzien na korte trips. Deze dubbele foerageerstrategie komt voor in verschillende soorten Buisssnaveligen, die vrijwel al hun tijd op zee doorbrengen, maar zou mogelijk ook voor de Kleine Mantelmeeuw voordelig kunnen zijn. Echter, uit onze resultaten blijkt dat de strategie niet voorkomt bij deze soort. 47 van de 48 individuen vertoonden immers geen duidelijk korte en lange trips. De afwezigheid van de dubbele foerageerstrategie in de Kleine Mantelmeeuw kan verklaard worden door de grote aanwezigheid van diverse voedselbronnen in de buurt van de kolonie, inclusief verschillende types marien en terrestrisch voedsel waarvan het geweten is dat deze intensief gebruikt worden door de Kleine Mantelmeeuw. Als gevolg hiervan is het onnodig om verafgelegen foerageerplaatsen op te zoeken, en kunnen de foerageertrips met succes worden afgelegd in slechts enkele uren. De foerageerstrategieën van de populaties van de Kleine Mantelmeeuw langs de Belgische en Nederlandse kust lijken dus niet de nood voor een dubbele foerageerstrategie op te leggen.

In het tweede deel van de studie werd nagegaan of ouders hun foerageertrips op elkaar afstemmen. Aangezien een foerageertrip van de Kleine Mantelmeeuw verschillende uren kan duren, zouden de jongen lang onbewaakt in de kolonie achterblijven wanneer de ouders tegelijk foerageren. Jongen die onbewaakt in het nest achterblijven beginnen soms rond te dwalen in de kolonie, waardoor ze een hoog risico lopen om aangevallen en opgegeten te worden door de andere vogels in de kolonie. Onze resultaten tonen aan dat ouders van de Kleine Mantelmeeuw actief hun foerageertrips coördineren om zo de tijd dat de jongen alleen in de kolonie achterblijven te minimaliseren. Het lijkt erop dat ouders dit doen door in de kolonie op hun partner te wachten, voordat één van hen een foerageertrip onderneemt. Daarnaast leveren onze resultaten ook bewijs voor de hypothese dat coördinatie het belangrijkste is in het vroege stadium van het grootbrengen van de jongen en dat dit belang afneemt doorheen het broedseizoen. De proportie van de tijd dat de jongen bewaakt werden was immers het hoogst tijdens de eerste dagen na het uitkomen van de eieren en nam af naarmate de jongen ouder werden. Daarbovenop werd de tijd dat de ouders in de kolonie doorbrachten tussen foerageertrips ook steeds korter doorheen het broedseizoen, wat wil zeggen dat, naarmate de jongen ouder worden, de foerageertrips van de ouders elkaar steeds sneller opvolgen. Een verklaring voor deze observaties is dat het risico op predatie het hoogst is voor de jonge kuikens, aangezien ze nog zeer klein zijn en zichzelf niet kunnen verdedigen, en het risico op uithongering toeneemt met de ouderdom van de jongen. Naarmate de jongen ouder worden, wordt het voorzien van voldoende voedsel dus belangrijker dan de constante bescherming tegen predatoren.

Hoewel binnen een kolonie een grote variatie aan foerageerstrategieën voorkomt, zijn individuele Kleine Mantelmeeuwen vaak erg gespecialiseerd in hun dieet. Daarom werd in het derde deel van de studie nagegaan wat de invloed is van foerageerstrategieën op de mate van coördinatie tussen ouders en op de tijd dat elk van hen doorbrengt in de kolonie. Eerst werd getest of gelijkenis in foerageerstrategieën tussen partners een effect had op de coördinatie van hun foerageertrips. Er werd verwacht dat partners die dezelfde voedselbronnen gebruiken in conflict zouden zijn met elkaar, omdat ze allebei tegelijk willen foerageren, namelijk wanneer de voedselbron het meest

