



# Common Guillemots *Uria aalge* Alter Trip Patterns During Breeding

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# Common Guillemots *Uria aalge* Alter Trip Patterns During Breeding.

*Sillgrisslor Uria aalge ändrar resmönster under häckning.*

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## Abstract

Seabirds are facing immense pressures, primarily induced by competition with commercial fisheries; this is of considerable concern due to the critical role that they play in marine food webs and their invaluable function as bioindicators. In this thesis, I studied the temporal change in trip duration for the Common Guillemot *Uria aalge*, a circum-arctic seabird species. Pre-recorded video footage that focused on a group of guillemot pairs residing on the Swedish island of Stora Karlsö during the 2021 breeding season served as the basis for this study. Five pairs were observed from egg-laying in May to chick-fledging in July. I hypothesized that there would be distinct shifts in trip duration and frequency following egg hatching, compared to egg incubation. Moreover, I investigated the possible development of a Storer Ashmole's Halo around the breeding colony; this would likely be evident due to an increase in trip duration as the season progressed and fish stocks near the colony progressively depleted. I found a significant increase in trip frequency following egg hatching. However, total time spent away from the nest did not appear to change; individual trips were, therefore, shorter once the chicks had hatched. The quantity of fish delivered to the chick fluctuated but did not show a clear correlation with chick age, or seasonal effects. Furthermore, the size of the fish delivered to the nest remained relatively stable throughout the breeding season. The results indicate that a Storer Ashmole's Halo most likely does not develop around the Stora Karlsö breeding colony; however, more research surrounding the topic is ultimately needed. The data that I collected allows for the investigation of potential variations in feeding rates leading up to chick fledging.

*Keywords:* Common Murre, Stora Karlsö, trip duration, trip frequency, central-place foragers, feeding rate, time-budget.

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# 1. Introduction

Decades of studies have demonstrated how seabirds can function as prominent indicators of environmental change and thus represent the health statuses of marine ecosystems (Zador & Piatt, 1999; Berglund, 2016). This is in part because of their sensitivity to changes in food density and distribution, primarily owing to their adaptations to flight (with the exception of a few bird species e.g., penguins), as well as that they require air to breathe and are terrestrially bound central place foragers during breeding.

The Marginal Value Theorem (Charnov, 1976) is an optimal foraging theory that describes how an animal's time and energy budget affects the optimal amount of food it should gather. For breeding birds provisioning their young, the load of food items collected or delivered should increase as transit time increases to compensate for the additional time and energy spent. Interestingly, some seabird species, such as the common guillemot, are single-prey loaders, delivering only one food item at a time to their chicks following a trip to the sea (Bradstreet & Brown, 1985). For single-prey loading seabirds, the typical strategy that parents often apply to increase the value of their load is to either bring larger fish to their chicks or a higher quality food source, such as a fish species with higher energy content. According to the MVT, there is an optimal relationship between distance and the size of the load to maximize rewards. In circumstances where a load of food items cannot be increased, any extra distance travelled is suboptimal due to it not resulting in any additional rewards. One such situation where animals will be faced with diminishing returns is when a Storer Ashmole's Halo (Ashmole, 1963; Gaston *et al.*, 2007; Elliott *et al.*, 2009) occurs. This theory describes how food depletion may arise in an area surrounding large stationary or centrally bound animal colonies (e.g., a colony of breeding seabirds) as a result of the extensive food requirements of the population (Ashmole, 1963; Gaston *et al.*, 2007). Fig. 1 provides a simplified illustration of two contrasting scenarios, one where a Storer Ashmole's Halo is present and another where one is not. The development of a Storer Ashmole's Halo may force provisioning parents to travel increasingly large distances to supply their chick with prey items of sufficient quality at a high enough frequency to fulfill the nutritional and energetic demands of a growing chick (Hentati-Sundberg *et al.*, 2021). However, a Storer Ashmole's halo should only occur if the food source is

insufficient compared to the predating population or if the food source fails continuously to replenish itself, for instance, through reproduction or migration.



*Figure 1. Plentiful fish stocks versus Storer Ashmole's Halo.*

During the summertime, common guillemots breed on high cliffs in densely packed colonies (Hentati-Sundberg *et al.*, 2018; Elliott *et al.*, 2009). Common guillemots are highly skilled divers that often forage at great depths, up to approximately 200 meters (Piatt & Nettleship, 1985). As for all air-breathing animals, when diving underwater for prey, the surface of the water becomes a central place that the foraging revolves around (Walton *et al.*, 1998; Carlsen *et al.*, 2021). Throughout the breeding season, an additional central place is added, which is the breeding colony; this signifies that, in theory, two levels of Ashmole's halo could materialize (Walton *et al.*, 1998), one surrounding the colony and another in the distance from the surface.

The vast majority of a common guillemot's diet consists of fish, specifically clupeids and sticklebacks. "Clupeid" is the collective name for a family of fish species; well-known members of this group include species such as European sprat *Sprattus sprattus* which are the guillemot's primary food source (Österblom & Olsson, 2002) and Atlantic herring *Clupea harengus*. A close link between sprat condition and the average weight of common guillemot chicks was observed in previous research (Österblom *et al.*, 2001). Elevated sprat populations caused by a reduction in cod populations notably led to reduced nutritional value in individual sprat. When sprat nutritional value decreased, the average weight of common guillemot chicks also decreased. Sticklebacks, or Gasterosteidae refer to another

family of small fish that lack scales and have characteristic spikes located on their dorsal fins. Fish from this family include the three-spined stickleback *Gasterosteus aculeatus* and the ninespine stickleback *Pungitius pungitius*.

