Faculty of Biosciences, Fisheries and Economics

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Differences in chick feeding frequency between parental sex and morph combination in the Common guillemot *Uria aalge*

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Cover photo by Malin Kjellstadli Johansen
Bridled (back) and unbridled (front) common guillemot *Uria aalge*
with a capelin *Mallotus villosus,* Hornøya

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Abstract

Provisioning food for the offspring stands as a major element of parental investment, yet the distribution between the parents is not necessarily equal. The Common guillemot (*Uria aalge*) is a monomorphic seabird who exhibits two colour morphs: a bridled and an unbridled. The aim of this study was to investigate which effect parental sex and morph had on the daily chick feeding frequency and during the chick-rearing period. To assess this, two fixed time-lapse cameras were used to document the chick feeding frequency for 27 Common guillemot families for 24 hours over a period of four weeks. The families were divided into two morph combination categories: mixed morph (n = 11) and same morph (n = 16). The results showed evidence of a diurnal chick feeding frequency among females and a nocturnal chick feeding among males. We also reported a strong trend of increased male contribution in chick feeding frequency after chicks turned 19 days old. There was no evidence for any daily differences in feeding frequency between the two morph combinations. However, there was statistical support for a higher feeding frequency among mixed morph pairs after the chicks turned 10 days of age. Our findings may indicate that there are some underlying mechanisms behind parental investment through chick provisioning for both parental sex and morph combination. In addition, future studies should include additional variables (e.g. parental stress-level, adult and chick diet, metrological data) in order to distinguish any possible underlying mechanisms. We suggest time-lapse cameras with short intervals to be a good method for long-term observational studies in a non-invasive way and it might be a good tool to highlight critical associations between the ongoing climate change, change in food resources, management and future breeding success of this species.

Keywords: chick feeding frequency, colour dimorphism, common guillemot, Hornøya, parental investment, seabirds, time-lapse camera, *Uria aalge*.

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1 Introduction

The main mating system among seabirds is social monogamy (e.g. Wiggins and Morris 1987). Most seabirds have a strong nest site fidelity and it can be challenging to protect this nest site and the chick in combination with foraging in a highly dynamic marine environment. Consequently, almost all seabird species practises a biparental care strategy, meaning that both parents contribute in chick-rearing (Elliot *et al.* 2010). Therefore, combining biparental care and social monogamy makes it possible for one parent to leave the nest site for foraging, while the other one remains defending the nest or the chick. However, even if social monogamous seabirds have biparental care, the parental investment and contribution between sexes are not necessarily equal (Paredes *et al.* 2006). Parental investment is any sort of investment (by the cost of the parent's ability to allocate their own resources) in an individual chick, clutch or brood, that increases the offspring's chance of survival (Trivers 1972, Wittenberger 1981). This definition includes everything from metabolic investment (e.g. primary sex cells), brooding, chick feeding, rearing and nest defence (Breitwisch 1989, Royle *et al.* 2004). Of these, the provision of food for the offspring stands as a major element (Thaxter *et al.* 2009). The effect of sexual differences in body size was earlier presumed to be the cause of differential parental investment between the sexes (Weimerskirch *et al.* 2000). However, this is not the case in several studies of sexual size monomorphic seabirds (e.g. Wanless and Harris 1986, Gray and Hamer 2001, Paredes *et al.* 2006, Thaxter *et al.* 2009, Burke *et al.* 2015, Huffeldt and Merkel 2016).

The Common guillemot (*Uria aalge*) is an example of a seabird with no sexual dimorphism in size (Gaston and Jones 1998). Guillemots are among the most numerous seabird species in the Norther Hemisphere (Birkhead 1977), yet the knowledge of the differences in parental investment is scarce. Previous studies on both Common guillemot and Brünnich's guillemot (*Uria lomvia*), have shown that females contributed significantly more in chick feeding than males (Wanless and Harris 1986, Paredes *et al.* 2006, Thaxter *et al.* 2009). In addition, studies have found a daily difference in chick feeding frequency between the sexes for both Common and Brünnich's guillemot (Thaxter *et al.* 2009, Elliott *et al.* 2010, Linnebjerg *et al.* 2015, Huffeldt and Merkel 2016).

There are many suggestions for predicting such sexual differences. Trivers (1972) proposed that all females in a monogamous relationship have the highest parental investment rate, as an evolutionary result of the initial variation in gamete size. For guillemots, Thaxter *et al.* (2009) proposed that this difference in investment is related to males spending more time self-feeding prior to the paternal-only care during the post-departure period. Others have suggested the male to be more present at the nest site during the day, as potential predators are most active in this period (Birkhead 1977), and males have been documented more aggressive in both the Common guillemot (Wanless and Harris 1986) and the Brünnich's guillemot (Paredes *et al.* 2006). These findings suggest that there might be some difference in the underlying parental investment strategies between the sexes.

The Common guillemot is also a colour dimorphic seabird, with a bridled and an unbridled morph, the former with a white eye-ring and stripe behind the eyes (figure 1).

Figure 1: *The unbridled morph (left) and the bridled morph (right) of the Common guillemot. Photos by Malin K. Johansen*

The morph variants are genetically different, where the bridled gene is the recessive variant and the unbridled gene the dominant variant (Jefferies and Parslow 1976). The two morphs mate randomly, and the bridled morph is not expressed until the birds reach adulthood (Lyngbo-Kristensen 2013). No apparent differences in additional morphology or behaviour between the morphs have been found (Birkhead *et al.* 1980, Lyngbo-Kristensen 2013). However, the frequency of the bridled morph increases towards the north, with the highest frequency of 50% at Bjørnøya in the Northeast Atlantic (Birkhead and Lock 1980), and it was therefore theorised that the bridled morph might be more adapted to a colder environment (Birkhead 1984). Studies in the Barents Sea showed the bridled morph to have a negative relationship, in terms of survival rate, to winter sea-surface temperatures (SST) while the unbridled morph showed a positive relationship (Reiertsen *et al.* 2012). In addition, Lyngbo-Kristensen *et al.* (2014) documented that mixed morph pairs produced larger chicks (in size) compared to chicks from pairs with same morph. Therefore, it was suggested that the two morphs have different parental strategies and could potentially be compensating for each other under different environmental conditions (Lyngbo-Kristensen *et al.* 2014).

The ocean is a highly dynamic environment, where both oceanographical conditions and prey availability fluctuate. The Common guillemot, as most seabirds, depends on the sea for food and must allocate resources optimally in order to sustain both themselves and their chicks. Guillemots are central place foragers, meaning that the net energy gain must be higher somewhere else away from the breeding site (the central place) compared to the areas around the breeding site itself (Orians and Pearson 1979, Elliott *et al.* 2009, Bugge *et al.* 2011). The cost of parental investment will consequently be affected by the variation of the optimal foraging conditions. However, guillemots and other seabirds are known to compensate for these dynamic changes by switching to alternative prey species or by altering their search effort and foraging range (Elliott *et al.* 2010, Ponchon *et al.* 2014, Kadin *et al.* 2016). The Common guillemot is a single prey loader and the adults utilize their own high wing-load as a trade-off for exceptional diving capacity (Paredes *et al.* 2006) – by using their wings to pursue its prey underwater (Matthews 1983, Thaxter *et al.* 2010). Which prey species they bring back to the chick is a trade-off between fish size, energy content necessary for the chick and energy cost for the parent (Sonntag and Hüppop 2005, Bugge *et al.* 2011). Therefore, the chicks' diet is constrained in several ways, depending on the oscillations of the marine environment and the parents' capability to allocate optimal resources.

Nonetheless, the mechanisms behind the Common guillemots' parental investment and possible differential strategies between sex and colour dimorphism are still unclear. Here, we investigated the Common guillemot chick feeding frequency by using two fixed time-lapse cameras to document the daily chick feeding frequency over a period of four weeks. The aim of this study was to examine the following questions: (1) Are there differences between parental sex and the feeding frequency of the chick? (2) Are there differences in chick feeding frequency between mixed morph pairs consisting of both a bridled and an unbridled variant, compared to same morph pairs consisting of parents with the same morph? (3) Are there any daily differences or variations during the chick-rearing period, in feeding frequency of the chick within parental sex and morph combination?

2 Material and method

2.1 Study area

The study was conducted at Hornøya (70º 22' N, 31º 08' E), a 0.5 km^2 small island located in the southern Barents Sea. Approximately 100 000 seabirds of 11 different species are present at Hornøya during the breeding season. Of these, the Common guillemot constitutes approximately 30 000 of them (Reiertsen pers. comm.) and the population has been steadily increasing since the mid-1980s when there was a collapse in the population (Erikstad *et al.* 2013). This increase reflects Hornøya as an important breeding site for this species, which is probably related to its adjacency to the Barents Sea. The Barents Sea is a highly productive ocean, with large local variability, both due to its relatively shallow shelf, and its density-driven currents with both Atlantic and Arctic water inflow (Ådlandsvik and Loeng 1991). These currents gradually mix and create locally high nutrient-rich areas, giving the Barents Sea the ability to maintain a high primary and secondary production, thereby supporting a large number of fish species (Loeng 1991, Falk-Petersen *et al.* 2000). The physical conditions of the Barents Sea, combined with the advective movement of water masses, play an important role in the life history of many fish species. Numerous fish larvae and eggs are transported by water currents from the Norwegian coast and into the Barents Sea, making this area a hotspot for seabirds and important for the population fluctuations of guillemots breeding at Hornøya (Olsen *et al.* 2009, Dalpadado *et al.* 2012, Hjermann *et al.* 2010, Erikstad *et al.* 2013, Sandvik *et al.* 2016).

2.2 Study species

The Common guillemot is the largest of the extant auk species (Alcidae). It is a long-lived seabird with a low Arctic, boreal and circumpolar distribution (Gaston and Jones 1998). Like most true seabirds, guillemots have a deferred maturity, high adult survival and low reproductive output (one egg per year), making them a typical slow species (Bielby *et al.* 2007, Jeschke and Kokko 2009). At Hornøya, the frequency of the bridled morph is approximately 30% (Reiertsen *et al.* 2012). The guillemots do not build any proper nest site, instead they breed in dense colonies where they lay one single egg directly on the ground. In addition, they have high nest-site fidelity and are socially monogamous. However, partner break-ups and extra pair paternity may occur, although rarely (Moody *et al.* 2005).

There are no visual characteristics that can be used to distinguish the sexes (Birkhead and Nettleship 1985). The incubation period lasts for 30-35 days and the chick is cautiously cared for until nest departure around 3 weeks old, after nest departure it is accompanied by their father at sea (Gaston and Jones 1998).