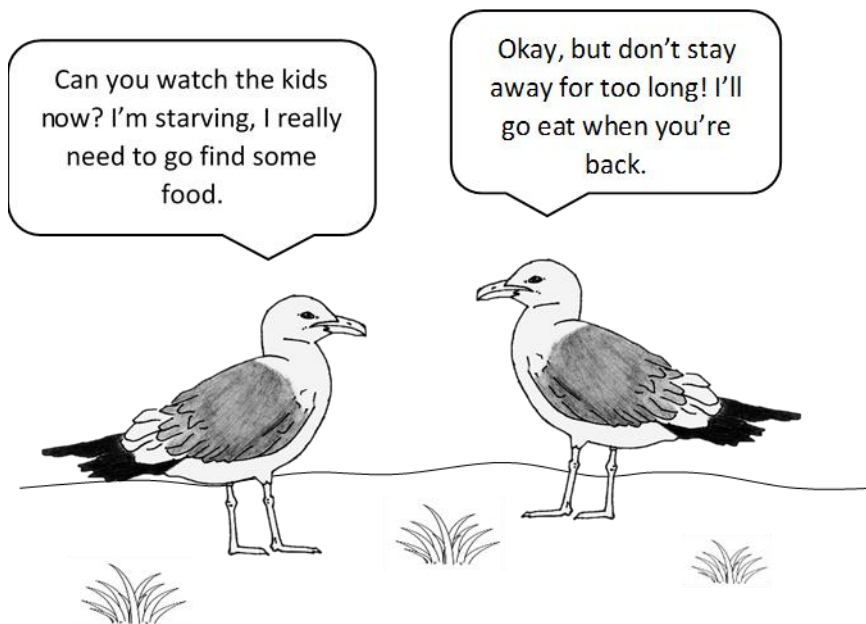
abundant is. Dit zou een negatieve invloed kunnen hebben op hun coördinatie. Onze resultaten leveren echter geen bewijs voor zulk conflict, aangezien de coördinatie tussen partners niet werd beïnvloed door de gelijkenis in hun dieet. Naast het effect van gelijkenis in habitatgebruik werd ook het effect bestudeerd van de individuele foerageerstrategieën van de ouders op de tijd dat ze in de kolonie doorbrachten en de mate van coördinatie die ze vertoonden. Mariene voedselbronnen zijn over het algemeen voordeliger dan terrestrische, en het kan dus verwacht worden dat de tijd die de ouders bij de jongen kunnen doorbrengen toeneemt naarmate ze meer gebruik maken van mariene voedselbronnen, wat mogelijk ook een effect heeft op de coördinatie tussen partners. Onze resultaten tonen echter aan dat de tijd die doorgebracht wordt in de kolonie onafhankelijk is van de eigen foerageerstrategie. Bovendien werd ook de tijd dat minstens één van de ouders in de kolonie aanwezig was en de tijd dat beide partners samen aanwezig waren niet beïnvloed door de foerageerstrategie van de ouders. Dit toont aan dat het vermogen van de ouders om hun foerageertrips te coördineren niet afhankelijk is van welke voedselbronnen zij verkiezen. Wel vonden we dat mannetjes minder tijd doorbrachten bij de jongen wanneer hun partner meer mariene voedselbronnen benutte, maar dit is hoogstwaarschijnlijk een artefact door een kleine steekproefgrootte.

In het laatste deel van de thesis werd gekeken naar hoe ouders hun eigen inspanningen aanpassen aan veranderingen in de investering van hun partner. Uit onze resultaten blijkt dat de Kleine Mantelmeeuw de duur van de foerageertrips niet aanpast aan de duur van de laatste trip van de partner, wat erop wijst dat ouders hun inspanningen niet op korte termijn aanpassen aan veranderingen in de investering van hun partner. Een verklaring hiervoor is dat, door hun lange foerageertrips, Kleine Mantelmeeuwen elkaar niet voortdurend in het oog kunnen houden, wat het moeilijk maakt om te reageren op kortstondige veranderingen in de investering van de partner. Het zou kunnen dat ze hun investeringen wel aanpassen op basis van de totale inspanning van de partner. Een alternatieve verklaring is dat ouderzorg mogelijk geen flexibele eigenschap is bij de Kleine Mantelmeeuw, en dat ouders op voorhand bepalen hoeveel ze zullen investeren, onafhankelijk van de partner, of dat onderhandelingen vroeger in het broedseizoen gebeuren.