Common guillemots have low fecundity, with just one egg being laid annually (Reiertsen *et al.*, 2012), except in situations where an egg is lost early in the breeding season, in which case the female may lay a replacement. During breeding, the male and the female alternate between staying at the nest to incubate the egg/provide care for the chick and leaving the nest to hunt for prey (Cameron-MacMillan *et al.*, 2006). Common guillemots routinely fly multiple kilometers (Hentati-Sundberg *et al.*, 2018) several times daily to forage, with a potential change in both trip distance and duration occurring once the chick has hatched and needs to be fed prey (Kadin *et al.*, 2015). Typically, eggs are incubated for around a month, and once the chick is approximately 20–24 days old, it will fledge (Ainley *et al.*, 2021).

## 1.2 Aims and Objectives

This study aims to determine the temporal change in trip duration for five common guillemot pairs residing at Tom's Ledge on the island of Stora Karlsö. The time budget of the selected pairs will be examined following the MVT based on foraging duration. Furthermore, chick provisioning will be described over a season to explore potential signs of a developing Storer Ashmole's Halo.

The first objective is to determine if a distinct shift in trip duration and frequency occurs succeeding egg hatching, compared to incubation. A change in the duration and frequency of trips could indicate a shift in foraging strategy, where shorter trips may be due to the birds foraging closer to the colony. If birds primarily forage near a densely populated breeding colony, it is highly plausible that a Storer Ashmole's Halo will occur. In the presence of a Storer Ashmole's Halo, one could hypothesize that parents will struggle to meet the needs of their chick; this could be visible in several ways, including fish size not corresponding with the MVT and thus not increasing with increased trip duration. If parents cannot source fish of a specific size or quality, then trip frequency must instead be increased to supply more fish of a lower value to meet their chick's needs. Consequently, more total time spent away from the nest site should result in an increased total amount of food being delivered to chicks if a Storer Ashmole's Halo is not present. In addition, when approaching the median egg hatching date of the population, there might be further changes in the duration of foraging trips due to increased competition from conspecific parents. Alternatively, if a distinct shift in total foraging time cannot be detected, this would suggest that the cost of raising a chick is perhaps comparable to that of incubating

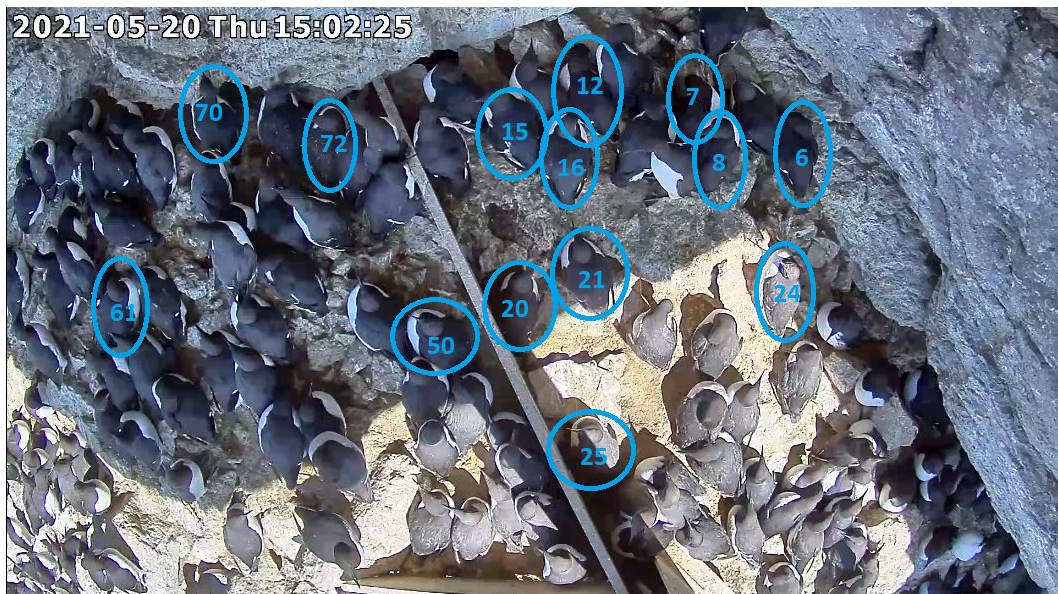


an egg. The next goal is to examine whether changes occur in connection to the chick's growth cycle or throughout the season. If differences in trip patterns are observed in relation to the chick growth cycle, this would indicate that parents adjust provisioning according to the age-specific needs of their chick. If seasonal changes are observed, shifts in prey size could be responsible for parents changing the frequency of trips or, more intriguingly, the development of a Storer Ashmole's Halo around the breeding colony. Alternatively, if no changes associated with the chick growth cycle are observed, this would imply that the chick's needs do not surpass beyond what parents already provide. Finally, if seasonal changes are not observed, this would indicate that a shortage of the prey sought in the preferred size does not occur.

To address the goals that were set, trip duration and frequency will be examined to determine if distinct changes are observed after egg hatching or if trip frequency/duration varies in accordance with chick age or with seasonal progression. Secondly, fish size will be analyzed in regard to chick age and seasonal progression. The hypotheses for this study are as follows: (1) There will be a significant decrease in trip duration after egg hatching due to the chick requiring frequent feedings; (2) There will be a significant increase in trip frequency following egg hatching in order to provide the chick with an adequate amount of provisions; (3) Trip frequency is related to the age of the chick, with older chicks requiring more food, resulting in more frequent trips; and (4) Trip duration will increase towards the end of the breeding season, as fish stocks in the vicinity of the breeding colony are gradually depleted due to the development of a Storer Ashmole's Halo.