In the North Atlantic, the overall number of Common guillemots have increased during the last decades (Barrett *et al.* 2006). In contrast, the Norwegian population has had a long decreasing period, going from 120 000 pairs in the 1960s to less than to 15 000 pairs by 2005, leaving only 5% of the original population (Brun 1969, Barrett *et al.* 2006, Erikstad *et al.* 2007). Causes for this decline have been widely discussed, but factors such as changes in the marine ecosystems (Erikstad *et al.* 2013) due to climate change, pressure from humans (e.g. bycatch from fisheries, habitat degradation and pollution), and predation from avian predators have been suggested (Steen *et al.* 2013). As a result, the Common guillemot was classified as critically endangered in the Norwegian Red List (Henriksen and Hilmo 2015). Despite the strongly depressed numbers from 2005, the Norwegian population has made a steady recovery, mainly as a result of high recruitment in certain breeding sites found around the Barents Sea (Fauchald *et al.* 2015).

At Hornøya mainly three fish species dominate the chick diet: capelin (*Mallotus villosus*), herring (*Clupea harengus*) and sandeel (*Ammodytes* sp.). However, chick growth in addition to adult diet and survival, also relates to the abundance of young cod (0-group, *Gadus morhua*), young haddock (1-group, *Melanogrammus aeglefinus*) and the coastal drift of fish larvae (Bugge *et al.* 2011, Erikstad *et al.* 2013, Myksvoll *et al.* 2013). Adult birds carry the fish back to the colony lengthwise in the bill (Barrett *et al.* 2007), leaving the bottom part of the fish visible for the observer, and can be identified by using binoculars or camera.

2.3 Fieldwork

2.3.1 Study design

The study was carried out between 16 June and 14 July 2018, wherein total 27 Common guillemot families were monitored during the breeding season. The pairs were chosen based on their location in a well-studied sub-colony located on the north-west part of Hornøya. The families were grouped in two different morph combinations: same morph pairs (n = 16) where both parents were the same morph (pure unbridled: n = 13, pure bridled: n = 3), and mixed morph pairs (n = 11) with a bridled and an unbridled parent.

As the chosen birds were a part of a larger demography study, the parents were captured two times during the breeding season (after hatching and 12 days after hatching) by using a noose-pole. In order to separate the chosen pairs from the rest of the colony, all parents were marked with green colour using a *Raidex stick*, each time captured. Adults caught for the first time were equipped with a stainless-steel ring with and a plastic ring on their foot, both with a unique code combination. The chicks were captured with a hook-ended pole two times (three if possible) during the breeding period (day 1, 15 and 20), and ~day 15-20 the chicks were equipped with a plastic and a metal ring. A small blood sample for genetic sexing was taken for all birds at first capture and all captures and sampling of guillemots in the field were conducted under legal permits by the Norwegian Food Safety Authority.

2.3.2 Observing feeding frequency

Two *Reconyx HyperFire HC500* cameras were installed right on top of the sub-colony. Each camera used 12 x AA (1.5 V) batteries, and they took a picture every 10th second 24 hours each day in the period from 16th of June to 13th of July. For each nest, all pictures were visually inspected for any parental chick feeding activity.

When an adult arrived with food, the following were noted: time of delivery, parent identity and parent morph. However, as there was no way to separate the adults' identity or sex unless it was a mixed morph pair, only the mixed morph pairs were used to determine the feeding frequency between sexes (n = 11). In addition, when the batteries were changed or of various reasons the camera angle became out of position, time gaps in the data set occurred.

Camera pictures were not always optimal for determining prey species as the image quality or camera angle varied, consequently fish species obtained by the camera were excluded in the analysis. Therefore, to observe potential changes in chick diet we conducted direct observations of the sub-colony using binoculars (10x42). Each day one to three observational feeding watches took place between 10:00-14:00h, 15:00-19:00h and sometimes including a night observational period between 21:00-23:00h. In total 21 days were spent observing chicks' diet, where only the prey species and birds' morph were noted, as it was not possible to determine the sex visually. The prey was divided into four categories: capelin, herring, sandeel and other small unidentified fish species. However, the general observation data obtained were not included in the analysis as they did not represent the chosen family birds and were carried out only for a few hours during the day (Appendix A, figure A1 – A3 and table A).

2.4 Molecular sexing analysis

A small blood sample was collected from all adults (n=54) and chicks (n=27) for molecular sexing. The blood samples were stored in 96% ethanol and analysed at a laboratory at Nord University in Bodø, Norway. In summary: the samples were 10 times diluted in phosphate buffered saline (PBS pH 7.2, Gibco). By using a Phusion Blood Direct PCR Master Mix kit (Thermo Scientific), sex was determined by polymerase chain reaction (PCR) in a total volume of 20 µl and contained 2 µl of the blood sample, with a forward primer P2 and a reverse primer P8. For most avian species, including Common guillemot, the P2-P8 sex-typing primers have been found useful to differentiate the sex-linked amplicons of the CHD-Z and CHD-W genes (chromobox-helicase-DNAbinding gene; Griffiths *et al.* 1998, Dawson *et al.* 2016). The PCR sample products were visualized on a 1.5% agarose gel, where the sexes can be distinguished by males showing a single band and females showing two bands. For more details, see the full procedure described in Griffiths *et al.* (1998).

2.5 Statistical analysis

Statistical analyses were performed using the open source software R, version 3.4.4 (R Core Team 2018). Generalized linear mixed models (GLMMs) were used to analyse the feeding frequency of parental sex and morph combination on a daily cycle and throughout the chick-rearing period. The GLMMs were fitted by using the *glmer* function from the "lme4" package (Bates *et al.* 2015). The response variable feeding frequency was the number of feeding events in a 3-hours interval, and we therefore used a Poisson distribution. Each day was divided into a “DayTime” category ranging from 1 to 8, starting from midnight. The chick-rearing period was divided into four “SeasonTime” categories, ranging from 1 to 4 with an interval on 7-day from early incubation to late chick-rearing period. For the specific time of the day and dates, see table 1. The real observation time was used as an *offset* (Zuur *et al.* 2009) to correct for the non-constant camera time (i.e. each 3-hours intervals may have less than 3 hours observations). Since not all functions used to fit models can use an *offset* (e.g. gamm4), a smoothing *B-spline* function from the package “splines”, was used to obtain a non-linear relationship, for the chick age, in the GLMM framework (Zuur *et al.* 2009). To take into account the repeated observations from all nests, nest was included as a random effect. Sex, morph combination as well as DayTime, SeasonTime and chick age were fixed factors. The statistical tests were conducted using the *Anova* function from the package “car”, implementing a chi-square test (hereafter χ^2) between nested models, starting with the interaction terms Sex/Morph*DayTime/chick age (Chambers and Hastie 1992, Fox and Weisberg 2011). We also used χ^2-ratios statistics to evaluate the degree of evidence (values much larger than their respective degrees of freedom indicated evidence for an effect, Howell 2007). A 95% confidence intervals of predicted effects were used in specific models (i.e. corresponding to the different predictions tested) to assess uncertainty and evidence of results. The raw data were first visualized by using the *ggplot* function from the “ggplot2” package with a *geom_smooth* function for the trends. The goodness of fit of different models was assessed using plot of predicted values versus observed and residual plots (Appendix B, figure B1 – B4).

Table1: *Descriptive list of DayTime and SeasonTime division and their respective time-period during the day (hours) and Julian dates to determine the feeding frequency of the* Common *guillemot pairs.*

Hour (From 00-24)	**DayTime**	**Dates (Julian day)**	**SeasonTime**
00-03	1	17.06 – 23.06 (168-174)	1
03-06	2		
06-09	3	24.06-30.06 (175-181)	2
09-12	4		
12-15	5	01.07-07.07 (182-188)	3
15-18	6		
18-21	7	08.07-14.07 (189-194)	4
21-00	8		

3 Results

In total 357 200 pictures were taken during the study period whereas up to 450 hours were spent analysing the photos. From these, 1459 feeding observations were found and the camera period covered a timespan from late incubation period to late chick-rearing period. Of the 27 nests, five chicks died during the nestling period. No chicks had yet departed the nest site when the study period ended on the 14th of July and all of the surviving chicks were by then older than 14 days. Chicks were fed at a daily average of 3.3 ± 0.18 fish.

3.1 Feeding frequency and parental sex

3.1.1 Daily feeding frequency rhythm

For the mixed pairs (n = 11) we found evidence for a sex-inverted rhythm in daily feeding frequency between the sexes (interaction DayTime:Sex: χ^2= 29.8, p = 0.001, df = 7, figure 2).

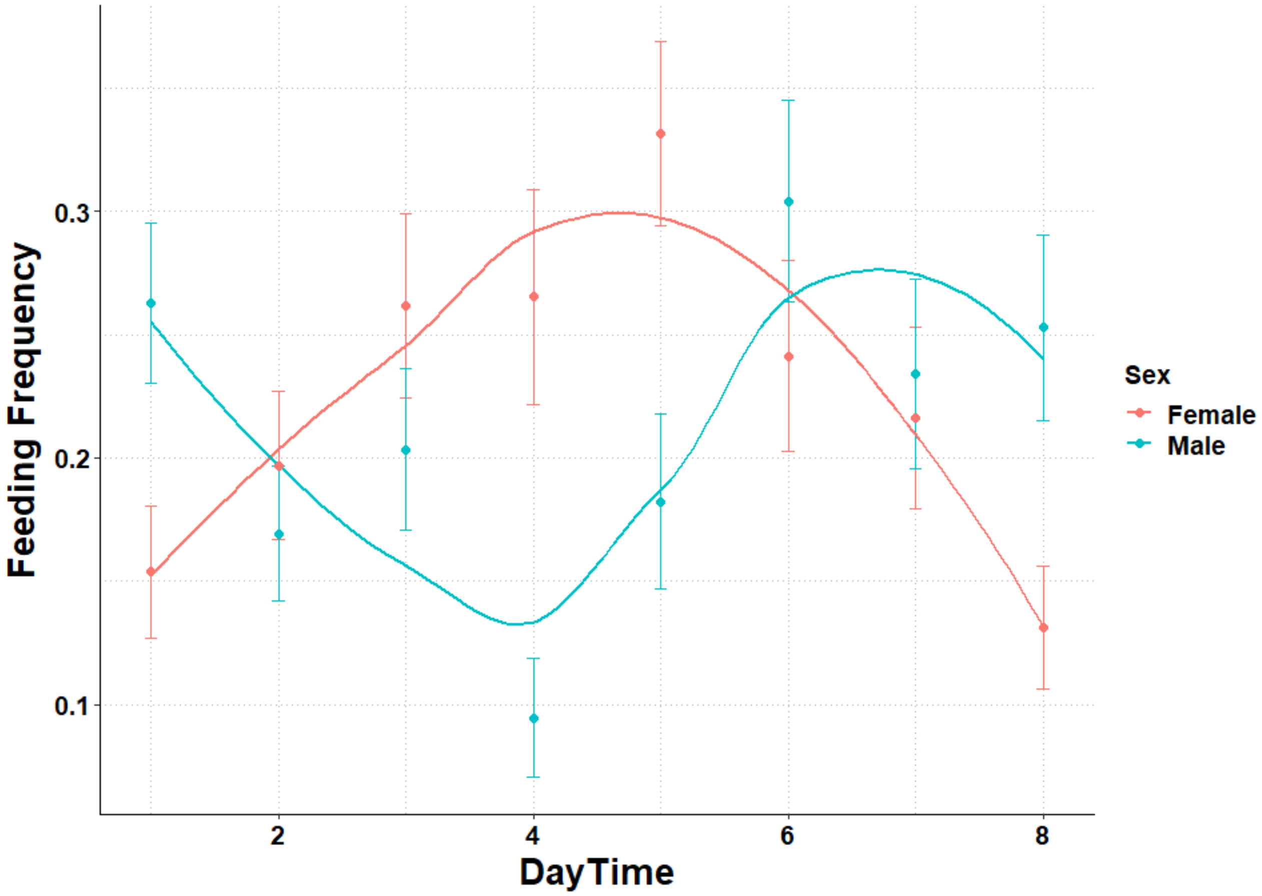

Figure 2: *Average feeding frequency for the male (blue line) and female (red line). The dots represent the feeding frequency over an average daily perspective (DayTime 1-8, table 1) for each sex. Each line shows the trend among the corresponding colour dots and are based on smoothed data. The bars indicate the standard error (SE).*

