

## Strategies for timing of nest departure in the common guillemot *Uria aalge*

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*BIO-3950 Master thesis in Biology*  
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Northern Populations and Ecosystems

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Cover photo by Malin Kjellstadli Johansen  
Bridled common guillemot *Uria aalge*

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## Abstract

Duration of parental care in avian species varies widely, from altricial to precocial species. The seabird family Alcidae is unique among birds in the variation of mass and age at nest departure. The common guillemot *Uria aalge* exhibits an intermediate nest departure, where chicks leave the nest flightless and only at a quarter of adult body size. The aim of this study was to examine factors controlling the age, weight and wing-length of the juveniles at nest departure. To assess this I followed common guillemot families including both parents and chick, from hatching to post-departure. The results showed that females in better body condition had older chicks at departure, than females in lower body condition. Both paternal and maternal stress-levels and their body condition had a significant influence on the weight and wing-length of the chicks at departure. Indications of strong synchronized departure events during the evening hours were found, where 30 juveniles, followed in the present study, departed the colony during five evenings. The synchronized departure events were highly weather dependent – strong winds were not favoured. I did not find strong support for that parental body condition or short-term changes in food availability during the chick-rearing period had any impact on the juveniles' age at departure. The findings indicate that only the maternal body condition affects the juvenile age at departure. Whether the maternal condition alone controls the timing of nest departure, or if it is controlled by high energy gain at sea and increased food availability, remains unknown.

*Keywords:* common guillemot, *Uria aalge*, nest departure strategy, parental stress and body condition, chick growth, synchronized departure





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## Introduction

Seabirds are long-lived species and highly adapted to a marine life. They spend most part of their life out at sea, and large periods in a seabird's life are still unknown. The juveniles' life after hatching and at sea after nest departure could be important knowledge to be included in the overall understanding of population dynamics. Avian species have many different developmental patterns, extending from altricial species whose young are highly dependent on a long period of parental care after hatching, to precocial species whose young are mobile and able to locate their own food (Ricklefs, 1968; Sealy, 1973). The family Alcidae, which composes 22 extant species, is unique among birds in the amount of variation in nestling growth strategies. In this family both precocial, intermediate and semi-precocial patterns of post-hatching chick development are found (Sealy, 1973). Three auk species exhibits an intermediate nest departure strategy, accompanied by one parent (the father) the juveniles leave the breeding colony at only a quarter of adult body size and with no ability to fly (Sealy, 1973). The common guillemot, *Uria aalge*, exhibit this strategy.

Ydenberg (1989, 2001) provided a model trying to explain at what age the common guillemot chicks leave the nest site. The model is based on the principles that mortality is greater at sea (or at departure) than in the colony, but energy gain is larger at sea than at the nest site (Ydenberg, 1989). Many studies suggest that this strategy have been selected for through the trade-off between foraging and predation risk (Birkhead, 1977; Birkhead and Harris, 1985; Ydenberg, 1989; Gaston and Jones, 1998; Ydenberg, 2001). Elliot et al. (2017) corroborated parts of the model, suggesting higher energy gain at sea, but they did not find higher mortality rate at sea than in the colony. The increased parental predation risk posed by frequent foraging visits to the nest and higher juvenile growth rate at sea may result in earlier nest departure (Ydenberg, 2001). Higher provisioning effort at the nest site would be favoured to achieve a short nestling period, and the chicks developmental pattern would evolve based on a high provisioning rate, leading to rapid growth (Ydenberg, 1989). Ydenberg (1989) also looked at parent-offspring conflict as an explanation for the nest departure strategy. Where he suggested an agreement between parents and offspring on the intermediate nest departure. The duration of parental care is an important aspect when looking at the length of nestling period – variation in parental care evolves in response to parent-offspring conflict, whereby parents benefit from decreased parental investment in current offspring and the offspring benefit from increased parental investment (Trivers, 1974). And the parental investment in

chick growth might be an important factor to timing of nest departure. It is thought that the chicks' wing-length and weight at departure may be important factors to timing of departure, where a sufficient ratio between wing surface and body weight might increase the gliding distance towards the sea when jumping off the breeding cliff. Hence, decreasing the predation risk from patrolling gulls under the cliff (Birkhead, 1977).