## 2. Materials and Methods

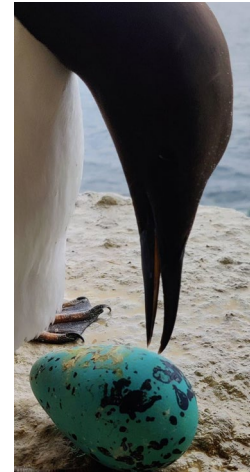
This study utilized pre-recorded video footage from 2021 of five Common Guillemot *Uria aalge* pairs living at Tom's Ledge on the Swedish island of Stora Karlsö, provided by The Baltic Seabird Project. The footage was recorded continuously (24 hours a day) from the 27th of April 2021 to the 18th of July 2021. However, only footage from the 6th of May (when the first egg was laid) to the 9th of July 2021 (when the last chick fledged) was closely examined and used to collect data for this study. All events were registered to a specific individual in a breeding pair nesting on the ledge (Fig. 2). Pairs 6, 8, 16, 20, and 21 were selected to be the focus of this study due to the high visibility of their nest sites on the video footage.



*Figure 2. Breeding pairs with nest identity, as seen on the monitor.*

## 2.1 Study Species: The Common Guillemot

The Common Guillemot *Uria aalge* (Am. Eng.: Common Murre) is a socially monogamous seabird species belonging to the auk family (Cameron-MacMillan et al., 2006). They are wing-propelled divers that have a circumpolar distribution in the Arctic. In their breeding plumage, guillemots are dark brown, with white feathers on their underside. Both sexes have the same external appearance, therefore gender cannot be visually determined. The common guillemot's bill is dark, long, and slender (Fig. 3) which easily distinguishes it from its relative, the razorbill *Alca torda*, which is also highly prevalent at Stora Karlsö. Eggs are pointed and speckled and vary in color from white to vivid turquoise (Fig. 3). Common guillemots typically weigh around a kilogram and usually return to the exact same nesting site each year to breed with their mate (Harris *et al.*, 1996). They are not particularly agile during flight, so travel that requires flying across great distances may therefore be problematic. Globally, common guillemot populations are on the decline, whereas in the Baltic Sea, populations are currently rising (Baltic Seabird Project, n.d.).



**Figure 3.**  
*Common Guillemot with its egg.*

## 2.2 Study Site: Stora Karlsö

Stora Karlsö (57°17'1N, 17°58'2E) is a 250-hectare island located six kilometers off the coast of Sweden's largest island, Gotland (Baltic Seabird Project, n.d.). Stora Karlsö is home to the Baltic's largest population of common guillemots, with a breeding population estimated at 27,500 breeding pairs in 2021 (J. Hentati-Sundberg, pers. comm.). The large seabird population at Stora Karlsö and highly accessible nesting sites have provided ample opportunity for research, beyond what was previously surmountable. The "Stora Karlsö Auk Lab" is an artificial nesting site constructed in 2008 by the Baltic Seabird Project to study breeding auks at Stora Karlsö (Hentati-Sundberg *et al.*, 2012). It is located directly above Tom's ledge (a natural breeding ledge), where all the birds in the study were nesting. This project is part of a more extensive study where breeding guillemots were caught by researchers and instrumented with telemetric loggers on their legs, which could also be used for identification. Pairs were primarily selected based on availability, with nest sites easily accessible from the hatch chosen, as well as bravery (individuals that were less reluctant to being captured).

## 2.3 Data Collection

The downloaded video footage was viewed at an accelerated rate using VLC Media Player for every second of each day in the breeding cycle of all observed pairs. Of the pairs selected for the extended study, five pairs were chosen for this study based on the visibility of their nest location. Initially, "Egglaying" events were recorded for all pairs, then one pair at a time was followed until the chick fledged. Individuals in a pair were defined as either individual one ("ID1") or individual two ("ID2"), with the egg-layer (the female) designated "ID1" and the mate (presumably the male) designated "ID2." Following periods when video footage was unavailable, or both parents were absent from the nest, and identification became uncertain/impossible, individuals were classified as either "IDX1" or "IDX2," where best estimates of ID were made. Physical characteristics and the pair's typical daily routine (when applicable) were taken into consideration to make assumptions regarding the identity of the individuals; for example, in some pairs, one individual was more likely to take overnight trips than the other. The nest's content was noted as "e" (egg present), "c" (chick present), or "0" (nest empty). After the first registered event, additional "events" were recorded; these were comprised of "departure" (when a parent left the nest), "arrival" (when a parent returned to the nest), "Overtake" (when egg incubation/chick roosting was switched from one parent to the other), and "Catch" (occasions when the bird was caught from their nest for data sampling and collection). Trips per day were noted and defined as the number of times a bird left its nest per day. Additionally, whether fish were returned to the nest (at "arrival") was noted as "Fish" no=0, yes=1. Furthermore, fish type ("FishType") was recorded as either "clupeid", "stickleback", "other", or "NA". "Fishsize" was determined in relation to the beak length of the bird carrying the fish, as either "1\*Beak length", "1.5\*Beak length", or "2\*Beak Length" (see Fig. 4). Fish that were between categories in terms of size were categorized as belonging to the category to which they were closest. For example, "1.8\*Beak length" was categorized as "2\*Beak length". Other information that was deemed significant was also recorded, such as when both parents were absent or when a fish was dropped and never ingested by either the chick or the parent.



**Figure 4.** Examples of fish size: 1\*Beak Length, 1.5\*Beak Length, 2\* Beak Length (in order from left to right).

## 2.4 Data Handling

All data treatment was performed in Excel, where averages regarding trip duration, frequency, number of fish delivered, and fish size were calculated, and graphs and tables were produced. Trip duration was calculated from the moment an individual in a pair left the nest until the moment they returned. Occasionally, individuals in a pair left the nest but were visible on the camera in other areas of the ledge. For such instances, the “trip” was disregarded, and the time the individual had been absent from the nest was not included in the production of figures. Additionally, in cases where there was missing or unfocused video footage and the number or duration of trips was uncertain, the data from that day was also disregarded. The breeding cycle was defined as beginning with egg-laying and ending once the chick fledged. Day “1” was defined as the date at which the egg was laid, and trips were counted from the moment of egg-laying onwards up until the moment the chick had fledged. Trips that overlapped onto the following day, as was typical of overnight trips, were categorized as belonging to the day that the individual made their departure from the nest. There were a select few occasions where a fish was brought back to the nest prior to egg hatching and the fish was ultimately eaten by the partner that had brought the fish. These rare occasions were not included in the figures that were produced. The average daily fish size was calculated as the average size of all the delivered fish each day. In cases where fish size could not be determined, average fish size was simply calculated based on the fish where the size was discernible.