The female Common guillemots had a diurnal rhythm with highest feeding frequency during the day, including a top peak between 09:00-15:00h (figure 2, DayTime 4-5), and a low peak between 21:00-03:00h (figure 2, DayTime 8-1). The male Common guillemots had a nocturnal rhythm with highest feeding contribution during night time, with a top peak during the period from 15:00-03:00h (Daytime 6-1) and a bottom peak between 09:00-15:00h (DayTime 4-5). The period between 03:00-06:00h (DayTime 2) and 15:00-18:00h (DayTime 6) both sexes contributed approximately equal. This daily sex-inverted rhythm was consistent over the season (SeasonTime, appendix C, figure C), except for SeasonTime 4 (08.07-14.07) where the feeding frequency for both sexes were highest in the time period around 15:00-18:00h (DayTime 6). The females having daily highest feeding frequency was consistent over the study period (SeasonTime, Appendix C, figure C).

3.1.2 Parental feeding frequency during the chick-rearing period

There was no statistical evidence for a change of the parental investment during the chick-rearing period as the chicks grew older (interaction Sex:spline(chick age): $\chi^2 = 3.47$, $p = 0.32$, $df = 3$). Both sexes had the highest feeding frequency when the chick was less than five days old (figure 3) and the female parent had in general the highest feeding contribution until the chicks were 19 days, however no statistical evidence was found for an effect of chick age (main effect spline(chick age): $\chi^2 = 0.94$, $p = 0.81$, $df = 3$). The maternal provisioning rates slowly decreased after the chicks were 15 days (figure 3). An increase of paternal contribution occurred after the chicks turned 18 days, resulting in males dominating feeding frequency by the end of the chick-rearing period. However, the trend of a different feeding frequency between the sexes, was not significant within this period (interaction Sex:chick age: $\chi^2 = 1.76$, $p = 0.18$, $df = 1$).

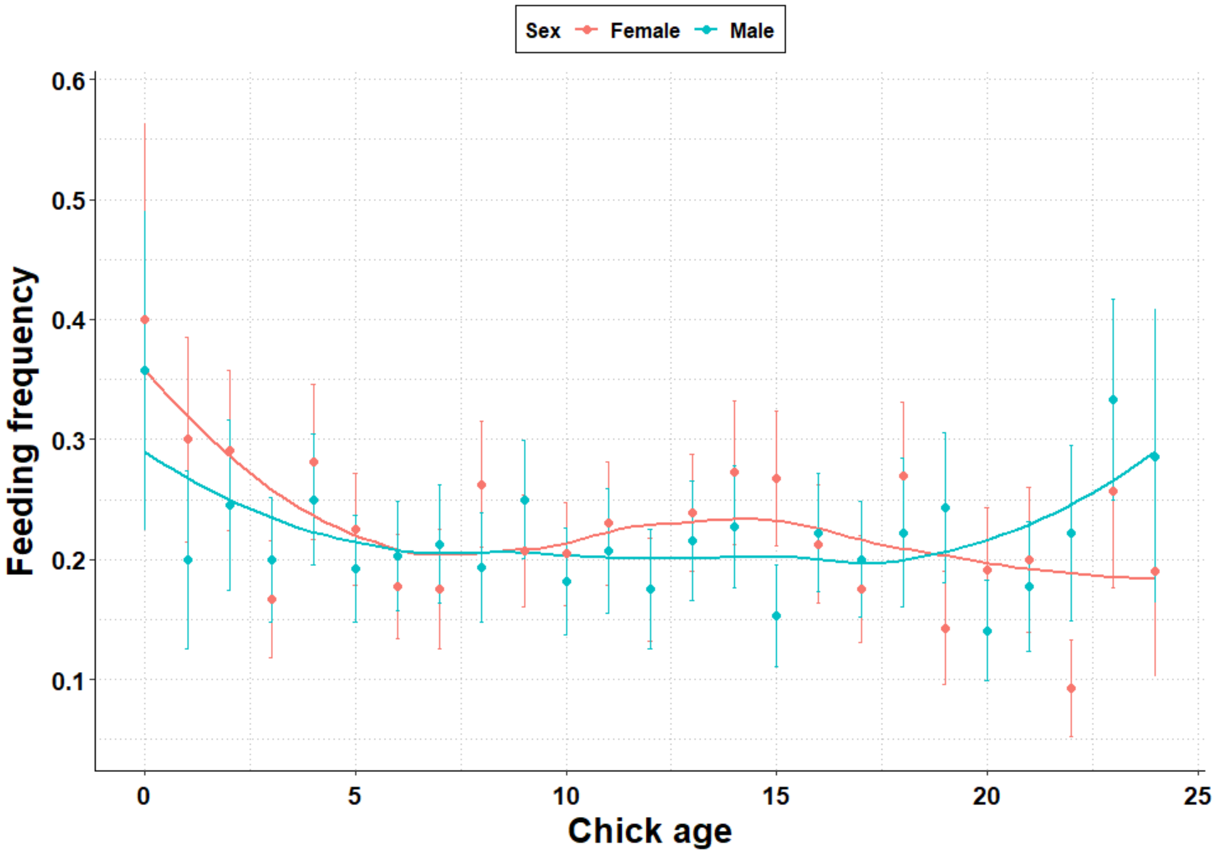

Figure 3: *The average observed feeding frequency between male (blue line) and female (red line). The dots represent the feeding frequency over a daily average in the period from day 0 (hatching) to the chick were up to 24 days of age. are based on smoothed data. Each line shows the trend among the corresponding colour dots and are based on smoothed data. The bars indicate the standard error (SE).*

3.2 Feeding frequency and parental morph combination

3.2.1 Daily feeding frequency rhythm

There was no evidence of any daily rhythms between the two morph combinations (interaction DayTime:Morph: χ^2= 10.2, *p* = 0.17, *df* = 7; main effect Morph: χ^2=0.57, p=0.45, *df*=1, figure 4). The mixed morph pairs had the overall highest feeding frequency, yet only in four DayTime periods did the two morph combinations differ from each other (DayTime 1, 2, 3 and 6, figure 4). The mixed morph pairs showed only one single peak between 15:00-18:00h (DayTime 6, figure 4). In contrast, the same morph pairs showed a bimodal distribution: one peak between 06:00-09:00h (DayTime 3) and another between 15:00-18:00h (Daytime 6). Both morph combinations had the lowest feeding frequency during the night time between 21:00-00:00h (DayTime 8, figure 4).

In addition, the weekly DayTime averages (SeasonTime) varied highly and no consistent trend could be found among the weeks (Appendix D, figure D).

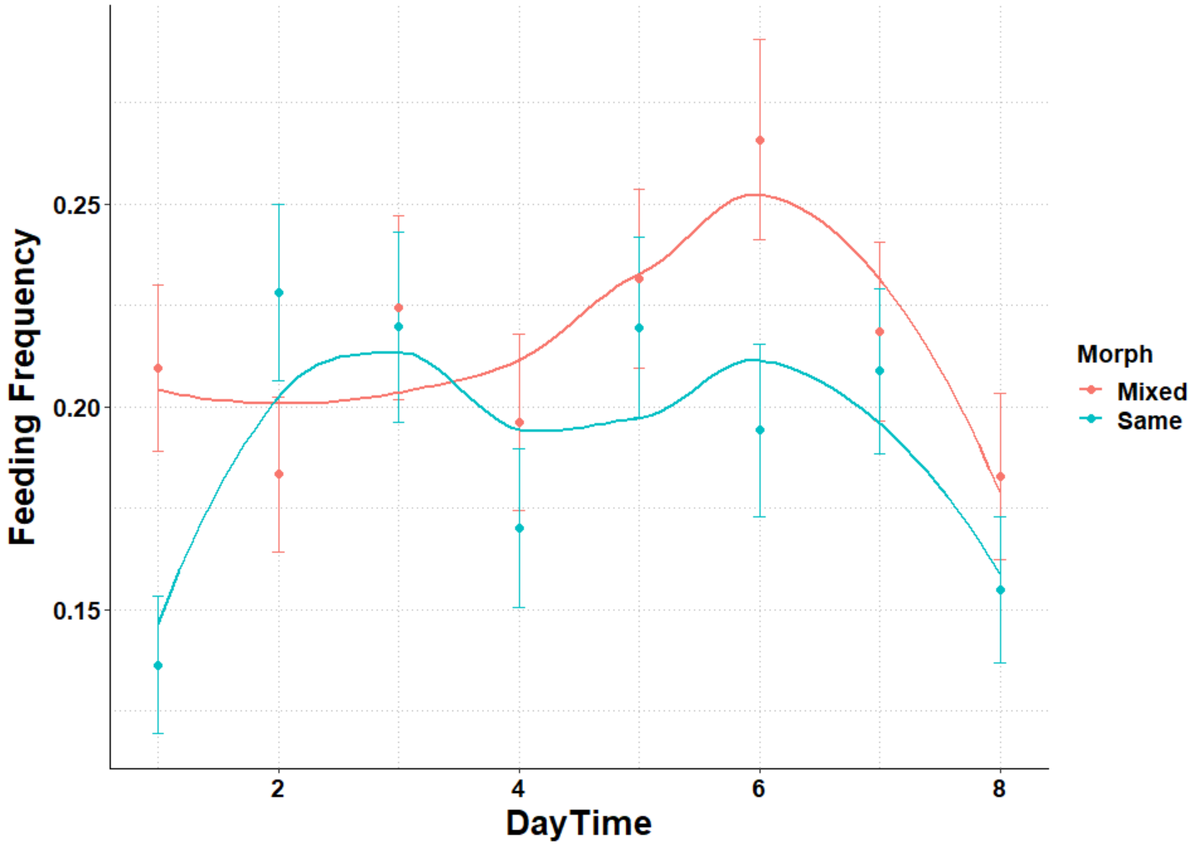

Figure 4: *The average daily feeding frequency for the mixed morph pairs (n = 11, red line) and the same morph pairs (n = 16, blue line). The dots represent the feeding frequency over an average daily perspective (DayTime 1-8, table 1) for both morph combinations. Each line shows the trend among the corresponding colour dots and are based on smoothed data. The bars indicate the standard error (SE).*

3.2.2 Feeding frequency and morph combination during the chick-rearing period

No statistical support was found for an overall change in feeding frequency for both morph combinations during the chick-rearing period (interaction Morph:spline(chick age): $\chi^2 = 3.06$, $p = 0.38$, $df = 3$).