We hebben met deze studie dus aangetoond dat Kleine Mantelmeeuwen hun foerageertrips op elkaar afstemmen door hun partner in de gaten te houden, ook al brengen ze het grootste deel van de dag zonder elkaar door. Onderhandelen over de investeringen lijkt echter niet noodzakelijk om deze coördinatie te bekomen, aangezien we geen bewijs vonden dat ze hun investering op korte termijn zouden aanpassen aan die van hun partner. Verder onderzoek is nodig om aan te tonen of dit een gevolg is van het gebruik van meer directe aanwijzingen voor de netto investering van de partner, of doordat ouderzorg en coördinatie geen flexibele eigenschappen zijn in de Kleine Mantelmeeuw, maar op voorhand bepaald worden.

## 9. TEXT FOR THE GENERAL PUBLIC

When we go out to the shop to buy food, we don't like to leave our small children at home alone, out of fear that something might happen to them. The same applies for Lesser Black-backed Gulls. By equipping 24 Lesser Black-backed Gull couples with GPS tracking devices, we studied the behaviour of the parents, and how they interact with each other. We found that parents take turns in going on a foraging trip. While one parent is away from the young to find food, the other stays at the nest. This way, there is almost always a parent present at the nest to guard and protect the young from potential predators. The parents seem to meet again in the colony before the other goes out to find food. We also found that older nestlings are left alone in the colony more often than young ones. Older nestlings are less vulnerable and the chance that they get attacked is therefore smaller. These interesting results help us to get a better understanding of how parental care is regulated in the Lesser Black-backed Gull.



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## 12. APPENDIX

### Material and methods

Colony	Boundary coordinates
Zeebrugge	51.351467 N, 3.168660 E
	51.362164 N, 3.186962 E
	51.346512 N, 3.202411 E
	51.335281 N, 3.178792 E
Vlissingen	51.457260 N, 3.686978 E
	51.437300 N, 3.727472 E
	51.434086 N, 3.711301 E
	51.449884 N, 3.677974 E

Table A.1: Coordinates for the colony boundaries used to define the polygons.

### Results

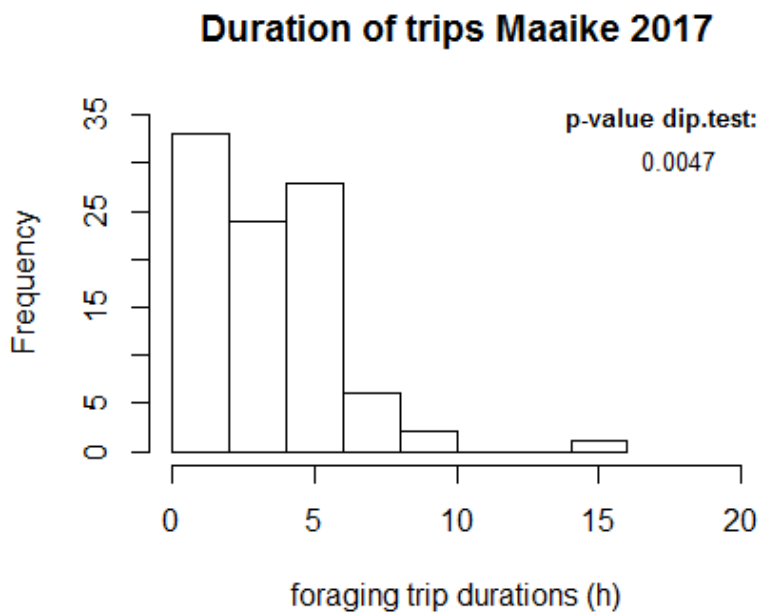


Figure A.1: Durations of foraging trips of Maaik (2017) with corresponding p-value obtained by the Hartigan's dip test for unimodality. This is the only bird which showed a significant deviation from unimodality according to the test.