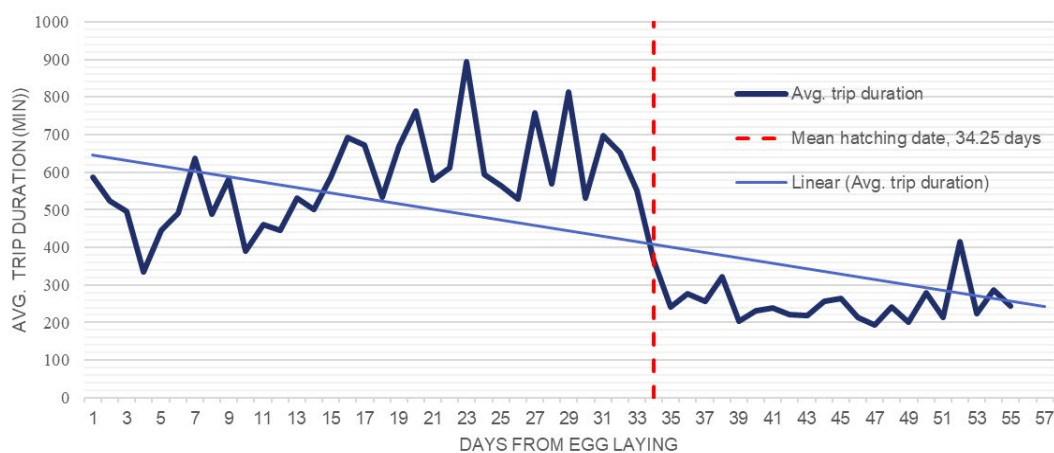
### 3. Results

Table 1. gives a summary of key observations for each of the nests. Egg incubation duration varied by +/- 2 days, fledgling age varied by +/- 3 days, breeding cycle varied by +/- 4 days and the total number of fish delivered to the chick varied by +/- 28 fish. On average chicks hatched 34.25 days after egg-laying began and the breeding cycle lasted 55 days.

**Table 1.** Observations regarding Common Guillemot pairs at Tom’s ledge (2021).

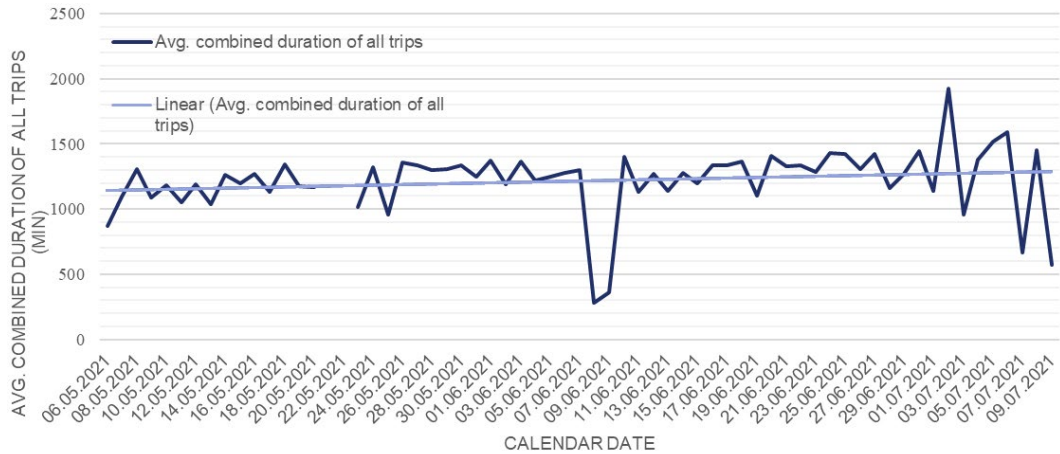
Nest ID	Egg Incubation Duration (days)	Fledgling Age (days)	Breeding Cycle Duration (days)	Total Number of Fish Delivered to Chick
6	35	20	55	120
8	35	20	55	96
16	34	23	57	106
20	33	21	54	120
21	33	20	53	92

#### 3.1 Trip Duration and Frequency



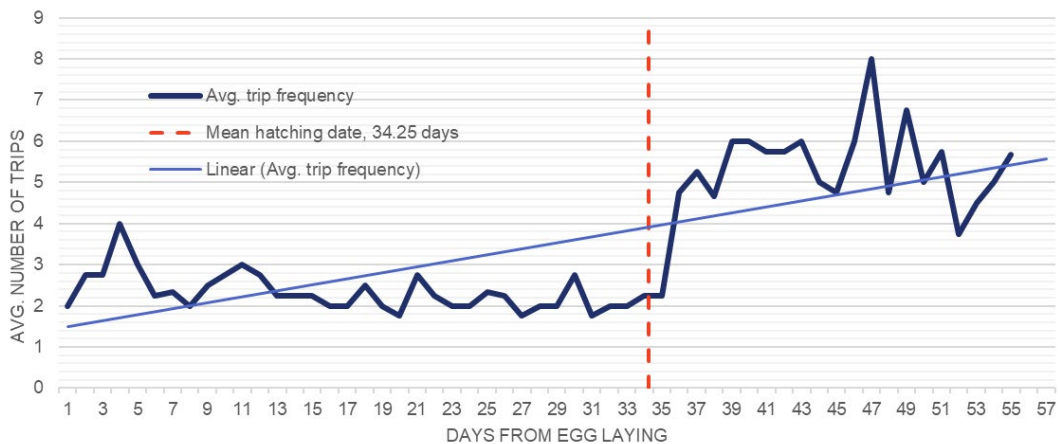
**Figure 5.** The effects of breeding cycle on trip duration. Average trip duration was calculated based on all observed pairs and plotted against days from egg laying to reflect the average duration of individual trips throughout the breeding cycle. In Appendix 1, Fig. A1 the relationship between trip duration and calendar date is plotted to demonstrate the effect of seasonal progression.