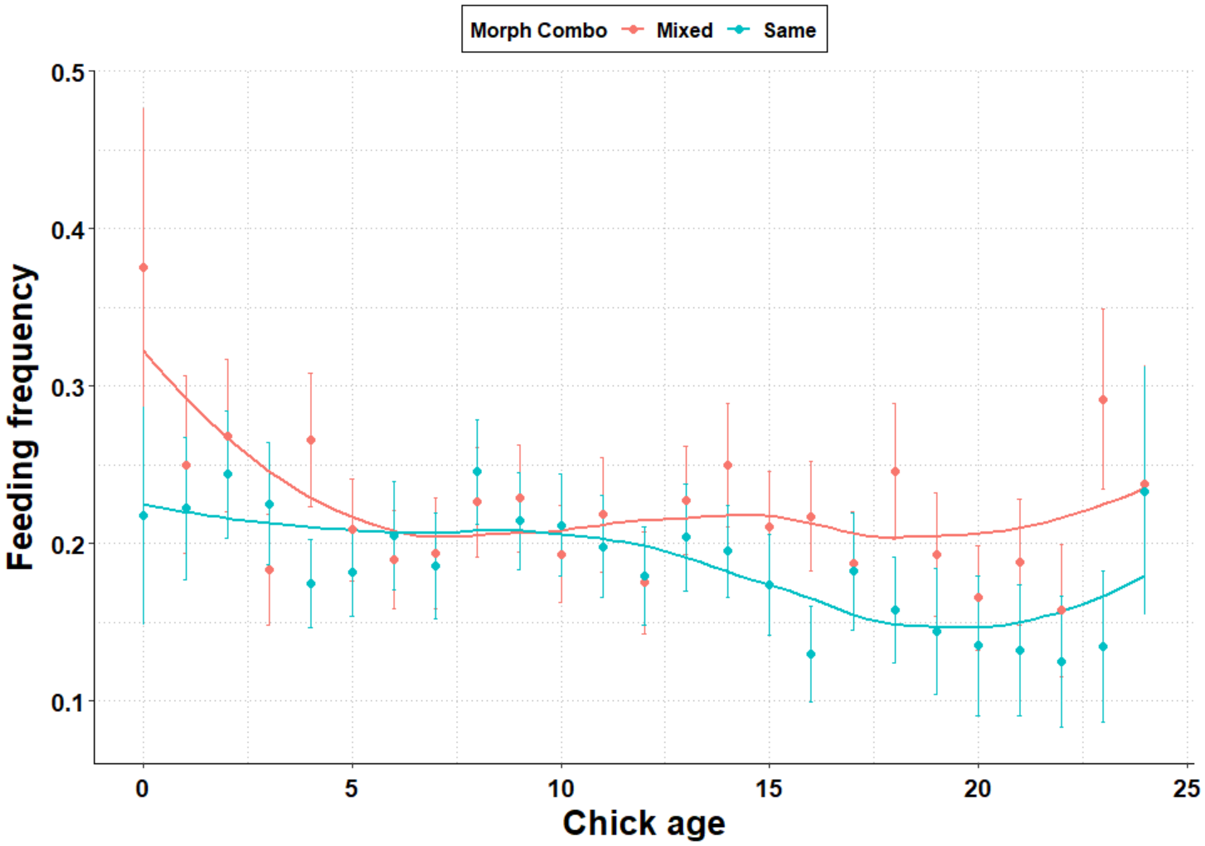

Figure 5: *The average observed feeding frequency between the mixed morph pairs (red line) and same morph pairs (blue line). The dots represent the feeding frequency over a daily average in the period from day 0 (hatching) to the chick were up to 24 days of age. Each line shows the trend among the corresponding colour dots and are based on smoothed data. The bars indicate the standard error (SE).*

For both morph combinations, the highest feeding frequency occurred before the chicks turned five days old. Similar to the daily feeding frequency in figure 4, the mixed morph pairs had a higher feeding frequency compared to the same morph pairs (figure 5). After chicks turned 10 days old, a significant segregation in feeding frequency between the two morph combinations occurred (spline(chick age): $\chi^2 = 4.07$, $p = 0.043$, $df = 1$; main effect Morph: $\chi^2 = 7.01$, $p = 0.008$, $df = 1$). In this period, the same morph pairs decreased in frequency while the mixed morph pairs kept overall the identical feeding rate. Both combinations showed an increase in feeding frequency after the chick was 20 days old (figure 5).

4 Discussion

The provision of food for the offspring stands as a major element in parental investment (Thaxter *et al.* 2009). For parental sex, we found evidence for a strong daily sex-inverted rhythm where females had a higher feeding frequency during the daytime and males during the night. Females also had the overall highest contribution throughout the chick-rearing period, but we observed a trend of increased male contribution in chick feeding frequency after chicks turned 19 days old. As for parental morph combination, we found no trend of any daily rhythms. However, we observed that the mixed morph pairs had a significant higher feeding frequency when chicks were older than 10 days.

4.1 Feeding frequency and parental sex

4.1.1 Daily feeding frequency rhythm

In this study, we found that the female Common guillemots at Hornøya had a diurnal chick feeding frequency, in contrast to males who had a nocturnal feeding frequency. This daily sex-inverted rhythm was consistent over the study period (SeasonTime, Appendix C, figure C) and are comparable to previous results for both Common guillemot and Brünnich's guillemot (Thaxter *et al.* 2009, Linnebjerg *et al.* 2015). However, several other studies have detected a nocturnal feeding frequency instead of diurnal among female guillemots (e.g. Jones *et al.* 2002a, Paredes *et al.* 2006). Elliott *et al.* (2010) suggested the variation among findings emerges as a result of different foraging risk partitioning between the sexes on a local scale. In their study, females took fewer foraging risks than males and they therefore argued, as some prey are more "riskier" than others, the prey species composition around the study location would determine the outcome of these rhythms (Elliott *et al.* 2010). Most previous studies used only a few hours per day to observe chick diet (e.g. Uttley *et al.* 1994, Cameron-MacMillan *et al*. 2006, Hipfner *et al*. 2006, Paredes *et al*. 2006, Thaxter *et al.* 2009, Barrett *et al*. 2013). Their study design may therefore have affected their results as feeding rates for guillemots are known to vary considerably depending on the time of day, weather and food availability (Finney *et al.* 1999).

Even so, several explanations have been suggested to interpret our findings of female diurnal and male nocturnal chick provisioning in guillemots. Firstly, males are known to interact more aggressively towards neighbours and predators, compared to females for both Common guillemot (Wanless and Harris 1986, Paredes *et al.* 2006) and the Brünnich's guillemot (Paredes and Insley 2010). If males are the optimal chick defender, it could explain why the females contribute to chick feeding mainly during the day - as the external-pressure from predators or intra-specific competition, might be highest in this period (Birkhead 1977). However, possibly due to constant sunlight (polar day), this might not necessarily apply in every seabird colony as white-tailed eagles (*Haliaeetus albicilla*) and other avian predators have been frequently observed disturbing the sub-colony at Hornøya during the night (pers. obs.). In addition, this period could potentially act as a parent-offspring bonding time for the males as recognition at sea is crucial for the post-departure period, when the male takes care of the chick at sea (Paredes *et al.* 2006).

Secondly, males have in several occasions been found to undertake longer foraging trips in both distance and duration – they also dive deeper and more often than females (Brünnich's guillemot: Paredes *et al.* 2006, Common guillemot: Thaxter *et al.* 2009; Burke *et al.* 2015). Therefore, Thaxter *et al.* (2009) suggested that males spend a greater time in daily self-feeding compared to females, in anticipation for the period after chick departure. In addition, Huffeldt and Merkel (2016) suggested that since a sex-inverted rhythm for guillemots persists both above and below the arctic-circle, despite the occurrence of constant sunlight, sex-inverted rhythms likely occurs as a result of divergent ways to allocate resources between the sexes. Consequently, there are reasons to believe the males' nocturnal feeding frequency might be a trade-off between optimal chick defence and self-provisioning. The males might also spend more time during the nights on scouting for potential locations for the upcoming post-departure period (Thaxter *et al.* 2009).

Thirdly, females showed the overall highest daily feeding contribution for all four study weeks (SeasonTime, Appendix C, figure C). Burke *et al.* (2015) linked their similar findings to female guillemots spending less time and being more efficient when out foraging compared to males (e.g. Common guillemot: Thaxter *et al.* 2009, Brünnich's guillemot: Elliott *et al.* 2010; Paredes and Insley 2010). Since the marine environment is a highly fluctuating system, this sex-inverted rhythm could potentially indicate some underlying preferences in adult diet. Therefore, daily weather fluctuation might affect the preferred prey species between sexes differently if they forage in different areas, as it is known the weather can affect the local prey species availability (Ådlandsvik and Loeng 1991, Finney *et al.* 1999).

4.1.2 Parental feeding frequency through the chick-rearing period

There was no significant variance in chick feeding frequency between the sexes throughout the chick-rearing period. However, similar to previous studies of the Common guillemot, the females had the overall highest feeding frequency (Wanless and Harris 1986, Thaxter *et al.* 2009) however with no statistical support for a sexual segregation. Nevertheless, in the present study, after the chicks turned 18 days old, males showed a strong trend of increased chick feeding frequency. This is in contrast to previous findings for both Common and Brünnich's guillemots (Paredes *et al.* 2006, Burke *et al.* 2015). Explanations behind the observed trend of increased male feeding frequency are relatively unexplored, thus several theories arise.