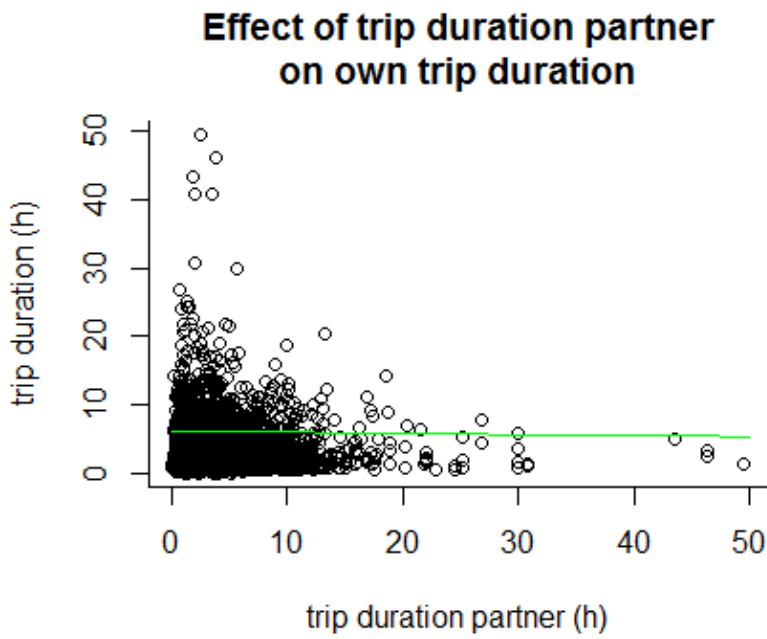


Figure A.2: Estimated effect of the duration of the last completed trip by the partner on the next trip of an individual, from the mixed effects model. No significant effect was found.

#### Model residuals

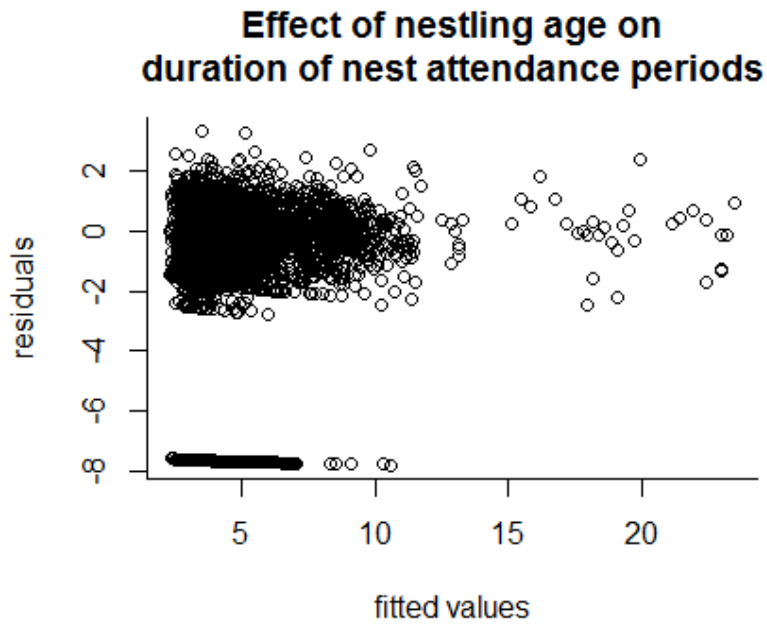


Figure A.3: Pattern of the residuals from the mixed effects model estimating the effect of the age of the nestlings on the duration of the periods spent in the colony in between foraging trips. The effect was modelled using a gamma regression.