A clear decrease in trip duration with a direct inflection point at day 34, corresponding to mean chick hatching was found (Fig. 5). Observation suggests that the plotted data more precisely follows a reverse sigmoid curve, as opposed to a linear regression line. However, the total number of minutes that the individuals in a pair were absent from a nest each day remained relatively stable throughout the entirety of the breeding season (Fig. 6).



**Figure 6.** The effects of seasonal progression on combined daily trip duration. Combined trip duration was calculated based on all observed pairs and plotted against calendar date to reflect the average amount of time that either individual in a pair was away from the nest. Gaps in the graph reflect days with missing, or incomplete data.

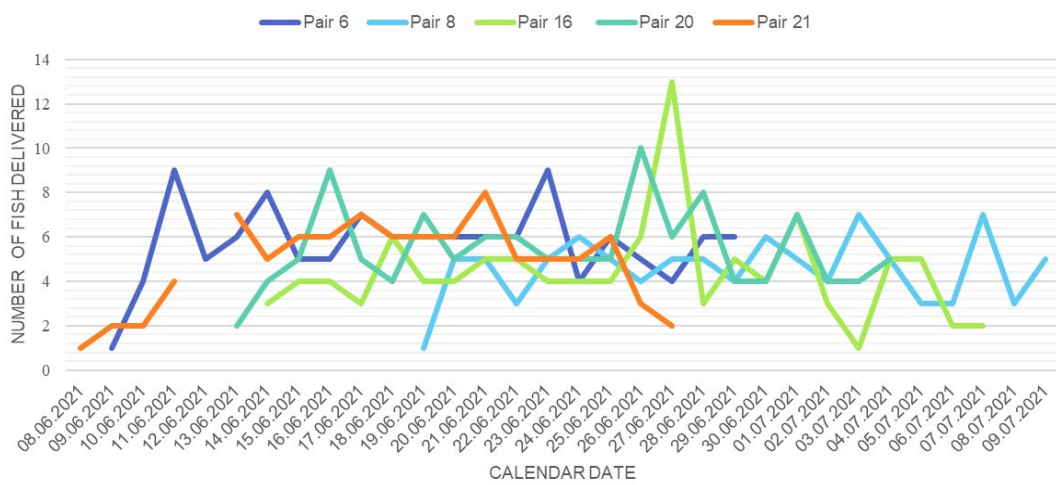
A substantial increase in trip frequency with a direct inflection point at day 34, corresponding to mean chick hatching was found (Fig. 7). The plotted data appears to follow a sigmoid curve. Trip frequency did not appear to be significantly impacted by seasonal progression (see Appendix 1, Fig. A2) and was instead more closely linked to the breeding cycle of each pair, as is demonstrated in Fig. 7.



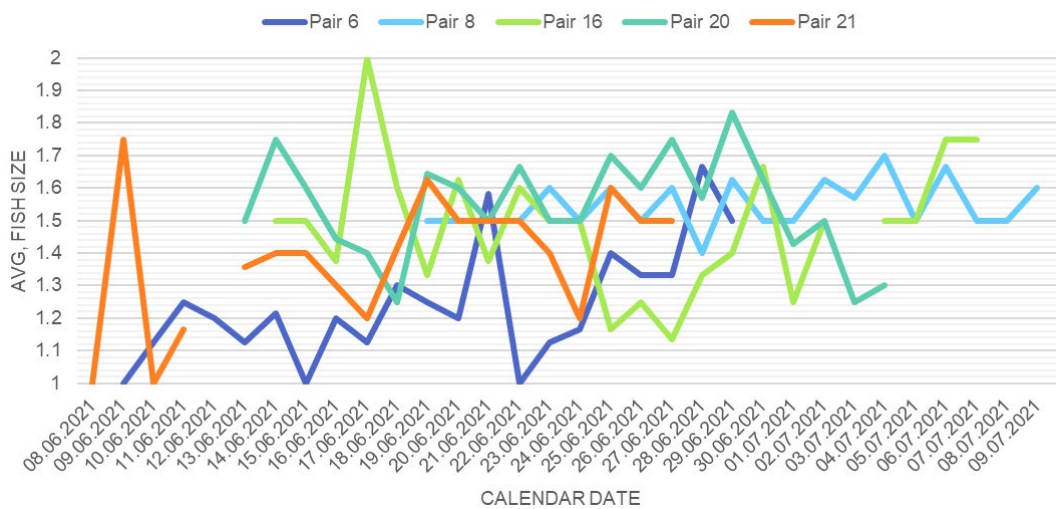
**Figure 7.** The effects of breeding cycle on trip frequency. Trip frequency was calculated as the average number of trips that all observed pairs made each day in the breeding cycle.

### 3.2 Quantity and Size of Delivered Fish

In Fig. 8, it can be seen that the number of fish delivered to the nest fluctuated prior to the chick fledging and did not appear to be strongly connected to the calendar date, or the point in the individual pair's breeding cycle. On average, a very slight upward trend was observed in regard to fish size as the season progressed; however, this was not true for all pairs. Spikes and troughs in fish delivery rates were observed for the various pairs at different points in both the breeding cycle and calendar date (Fig. 8).