We might speculate these findings relating to parental body condition and stress. Maternal body condition around egg hatching was in the same study population found to have a positive effect on the chick age at departure (Johansen *et al.* in prep.). Therefore, females in better body condition prior to the chick-rearing period, can provide for the chick longer at the nest site (Wanless and Harris 1986, Johansen *et al.* in prep.). This could potentially explain the overall female dominating contribution, as the maternal resource allocation differ from the paternal, because of distinct resource allocation prior to the paternal-based post-departure period. Females do not have such period and might therefore allocate their resources more in chick provisioning instead of self-maintaining, thereby resulting in a higher parental effort compared to males. High parental effort is known to be linked with elevated stress-levels in several species (e.g. Harding *et al.* 2009, Bonier *et al.* 2011, Riechert and Becker 2017. High stress-level could potentially trigger nest desertion due to low parental body condition (Jones *et al.* 2002b, Angelier *et al.* 2009, Spée *et al.* 2010). Our observed trend of decreased maternal feeding frequency after chicks turned 19 days, might arise as a result of females having too high stress-levels. Thereby entering a period where males increases their chick feeding frequency in order to compensate for the females.

On the other hand, Thaxter *et al.* (2009) found that females foraged closer to the colony compared to males. Therefore, the female Common guillemots at Hornøya could potentially be restricted by their own foraging range and the availability of preferred prey. However, we have no data on this. It is well known that the abundance of fish and their distribution in the Barents Sea is fluctuating both inter- and intra-seasonal (Sakshaug 1997) and a shift in fish distribution normally occurs in late summer period as capelin follows their main prey northwards (Gjøsæter 1998).

Therefore, we might speculate that the observed shift in parental investment, may have happened as a result of fluctuations in the marine environment, which might have caused a change in preferred or optimal prey species.

However, we were not able to detect any changes in prey in the general chick diet throughout the study period (Appendix A, figure A) despite this being observed in previous years at Hornøya (e.g. Barrett 2002, Johansen *et al.* in prep.). In contrast, as we were not able to separate the sexes by binoculars nor could the cameras be optimally used for determining the fish species, we cannot exclude the possibility that there might be a change in the adult preferred prey species between sexes over the breeding season. Although, little is known about sex dependent prey preferences in adult guillemots and therefore we cannot ignore the possibility of different reactions between the sexes when the marine environment fluctuate. It is also no way to know if our observed decrease of female feeding frequency are a result of a change in prey size as it has been found to change during the breeding season among other seabird species like in the little auks (*Alle alle,* Gaston and Jones 1998) and kittiwakes (*Rissa tridactyla*, Ponchon *et al.* 2014).

Nevertheless, even though we found no statistical evidence for different feeding frequency between the sexes, it is possible that we could have found stronger evidence for increased parental feeding frequency which might have been significant if the study period had continued until chick departure. It is therefore hard to draw any conclusions based only on the feeding frequency, and the mechanisms behind our observed feeding frequency shift remains unanswered. Future studies are therefore encouraged to include data on parental body conditions, stress-levels, nest attendance, adult- and chick diet and environmental data, such as weather, in their statistical analyses. Adding further data might help detecting and to understand any underlying mechanisms behind parental feeding frequency.

4.2 Feeding frequency and parental morph combination

4.2.1 Daily feeding frequency and the effect of morph combination during the chick-rearing period

There was no evidence for a difference in daily feeding frequency between the two morph combinations and we found no daily trend over the study period (SeasonTime, Appendix D, figure D). As for the chick-rearing period, mixed morph pairs had the overall highest feeding frequency, yet not significant until after the chicks were 10 days old. Hereafter, same morph pairs decreased their feeding frequency while the mixed morph pairs continued steadily, resulting in a significant feeding frequency segregation between the two morph combinations. To our knowledge, this is the first study to document the feeding frequency throughout the chick-rearing period between the two morph combinations. Therefore, we can only assume what our findings might indicate and the potential explanations for our observed difference in chick feeding frequency, between mixed morph and same morph pairs.

For Brünnich's guillemot, Elliott *et al.* (2009) suggested chick growth rates after 10 days of age are affected by the distance of prey away from the central place – as chicks energy demand is highest after this point. Therefore, our findings might indicate that mixed morph pairs for some reasons are able to cope better with the increasing energy demand of the chick. This might explain why Lyngbo-Kristensen *et al.* (2014) found chicks of same morph pairs to be smaller than chicks of mixed morph pairs. This suggests that there might be some underlying explanations behind the chick feeding frequency induced by the parental morph combination.

The bridled morph has been suggested to be better adapted to a colder environment because of a northward increase in numbers (Birkhead and Nettleship 1985, Harris and Wanless 1986) and its negative relationship to increased SST (Reiertsen *et al.* 2012). In contrast, unbridled individuals have been suggested being more tolerant to warmer conditions compared to the bridled morph (Reiertsen *et al.* 2012). If the bridled and the unbridled morphs can cope with different environmental conditions, mixed morph pairs could potentially compensate for each other in a fluctuating environment as suggested by Lyngbo-Kristensen *et al.* (2014). Should one type of climate dominate more than others, pairs consisting of only the same morph might experience more challenges to maintain the increasing energy demand from their chick.

On the other hand, Reiertsen *et al.* (2012) suggested that bridled birds are more dependent on cold-water species such as capelin and unbridled birds more on warmer water species such as cod and herring. Through the study period, we found no such prey species preference for the two morph combinations (Appendix A, figure A2-A3, table A), which is consistent with previous findings in the Common guillemot (Thaxter *et al.* 2009, Barrett 2013). For the unbridled birds, there is a tendency of higher frequency of herring happening early in the chick-rearing period (Appendix A, figure A1) compared to no such tendency for the bridled birds (Appendix A, figure A2). However, it is hard to draw any assumption without adding the sufficient data such as weather data and SST in the analysis.

Nevertheless, we have no data on adults' diet, and therefore we cannot exclude the possibility that adult guillemots might be affected by environmental fluctuating of preferred prey species (Bugge *et al.* 2011). Our observed decrease of chick feeding frequency could potentially be affected by a change in adults' foraging efficiency, induced by fluctuating variables in the marine environment. In contrast, it is no way to know if our observed decrease of the same morph pairs feeding frequency are a result of any changes in prey size, and we do not know how this might relate to the two different Common guillemot morphs.

The observed feeding frequency differences occurring after chicks turned 10 days old, are most likely a result of either a shift in the adults' prey or climatic fluctuations that favours one morph more than the other, in the period with increasing chick energy demand. The ability to adapt and comprehend with both short- and long-termed environmental changes, in addition to preserve the increasing chicks' energy demands, is vital for the future population.

4.3 Conclusion and recommendations

In conclusion, in this study we showed that parental sex had a clear daily sex-inverted rhythm persistent over the study period, while no such rhythm or trends could be found for the parental morph combinations. During the chick-rearing period, food provisioning between the parent sexes were overall female dominated until a shift occurred after the chicks turned 19 days, thereby entering a male dominated period. In addition, the two morph combinations showed no segregation in feeding frequency until after chicks were 10 days old, hereafter the mixed morph pairs had significant higher feeding frequency than same morph pairs.

Our findings may indicate that there are some underlying mechanisms behind parental investment through chick provisioning for both parental sex and morph combination. For future studies, we recommend adding sufficient data in order to distinguish possible underlying mechanisms that should be of interest. Suggested variables include data on parental body condition and stress-levels, brooding time, adults' and chicks' diet, foraging behaviour and various climatic measurements over the breeding season. In addition, we also recommend to visually separate the same morph pairs, in order to compare sex dependent strategies in relation to morph and enhancing the sample size.

To our knowledge, this is the first study to investigate the Common guillemot chick feeding frequency by using two time-lapse cameras throughout the chick-rearing period. Overall, using time-lapse cameras on short intervals seems promising as a method to study the Common guillemot on a long-term scale in a non-invasive way. Providing insight on how the breeding system today might have evolved, is an important factor to comprehend in order to highlight critical associations between the ongoing climate change, management and future breeding success of this species.

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Appendix A

In total 1772 general feeding observations were obtained with binoculars, with mainly capelin dominated the chick diet (77.8%) while herring and sandeel contributed in total 8.52% and 12.42% respectively (figure A1). The last remaining proportion of the chicks' diet consisted of 1.24% unidentified fish species. The composition of the chicks' diet varied significantly in fish species during the 21 observation days (χ^2= 365.05, $p < 0.001$, $df = 69$). We observed a decrease of species such as herring and sandeel, while the proportion of capelin varied over the season but was nearly always high around 75-80%. No overall preference of fish species was found between the bridled and the unbridled morphs as they both brought back almost identical proportion of fish species (table A, $\chi^2 = 0.57308$, $df = 3$, $p = 0.9026$). Nor were there any differences in fish proportions between the morphs during the observational period (figure A2 – A3, χ^2= 26.983, $p = 0.14$, $df = 20$).