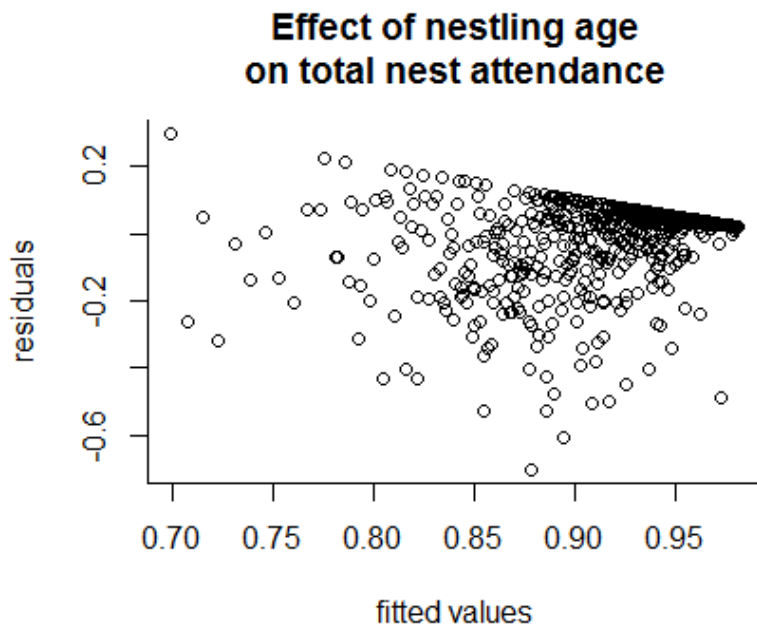


Figure A.4: Pattern of the residuals from the mixed effects model estimating the effect of the age of the nestlings on the proportion of time that at least one parent is present in the colony. The effect was modelled using a beta regression.

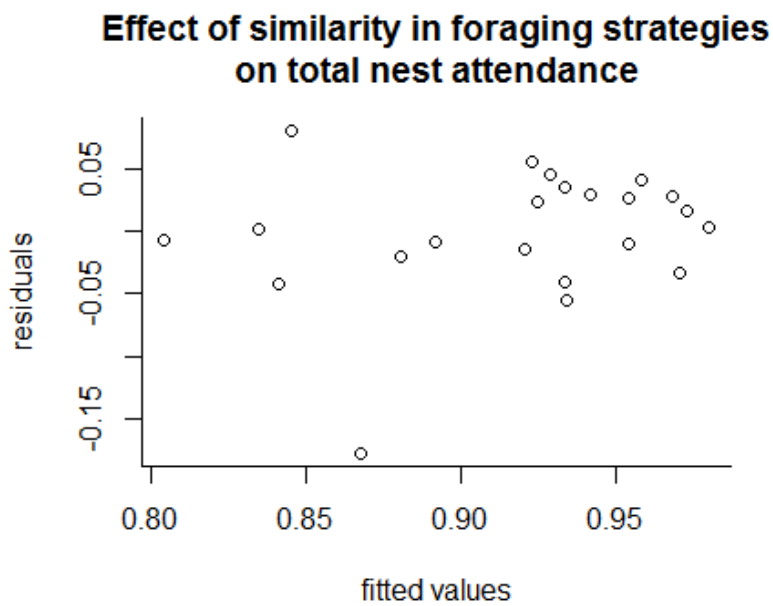


Figure A.5: Pattern of the residuals from the mixed effects model estimating the effect of similarity in foraging strategies on the time that at least one parent is present in the colony. The effect was modelled using a beta regression.