**Figure 8.** The effects of seasonal progression on fish delivery rate. Fish delivery rate was calculated as the number of fish delivered daily to each nest. Gaps in the graph reflect days with missing or incomplete data.



**Figure 9.** The effects of seasonal progression on fish size. Average fish size was calculated as the mean fish length for all fish delivered to each nest per day, Gaps in the graph reflect days with missing or incomplete data.



Fish size did, in some circumstances appear to be tied to calendar date and breeding cycle, demonstrating a very slight upward trend as the season progressed and chicks got older, however a strong correlation was not found (Fig. 9).

## 4. Discussion

There was a distinct shift in trip duration and frequency following egg hatching compared to egg incubation. After chicks hatched, the combined duration of all trips (each day) remained approximately the same as during egg incubation. Thus, parents were spending more or less the same amount of time together at the nest site each day, as virtually the only time that they weren't together was when one of them was away on a foraging trip. Trips were, however, significantly more frequent and each individual trip had a shorter duration. As was discussed earlier, a decrease in average trip duration suggests that birds must have been foraging closer to the breeding colony. Previous research indicates that 2.7-9.6% of each foraging trip for guillemots is spent flying and that their flight speed is roughly 69km/hr (Pennycuik, 1987; Österblom & Olsson, 2002). Using this information, it was calculated that the birds in this study most likely traveled 6.21 - 22.08km each trip to forage during chick rearing (given that the average trip duration was approximately 200 minutes). On rare occasions, trips were incredibly brief and lasted less than 5 minutes, yet still resulted in a fish being brought back to the chick. During such events, parents must have been foraging extremely near the nest site and probably spent a much larger percentage than 9.6% in transit to and from the nest. In fact, the maximum possible distance that they could have traveled would have been <3km (not taking into consideration diving time). No noteworthy changes in trip duration or frequency were observed when approaching the median egg hatching date of the colony (20/06/2021, based upon colony-specific averages collected from the Auk Lab).

Guillemots act according to the MVT (Walton *et al.*, 1998) and adjust their trips to fulfill their chick's needs (Kadin *et al.*, 2015). Flying is a highly costly activity for guillemots (Kadin *et al.*, 2015). The duration and frequency of foraging trips, therefore, have a significant impact on a bird's daily energy expenditure. Shorter flying distances likely give room for higher trip frequency. However, many brief trips are presumably more costly than fewer longer ones because the most energy-intensive components of flight are take-off and landing (Nudds & Bryant, 2000). Assuming the total distance traveled each day remained the same as during egg incubation, parents were assumably increasing their own daily energy expenditure as a consequence of an increased number of take-offs and landings during chick

rearing. Nevertheless, being able to forage near the breeding colony is most likely ideal due to reduced risks. For instance, when foraging is unsuccessful, birds incur a greater loss when they have traveled a further distance away from the colony, versus a shorter one. In Thick-billed Murres *Uria lomvia* (a close relative of the guillemot) energy expenditure during flight and diving was compared, and it was established that diving was significantly less costly compared to flying (Elliot *et al.*, 2013). When a smaller percentage of each foraging trip is spent in transit, there is more opportunity for time to be spent actively foraging and diving for prey.

As I predicted earlier, parents radically altered their trip patterns to meet their chick's needs. Kadin *et al.* (2015) found that guillemot parents at Stora Karlsö made efforts to adjust both feeding rate and prey size to compensate for prey of inferior quality. However, they discovered that parents were, for the most part, not successful in regulating prey size and were instead more successful at adjusting feeding rate. My results were quite similar, in that I found that fish delivery rate and size did not appear to have strong ties to the chick's growth cycle. This could either indicate that there is little correlation between the chick's growth cycle and its nutritional demands, or the more logical answer that parents had little success in terms of their ability to regulate prey-size according to their chick's age-specific needs. I did however on average observe a very slight upward trend in both fish-size and feeding rate with increasing chick age and seasonal progression. Yet, I did not find that parents were markedly better at adjusting feeding rate, compared to fish size. Slight differences in my results, compared to Kadin *et al.* (2015) are plausibly a result of vastly contrasting methodologies. For instance, Kadin observed more pairs (a median of 17) than I did and observed them in-person using binoculars during select periods over the course of several years, whereas I studied fewer pairs using video footage and followed them throughout their entire breeding cycle.

There are a multitude of factors that could be behind parents being unable to successfully regulate prey size. For example, during dives, birds may struggle to distinguish between fish of differing sizes. Little is currently understood about guillemot vision and how it influences their hunting behavior (Regular *et al.*, 2011). Perhaps their vision doesn't enable them to see well enough to accurately assess fish size deep below the surface where little light penetrates. Regular *et al.* (2011) found that guillemots sometimes forage during periods of starlight and suggested they might be relying on randomly encountering prey at a close distance and, or utilizing non-visual cues to capture prey successfully. If this theory is correct, it would be highly plausible that guillemots would have little opportunity to regulate prey size when hunting under such conditions. It could also be the case that the majority of fish in the areas that are most advantageous for guillemots to hunt are of a relatively similar size and there simply isn't much variation to choose

from. Decades of research has proved that development is often not linear (Roberts, 1986; Grimm *et al.*, 2011). While the growth patterns of many wild bird species have not been studied closely, domestic birds such as Japanese Quail *Coturnix japonica* have been documented to follow non-linear growth curves (Akbas & Oğuz, 1998). Logically, this would also be true for guillemots, which suggests that chicks must be at some points of development getting an excessive quantity of food, as prey size and quantity remains largely consistent throughout their entire time spent at the nest site. Perhaps the chick's non-linear development adds further difficulty for parents trying to regulate prey size and feeding rate successfully.