The common guillemots are distinguished by very high wing-loading, which reduces drag and permits more effective underwater pursuit of prey. However, it also decreases aerial manoeuvrability and increases energy expenditure during flight (Witter and Cuthill, 1993; Thaxter et al., 2010). This high wing-loading rendering them unable to carry large loads of fish back to the colony, and with high-energy provisioning effort makes it costly for the parents to feed their chicks in the colony. Hence, it may be in the interest of the parents to bring the chick out at sea and closer to the feeding areas at an early stage of development. However, due to the lower predation risk of the chicks at the nest site compared to at departure and potentially at sea, the chicks will prefer a longer nestling period. The intermediate nest departure may have evolved as a result of the parents provisioning ability being lowered throughout the nestling period (Gaston and Nettleship, 1981).

One of the mechanisms that may affect the timing of nest departure is food-conditions during the breeding season, which may be observed indirectly through changes in parental stress-levels and body-condition throughout the season in relation to chick growth. The breeding season is timed to coincide with the peak of prey items, increasing ocean temperature may lead to a mismatch between energy demand and food availability, and in turn affect the breeding success of the seabirds. Measuring endocrine changes have shown to be a helpful tool in indirectly assessing the within-season changes in prey abundance (Barrett et al., 2015). Increased secretion of the stress hormone, corticosterone (CORT) is a response to decreasing energy availability in the environment (Kitaysky et al., 2007; Kitaysky et al., 2010; Barrett et al., 2015). The baseline concentration of the hormone in blood plasma rises during food shortages, therefore CORT-levels can be used as a proxy for altering food availability (Kitaysky et al., 2007; Benowitz-Fredericks et al., 2008; Doody et al., 2008; Barrett et al., 2015; Barger et al., 2016).

Another important factor to be included when seeking to understand the timing of nest departure, is the drive towards synchronicity in departure. In colonial birds, synchronized egg laying and -hatching is selected for to increase reproductive success (Benowitz-Fredericks and Kitaysky, 2005). However, we might hypothesize that nest departure may be more synchronized than egg-laying because of a swamping effect to avoid predation. In colonies with many avian and terrestrial predators this synchronicity in departure may have large impact on reproductive success. Even in the absence of strong daily fluctuations in luminance during the Arctic summer, enough environmental information on the phase of earth rotation avails to synchronize circadian rhythms (Krüll, 1976). Large synchronized departure events take place in the evening hours (Daan and Tinbergen, 1979). Synchronization in departure is highly connected to mortality, and chicks that depart from the colony later in the breeding season have a higher mortality rate mainly due to lack of predator swamping and decreased local density (Williams, 1975; Daan and Tinbergen, 1979; Gaston and Nettleship, 1981; Hatchwell, 1991). As the differing predation risk at nest site and at sea have shown to be an important mechanism behind the intermediate nest departure, the synchronicity in departure may also be an important aspect to examine in detail. Weather conditions may also play an important role in the timing of these synchronized departure events (Greenwood, 1964). The conditions the chick experience when departing the colony may be critical to survival, and strong winds directed straight into the cliff could be devastating.

The aim of this study was to examine how environmental resources and parental body condition may affect timing of nest departure and chick growth. I wanted to approach this through Ydenberg model (Ydenberg, 1989; Ydenberg, 2001). Two hypothesis arises. (1) Nest departure is determined by the increased costs experienced by parents from the chicks increasingly food demand throughout the breeding season. When the costs in food provisioning reaches a threshold, parents benefit from bringing the chick to sea in order to increase the chick growth rate and lower the cost of transporting food to the chick. (2) The nest departure is being synchronized in order to minimize predation risk. On the background of these hypothesis I made four predications I wanted to test. (1) By using levels of stress hormones (CORT) from parents' blood as proxy of environmental prey resources available and observations of chicks' diet, I predicted that if resources were the determining factor for timing of nest departure a negative relationship between available resources and age at departure would be found. (2) I predicted that greater parental body condition would prolong the nestling period and increase the chicks' wing-length and body weight. (3) I also predicted

that higher rate of synchronized departure would decrease the predation risk by predator swamping, (4) and if unfavourable weather conditions played a role I also predicted that strong winds would further increase the synchronicity.