### Effect of similarity in foraging strategies on individual nest attendance

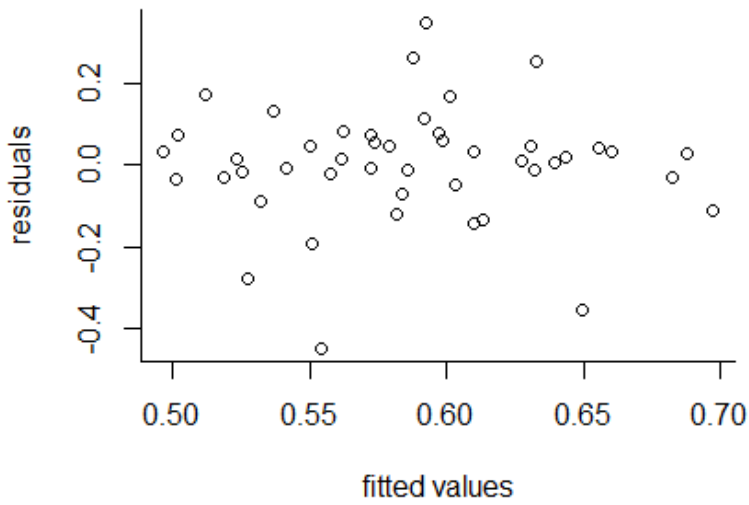


Figure A.6: Pattern of the residuals from the mixed effects model estimating the effect of similarity in foraging strategies on the time that the individuals spent in the colony. The effect was modelled using a beta regression.

### Effect of similarity in foraging strategies on overlap in nest attendance

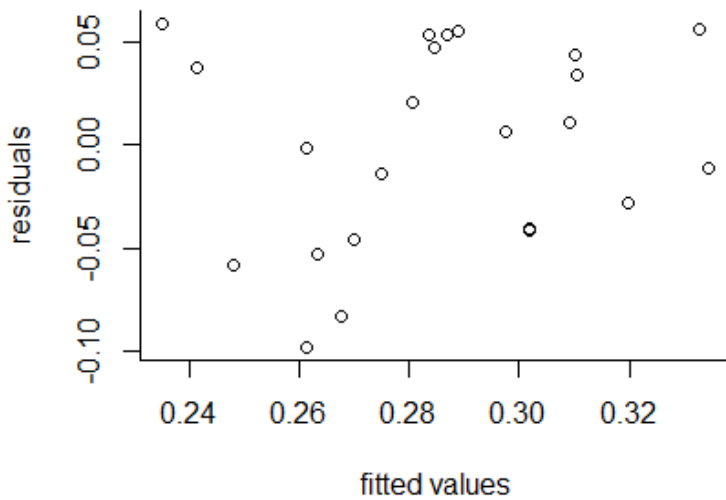


Figure A.7: Pattern of the residuals from the mixed effects model estimating the effect of similarity in foraging strategies on the time that the partners spent in the colony simultaneously. The effect was modelled using a beta regression.

### Effect of similarity in foraging strategies on trips started with partner present

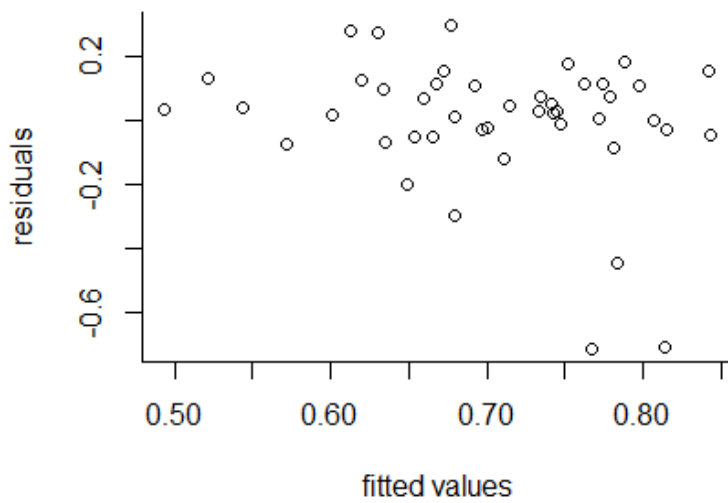


Figure A.8: Pattern of the residuals from the mixed effects model estimating the effect of similarity in foraging strategies on the proportion of trips the individuals started when their partner was present in the colony. The effect was modelled using a beta regression.