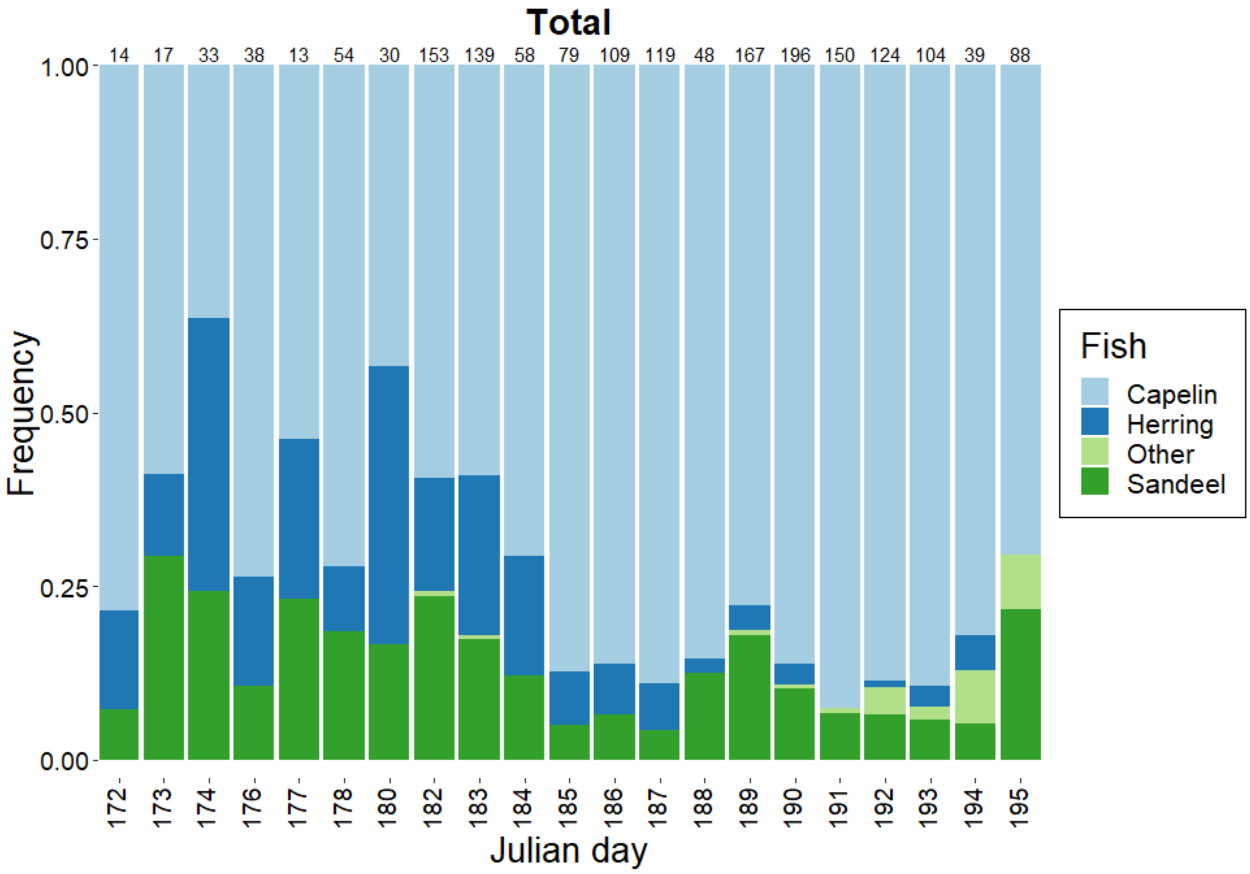

Figure A1: *Daily proportion of fish species in chicks' diet (n = 1772) obtained through binoculars during the observational period from 21*st *of June until 14*th *of June (Julian day 172 to 195). The daily sampling size is indicated above each column.*

In total 607 general feeding observations for the bridled morph were obtained with binoculars (figure A2). The composition of the chicks' diet varied significantly in fish species during the 21 observation days (χ^2= 176, *df* = 60, *p* < 0.001). Total percentages for each fish species are listed in table A.

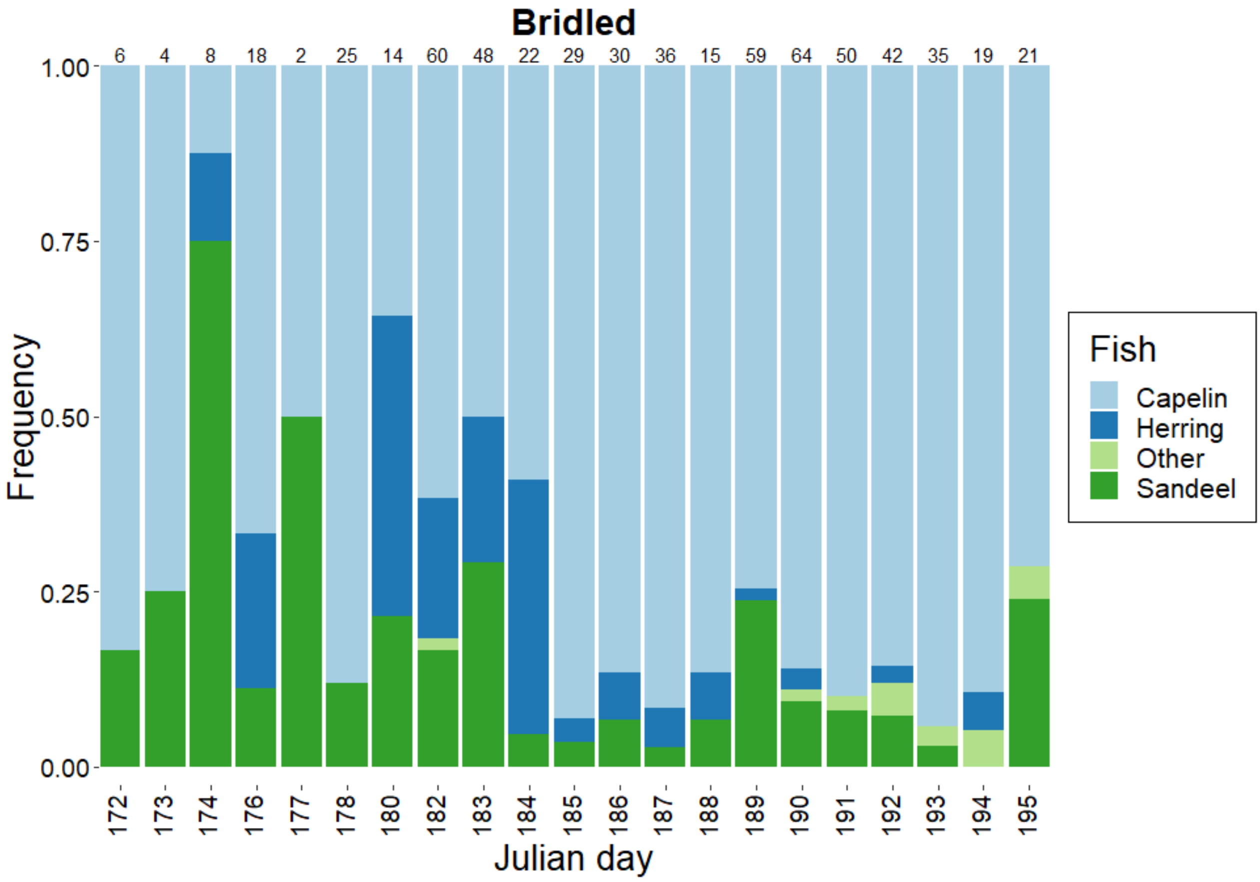

Figure A2: *Daily proportion of fish species in chicks' diet (n = 607) from the bridled morph parents, obtained through binoculars during the observational period from 21st of June until 14th of June (Julian day 172 to 195). The daily sampling size is indicated above each column.*

In total 1165 general feeding observations for the unbridled morph were obtained with binoculars (figure A3). The composition of the chicks' diet varied significantly in fish species during the 21 observation days ($\chi^2 = 268$, $p < 0.001$, $df = 60$). Total percentages for each fish species are listed in table A.

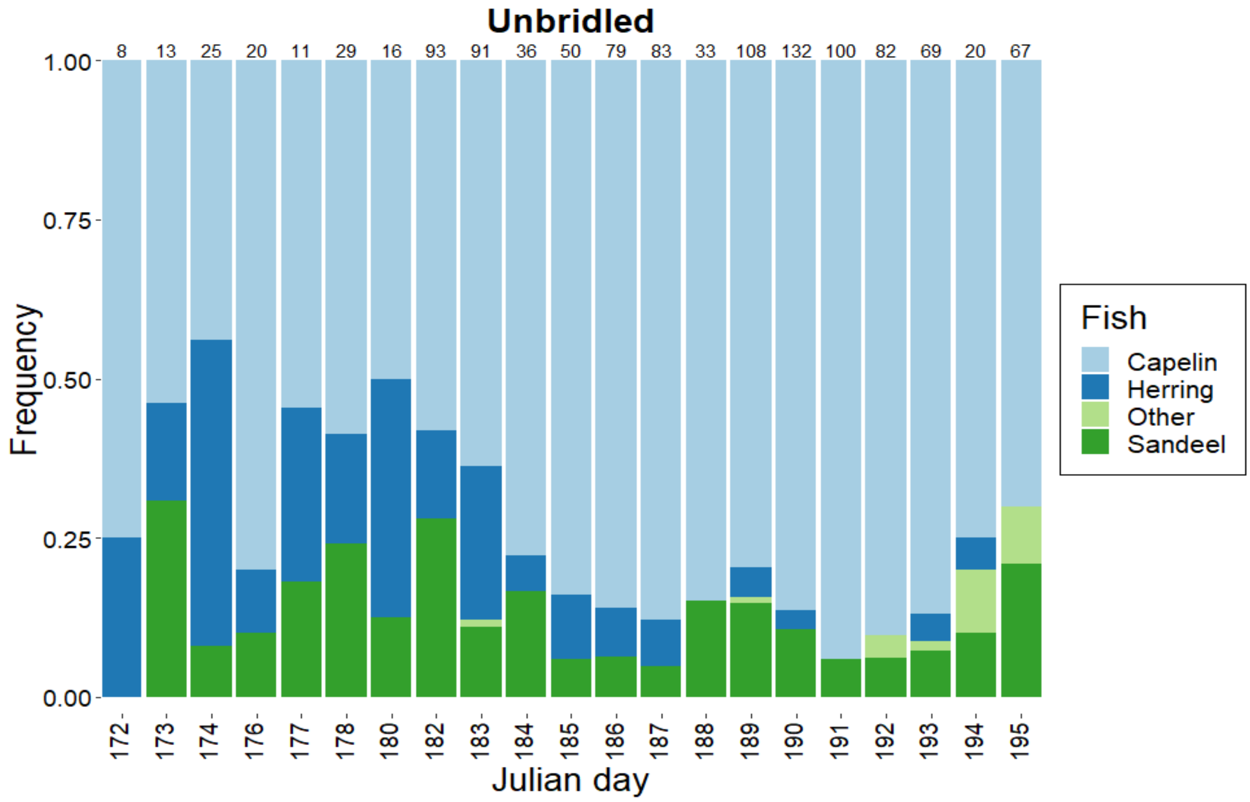

Figure A3: *Daily proportion of fish species in chicks' diet (n = 1165) from the unbridled morph parents, obtained through binoculars during the observational period from 21st of June until 14th of June (Julian day 172 to 195). The daily sampling size is indicated above each column.*

Table A: *A summary of the total observed amount of fish (% of total listed in the brackets) brought to chicks by the bridled and the unbridled morph between 21st of June to 14th of July based on the data from figure.*

Fish	**Unbridled**	**Bridled**
Capelin	912 (78.3%)	467 (76.9%)
Herring	99 (8.5%)	52 (8.6%)
Sandeel	140 (12%)	80 (13.2%)
Other	14 (1.2%)	8 (1.3%)
Total	1165	607