These predictions were tested by following families, including both parents and chicks during their nestling period, from hatching to post-departure. Parental stress-levels, body condition and biometric measurements was sampled to assess whether they affected the chick growth and age at departure. Weather and chicks' diet was used to assess if such factors had an impact on the timing of nest departure.

## Methods

### Study area

The study was carried out at Hornøya (70° 23' N, 31° 9' E), a 0.5 km<sup>2</sup> island in northeast Norway (Figure 1). Hornøya is a part of the Hornøya and Reinøya Nature Reserve and located in the southern Barents Sea. The nesting cliffs for the common guillemot are facing north-west at Hornøya. It is one of the few areas in mainland Norway that is characterized as Arctic. It is located in the bioclimatic subzone E, the warmest zone of the Arctic tundra, with mean July temperature between 9-12 degrees Celsius (Walker et al., 2005). However, the plant ecology of this bird island, does not reflect the Arctic tundra. The landscape is characterised as typical bird cliff, with its lush vegetation that is highly fertilized by the bird guano.

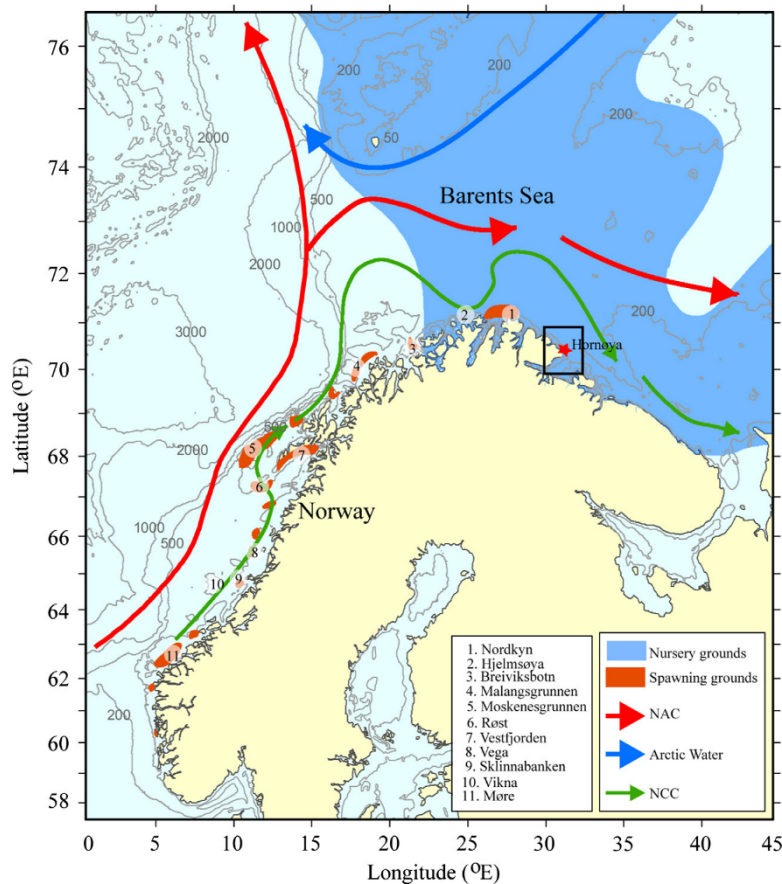


Figure 1: Common guillemot colony at Hornøya (red star) centered in the approximate foraging area of chick-feeding adults (black box). Illustrating the most important current features, the Norwegian Coastal Current (NCC), and the Norwegian Atlantic Current (NAC), the Northeast Arctic cod spawning areas numbered from north to south (from Barrett et al. (2015)).

The breeding population on Hornøya is approximately 25 000 individuals (Reiertsen et al., unpublished). Hornøya is a key site for the SEAPOP monitoring program, with one of the longest time series on population size, survival and breeding biology of seabirds in Norway (Anker-Nilssen et al., 2005). Almost 30 years of data have been collected from the common