### Effect of individual foraging strategies on individual nest attendance

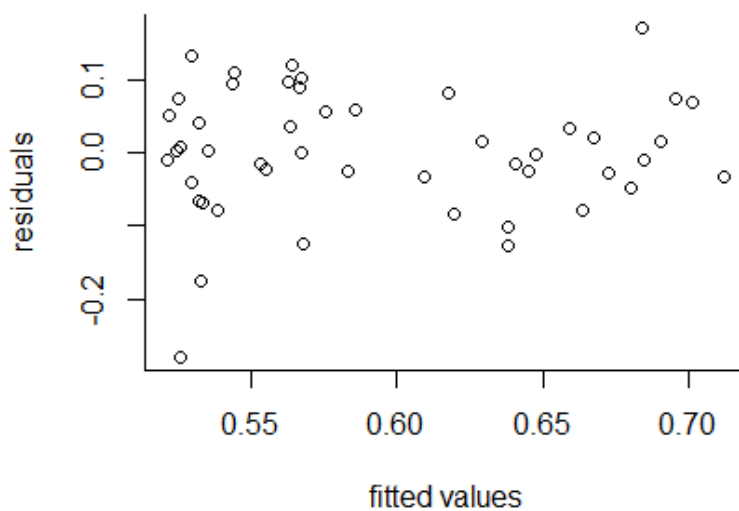


Figure A.9: Pattern of the residuals from the mixed effects model estimating the effect of individual foraging strategies on the time that the individuals spent in the colony. The effect was modelled using a beta regression.

### Effect of individual foraging strategies on trips started with partner present

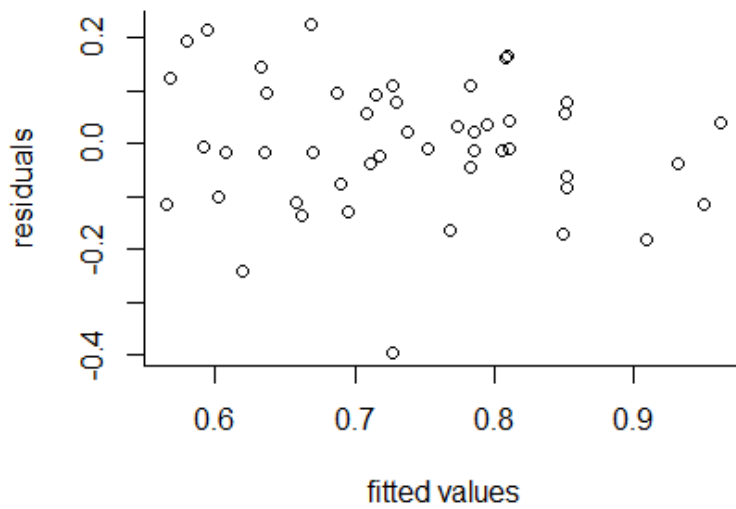


Figure A.10: Pattern of the residuals from the mixed effects model estimating the effect of individual foraging strategies on the proportion of trips the individuals started when their partner was present in the colony. The effect was modelled using a beta regression.

### Effect of individual foraging strategies on total nest attendance

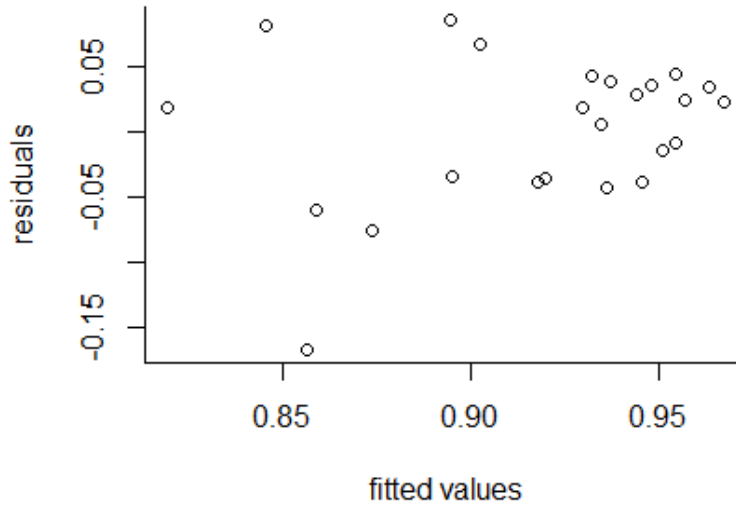


Figure A.11: Pattern of the residuals from the mixed effects model estimating the effect of individual foraging strategies on the time that at least one parent is present in the colony. The effect was modelled using a beta regression.