Appendix B

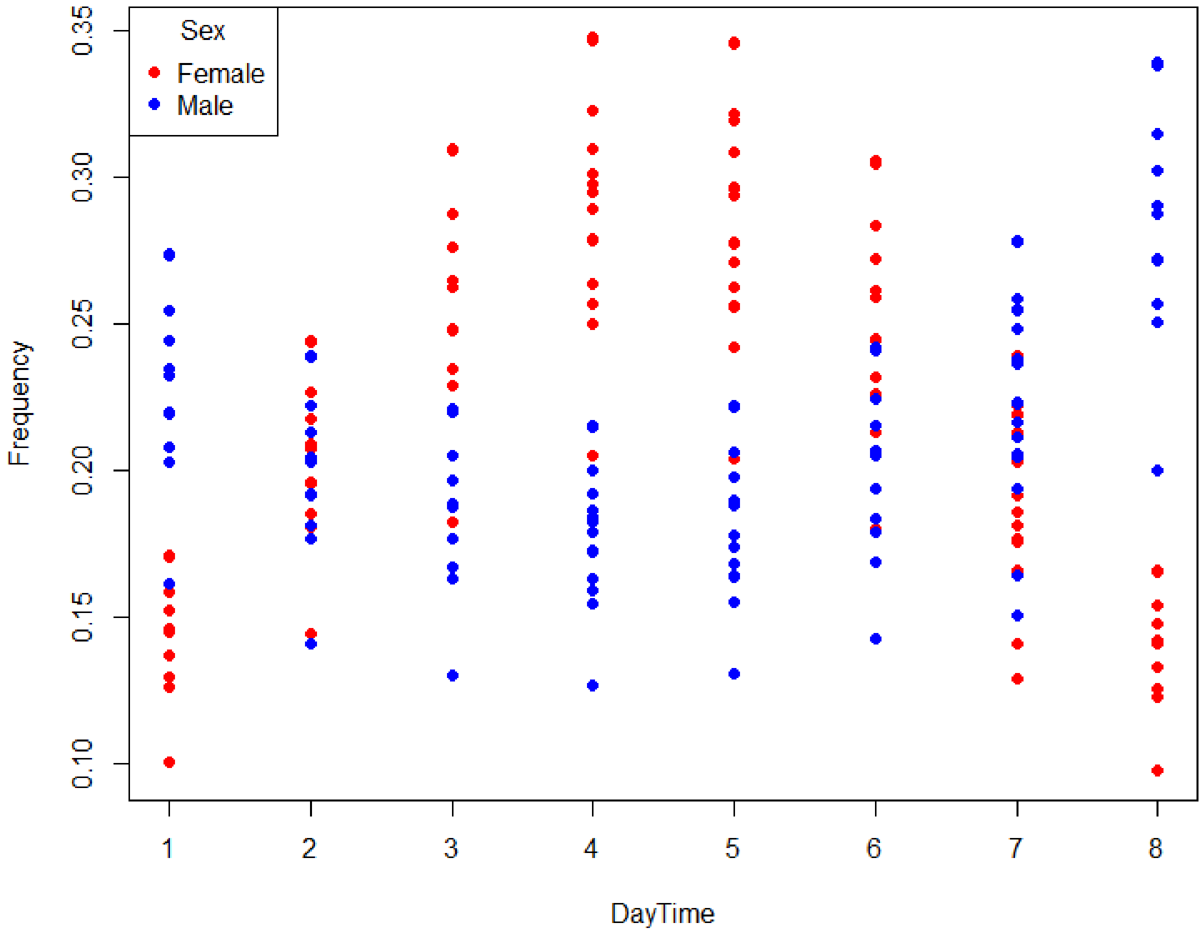

Figure B1: *The predicted feeding frequency values for males (blue dots) and females (red dots) from the model over an average daily perspective (DayTime 1-8, table 1).*

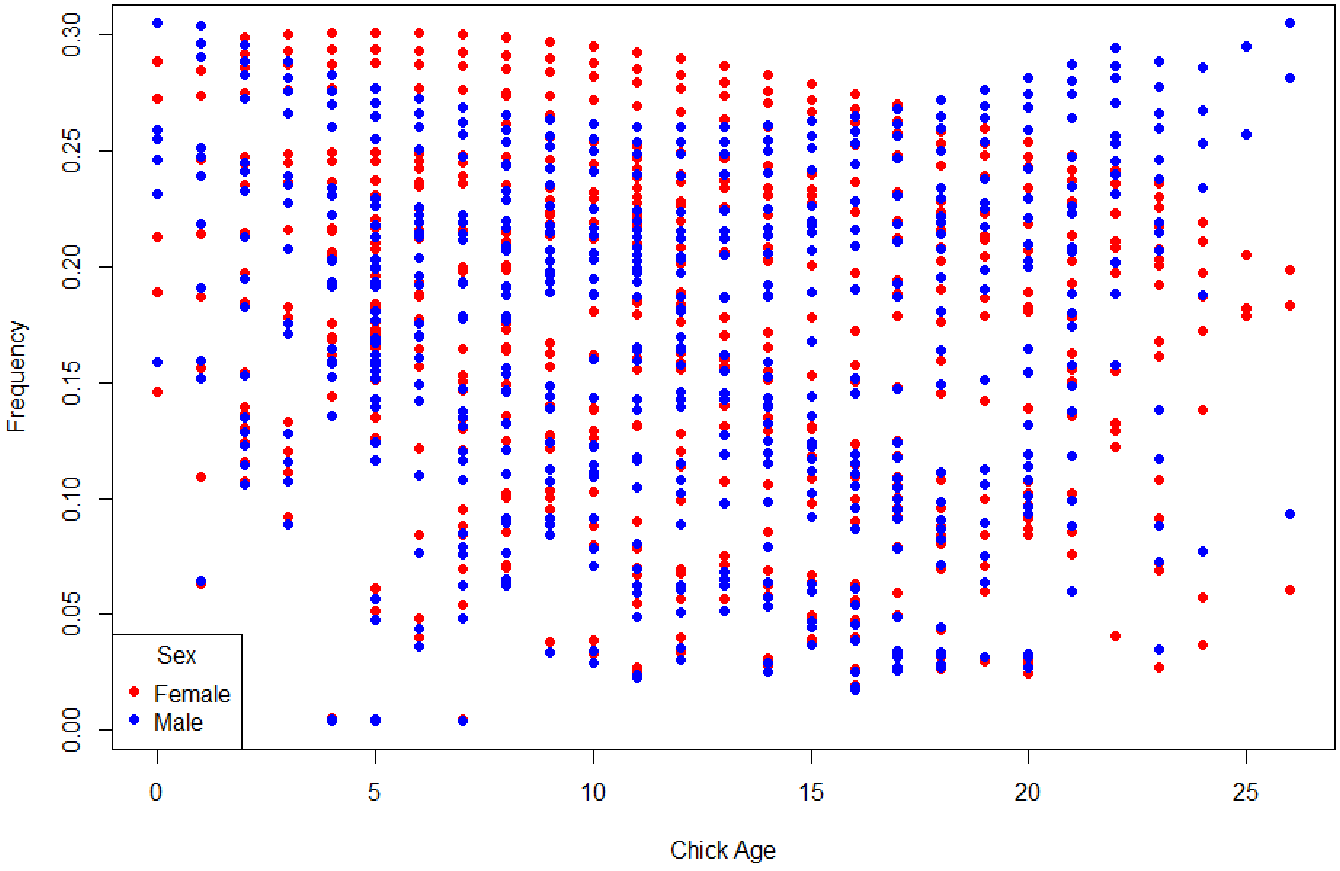

Figure B2: *The predicted feeding frequency values for males (blue dots) and females (red dots) from the model over chick age.*

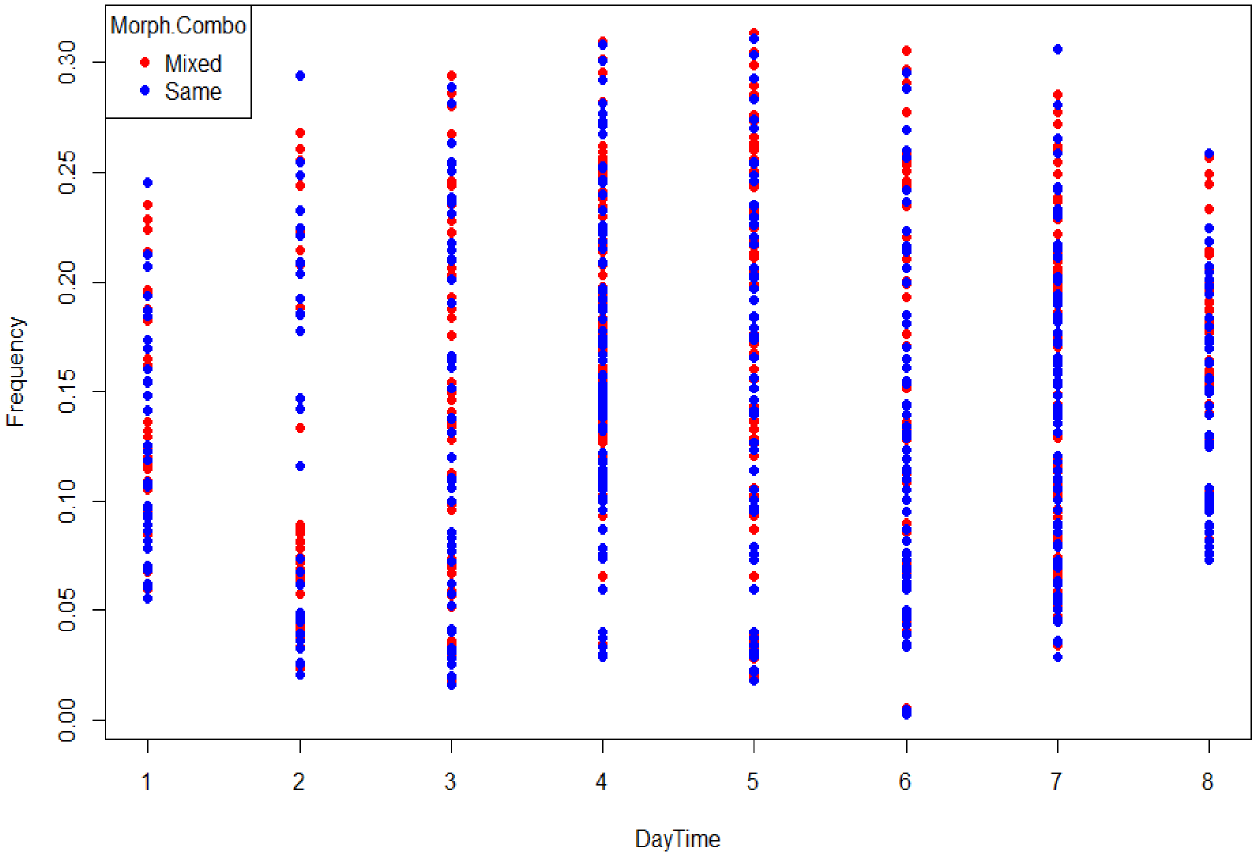

Figure B3: *The predicted daily feeding frequency values for the mixed (red dots, n = 11) and same morph (blue dots, n = 16) from the model over an average daily perspective (DayTime 1-8, table 1).*