If prey depletion were occurring, parents would be expected to be under increased pressure and subsequently decrease the time they spent with their partner at the nest site (Berglund, 2016). However, even if a decrease in total time spent at the nest were observed, this could have been due to other factors. Extreme heat, for instance, is uncomfortable or even dangerous for many seabird species, and on such days, birds can be forced to abandon the nesting site temporarily to cool off (Hand *et al.*, 1981). Additionally, if a Storer Ashmole's Halo were developing, it would have been expected that trip duration increased as the season progressed due to prey depletion in the area surrounding the breeding colony and parents being forced to travel greater distances to forage. Furthermore, it would be logical that a decrease in the average fish size may be observed due to parents choosing less valuable prey items in the absence of the optimal prey size; evidently, this was not the case based on the findings of this study. Conversely, the findings indicate that birds do not struggle to provision their chicks later in the breeding season because average trip duration decreases, and fish size does not decrease. Once chicks had hatched, there were very few instances where parents returned to the nest without a fish.

## 4.1 Possible Limitations

Only five breeding pairs were observed, all living in close proximity. It seems unlikely that the close proximity of the nests in this study would have affected the foraging behavior of the parents. However, it could be possible that the amount of time spent at the nest site is affected by its location. For instance, the nests in this study were all in a relatively safe location, with a fair amount of shelter from the elements and a low risk of predation. In a less optimal location, with greater predation risk and less protection from extreme weather, it would be plausible that parents might spend less time at the nest. Also, as was mentioned previously, the pairs in this study were partially selected due to their temperament. It is possible that selecting birds with a tendency towards a specific temperament (in this case,

bravery) might have had some impact on the findings. However, for this study it would have been significantly more difficult, if not impossible, to select pairs on an entirely random basis. Moreover, I do not believe that catching individuals who were incredibly frightened or nervous, would have been an ethically responsible decision. Several other limitations must be noted regarding the findings. Firstly, could parents have decreased their own food intake to provide their chick with a sufficient amount of food? If this were the case, a Storer Ashmole's Halo could develop without a change being necessarily visible in trip duration or the number and size of fish being brought back to the nest. To be able to rule this out, it would be beneficial to continuously record the weight of parents to see how their weight fluctuates throughout the breeding season. In the Stora Karlsö Auk Lab, for instance, Baltic Seabird Project researchers weigh birds when they are caught and recently introduced an outdoor scale that records the weight of birds who stand on it. Electronic scales, which automatically record the weight of birds, have also been utilized in other locations and have provided data that has served as the foundation for a variety of studies (Wendeln & Becker, 1996; Vertigan *et al.*, 2012). Developments such as these allow for a more comprehensive understanding of prey availability and seabird foraging behavior. It is, however, unlikely that parents would sacrifice their own food intake to a dangerously low level. For instance, in the presence of threats (actual or perceived), parents often abandon their egg/chick to seek safety; this was observed both in person at the auk lab as well as on the video footage. A parent will likely survive until the next season and be given another opportunity to reproduce, whereas an egg/chick has a much smaller chance of surviving long enough to begin reproducing (Olsson *et al.*, 2000). In order for a parent to maximize their own fitness, it is therefore logical that they exercise self-preservatory behavior and place greater value on their own survival than that of their offspring (Berglund, 2016).

In the video footage that was examined, there were several instances in which the footage was either missing or not usable due to it being out of focus. These instances have been compiled in a table (see Appendix 1, Table. A1). Efforts were made to establish accurate identities for the individuals within a pair in such instances or when both adults were away from the nest. However, there were several occasions for many of the couples where the identities could have potentially swapped. For this reason, the individuals within a pair were viewed as a team, and sex-based differences were impossible to evaluate. Fish species for fish brought back to the nest was not possible to determine for the vast majority of events, primarily due to video quality, but also the angle of the nests in many cases. Due to this, differences in the fish species being brought back to the nest were not evaluated. If it were possible to determine fish species, this would have been beneficial due to there being variations in the nutritional value of different

species; for example, a smaller fish of one species could have a higher caloric value than a larger fish of another species. In most cases, it was possible to establish fish size with a relatively high level of accuracy. In cases where it was not possible to accurately determine the fish size, the field was left blank. Visibility due to fish size is a bias that potentially affected the results. It was more difficult to assess the size of smaller fish accurately. It is therefore highly plausible that cases where fish size was not determined consisted primarily of fish that were one beak length or less. Likewise, the angle at which the parent was facing towards the camera when fish size was determined could also have impacted the results. When the fish size was determined from an aerial view, fish often appeared larger because it was more challenging to establish the bird's beak length. This contrasts occasions where fish size was determined from a side view, where it was much clearer where the beak began. Due to this, fish size was determined from a side view whenever possible; however, in many instances, the fish could only be viewed from an aerial view in the video footage. Additionally, there was a great deal of variation between the pairs and even the individuals within a pair when it came to feeding their chicks. Some individuals held the fish in their beaks for quite some time before feeding the chick, thus making it more likely that fish size could be determined. Others fed their chick extremely quickly, increasing the likelihood that fish size could not be determined.

## 4.2 Conclusions and Future Recommendations

Parents spent approximately the same amount of time away from the nest site throughout the entire breeding season. Average trip duration dramatically decreased once chicks hatched, and trip frequency drastically increased. Fish size and feeding rate did not appear to change significantly as chicks got older, or as the season progressed, but a very slight increase in both was noted. The results imply that a Storer Ashmole's Halo does not form around the breeding colony at Stora Karlsö. Parental care was likely more demanding when caring for a chick, compared to an egg, at least regarding foraging costs due to increased trip frequency. I anticipate that the findings of this study will most likely apply to the majority of established guillemot breeding pairs at the Stora Karlsö colony. In order to further increase the reliability of the results, it is recommended that more breeding pairs are analyzed, and more in-depth research is conducted. For example, higher quality cameras, or ones that are located closer to the nest sites, could enable the collection of valuable data regarding fish species and more precise measurements of their size.