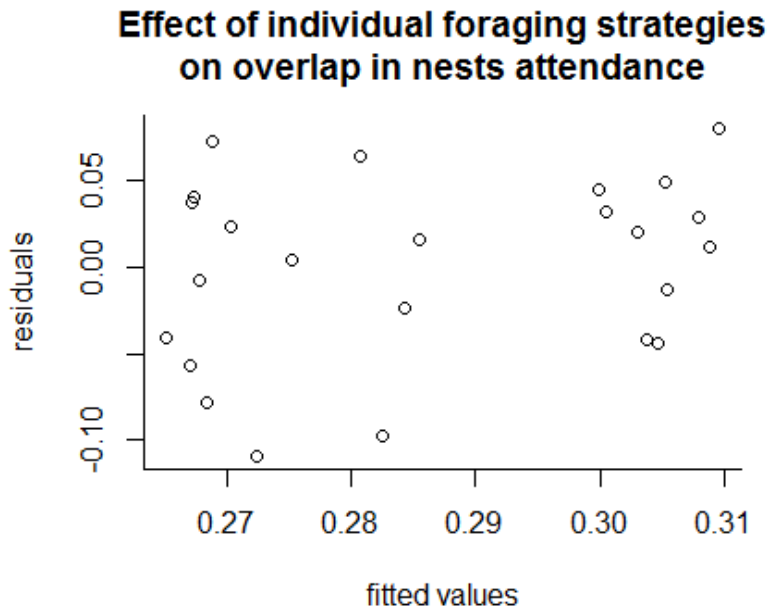


Figure A.12: Pattern of the residuals from the mixed effects model estimating the effect of individual foraging strategies on the time that the partners spent in the colony simultaneously. The effect was modelled using a beta regression.

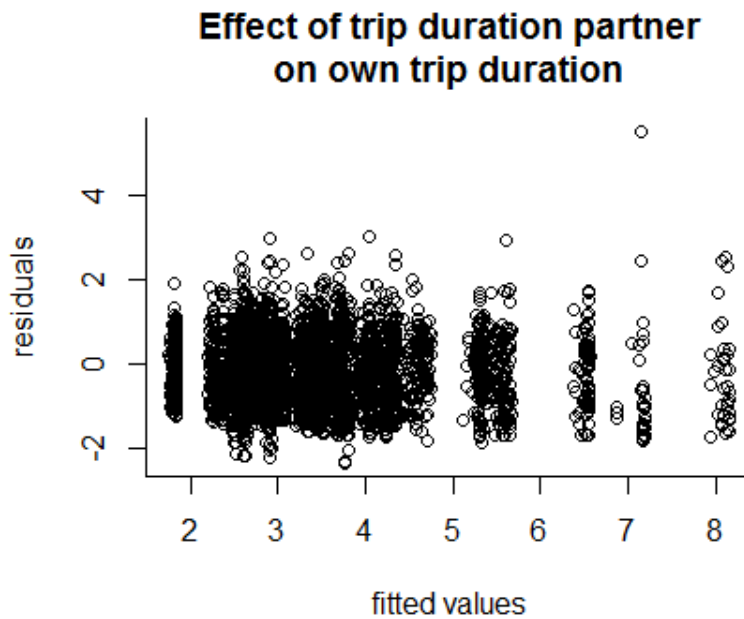


Figure A.13: Pattern of the residuals from the mixed effects model estimating the effect of the duration of the last foraging trip of the partner on the own trip duration. The effect was modelled using a gamma regression.