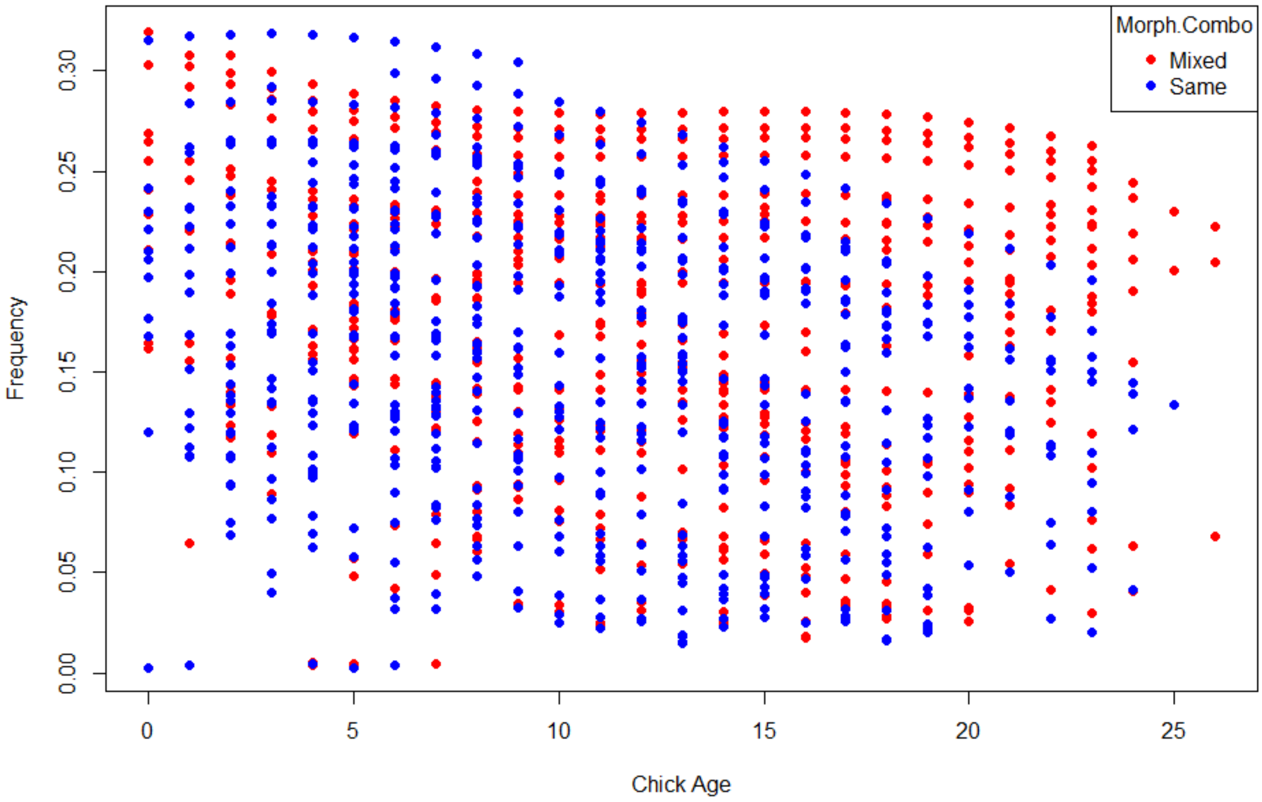

Figure B4: *The predicted feeding frequency values for the mixed (red dots, n = 11) and same morph (blue dots, n = 16) from the model over chick age.*

Appendix C

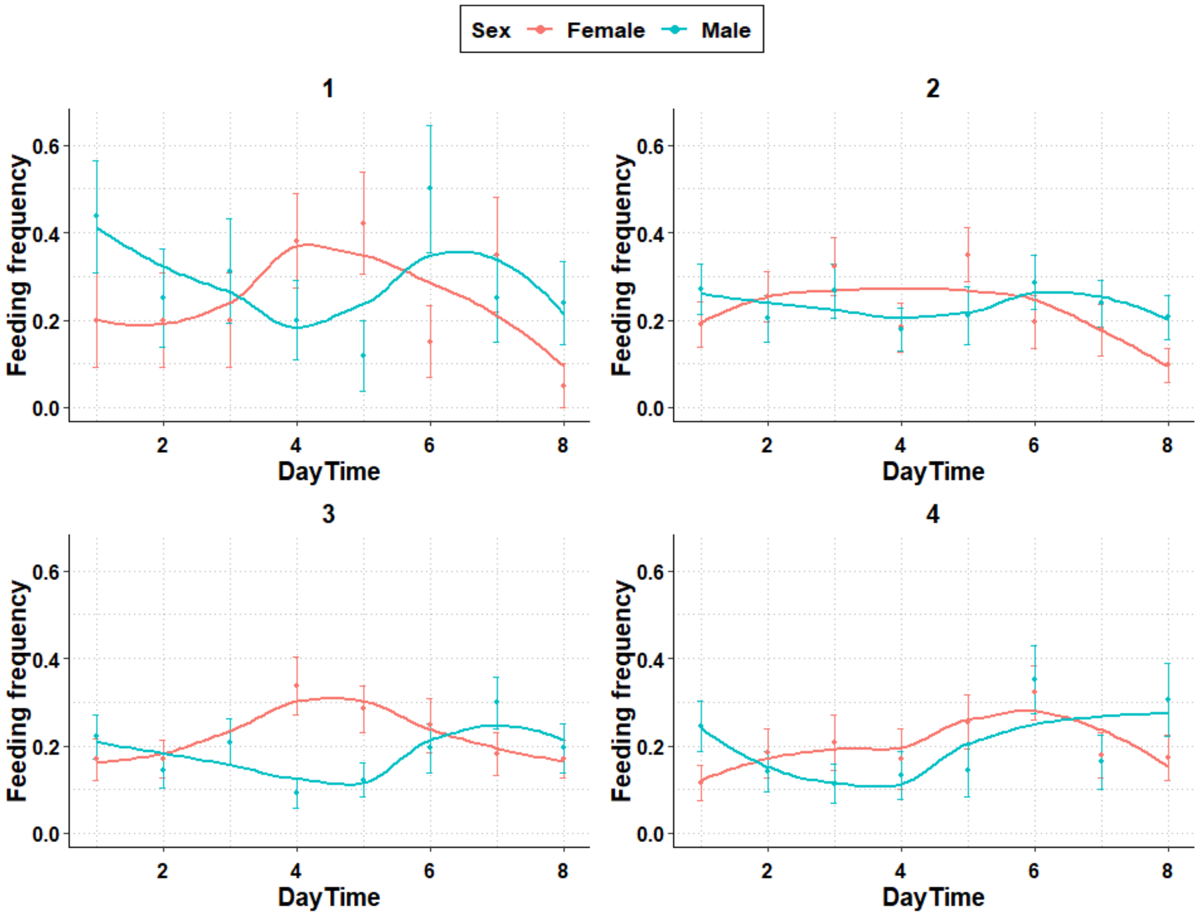

Figure C: *The observed weekly average of the daily feeding frequency between the male (blue line) and female (red line). The dots represent the feeding frequency over a daily perspective (DayTime 1-8) in the four SeasonTime weeks (SeasonTime 1-4, table 1) for both sexes. Each line shows the trend among the corresponding colour dots and the bars indicate the standard error (SE).*

Appendix D

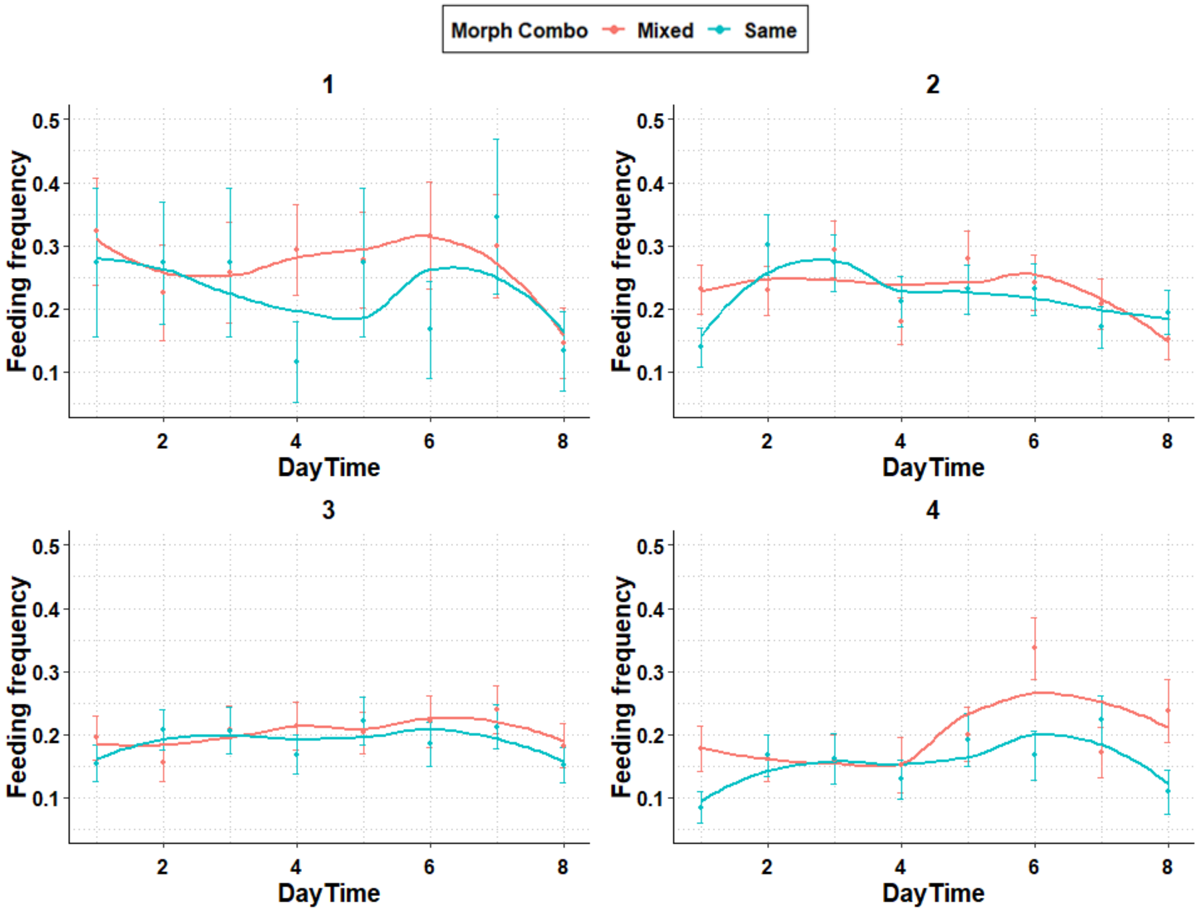

Figure D: *The observed weekly average of the daily feeding frequency between the mixed (n = 11, red line) and same morph pairs (n = 16, blue line). The dots represent the feeding frequency over a daily perspective (DayTime 1-8, table 1) for both morph combinations. Each line shows the trend among the corresponding colour dots and the bars indicate the standard error (SE).*