Due to time constraints, fish size was not analyzed regarding individual trip durations. However, the compiled dataset allows for this to be investigated. Another

exciting area of data exploration that researchers can delve into includes comparing feeding rate to fledgling age to determine whether increased provisions lead to chicks fledging at an earlier date. Technological advancements, especially in AI technology, will in all likelihood be at the forefront of research in the future. With technological innovations facilitating extraordinarily rapid and efficient data collection and handling, many more seabirds and other animal species can be studied in intricate detail on an unimaginably large scale. As was stated previously, although Baltic guillemot populations are on the rise, their populations are declining in many areas throughout the world (Baltic Seabird Project, n.d.). Seabirds are particularly vulnerable to climate change, water pollution, and commercial fishing practices (Thompson & Hamer, 2000). In recent months, avian influenza has afflicted several seabird species, including the common guillemot, throughout Europe (Adlhoch *et al.*, 2022). While it is yet to be fully understood what impact the current avian influenza outbreak will have on Baltic guillemot colonies, increased knowledge about the species is of the utmost importance in ensuring that populations remain robust.

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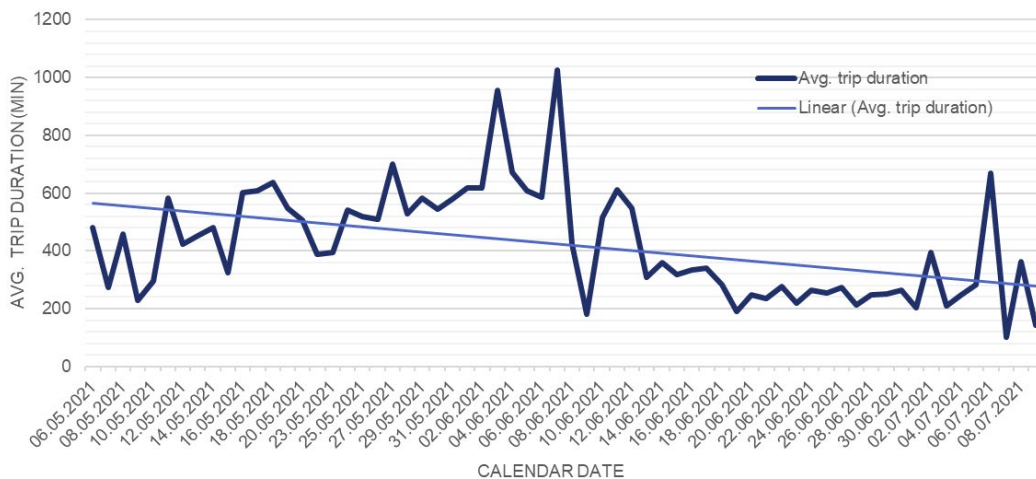
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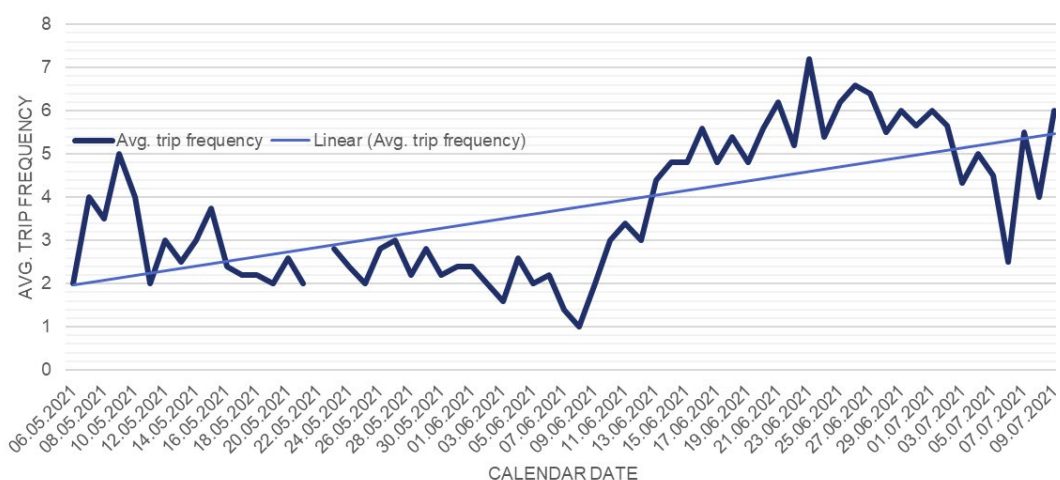
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## Appendix 1



**Figure A1.** The effects of seasonal progression on trip duration. Average trip duration was calculated based on all observed pairs and plotted against calendar date to reflect the average duration of individual trips throughout the breeding season.



**Figure A2.** The effects of seasonal progression on trip frequency. Trip frequency was calculated as the average number of trips that all observed pairs made each day in the breeding cycle. Gaps in the graph indicate days with missing or incomplete data.

*Table A1. Missing video-footage.*

<b>Date</b>	<b>Time</b>	<b>Explanation</b>
21.05.2021	18:03:30-15:00 (of next day)	Video footage unavailable, or blurry
22.05.2021	15:23:57-21:01:20	Video footage unavailable, or blurry
07.06.2021	03:19:42-05:35:27	Video footage unavailable
08.06.2021	10:47:13-12:40:57 (of next day)	Blurry video footage
12.06.2021	21:43:52-22:05:29	Video footage unavailable
13.06.2021	00:21:14-1:05:32	Video footage unavailable
18.06.2021	13:15:12-14:00:18	Video footage unavailable
19.06.2021	10:06:29-11:00:31	Video footage unavailable

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