guillemot colony at Hornøya, providing scientists with exceptional data on annual fluctuations in both demographic rates and population size (Barrett, 2001; Barrett and Erikstad, 2013; Erikstad et al., 2013). There is no terrestrial predator such as red fox *Vulpes vulpes* and arctic fox *Vulpes lagopus* at Hornøya and the main predators on the common guillemots are great black-backed gull *Larus marinus*, herring gull *Larus argentatus* and raven *Corvus corax*. The seabirds on Hornøya gets their energy resources from the highly productive Barents Sea. The local variation in productivity is highly dependent on the transport of water by the offshore Norwegian Atlantic Current (NAC) or by the nearshore Norwegian Coastal Current (NCC) (Figure 1) (Loeng, 1991). High productivity through both primary and secondary production supports large stocks of cod *Gadus morhua*, herring *Clupea harengus* and capelin *Mallotus villosus*. The cod spawning occurs in early spring, and the spawning grounds are widely distributed along the Norwegian coast (Figure 1). The egg and larvae are transported by the NCC and NAC along the coast into the Barents Sea (Dalpadado et al., 2012). The larvae drifts past many seabird colonies within the foraging range of breeding adults, providing good breeding condition for the colonial seabirds (Figure 1) (Barrett et al., 2015). The distribution of prey items in the Barents Sea may be driven by changes in oceanographic parameters with temperature as the most important (Hjermann et al., 2004). These fluctuations in the marine climate may cause severe changes in distribution and composition of fish communities both between and within seasons in main feeding areas.

### Study species

The common guillemot is a long-lived seabird with a boreal, circumpolar and low-Arctic distribution (Gaston and Jones, 1998). It is the largest of the extant auk species, with its 39-43 cm in length and weighing approximately 900-1300 grams (Gaston and Jones, 1998). There are no differences in morphological characters between the sexes, however the males are usually 3-5% larger than the females. The common guillemots are socially monogamous, and have high site fidelity – breeding in colonies located at rocky cliffs and produce a maximum of one chick a year. In the North Atlantic the common guillemot occurs in two colour morphs; one bridled-morph with a white eye-ring and a stripe behind the eye and a non-bridled morph with a complete dark brown/black head. No apparent differences in behaviour have been documented and mating between the morphs appears to be random (Harris and Wanless, 1986; Kristensen et al., 2014). The increase in the abundance of bridled individuals towards the north may be an indication that they are better adapted to a colder environment (Birkhead,



1984; Harris and Wanless, 1986; Harris et al., 2003; Reiertsen et al., 2012). The overall abundance of the common guillemot in the North Atlantic have increased during the twentieth century, with a population of nearly 3 million pairs (Mitchell 2004). However, the Norwegian population has declined dramatically from 120-160 000 pairs in the 1960s to approximately 15 000 pairs in 2005 (Barrett et al., 2006). Thus, the common guillemot is classified as critically endangered in the Norwegian Red List (Henriksen and Hilmo, 2015). Despite these declines in the Norwegian mainland population of common guillemots, the population at Hornøya has increased steadily since mid-1980s to have reached a population of 25 000 individuals (Erikstad et al., 2013, Reiertsen et al., unpublished). Food shortage and alternating food composition may have a major influence on the survival and breeding success of the common guillemot and may be one of the drivers for the massive decline in the Norwegian population.

The common guillemot is a pelagic pursuit-diver, feeding mainly on small fish such as capelin, 1-group herring, 0-group cod and sandeel *Ammodytes* sp. It is a prominent resident bird in the Barents Sea area, and is highly dependent on these fish species during their breeding season (Loeng, 1989; Barrett et al., 1997; Barrett, 2002). During the winter 1986/1987, the common guillemot population collapsed by more than 80%. The collapse occurred in a period when the abundance of capelin, 1-group herring and 0-group cod were all very low, indicting the importance of these fish species (Erikstad et al., 2013). Important food items in the chicks' diet is both capelin and 1-group herring, but also sandeel have been shown to make up significant proportion of the chicks' diet (Loeng, 1989; Barrett et al., 1997; Barrett, 2002; Barrett and Erikstad, 2013). In addition, 0-group cod and 1-group haddock *Melanogrammus aeglefinus* has been shown to be more important in the diet of adult birds (Bugge et al., 2011).

### Field work

In total, 41 families, including mother, father and chick, were followed and studied intensively during the field season from the 20<sup>th</sup> of June to the 19<sup>th</sup> of July 2016. The families were chosen randomly from a sub-colony on the north-west side of the island, including both early and late hatchers. This sub-colony has been monitored since 2009, where families of chicks and adults have been followed from hatching to near departure (Kristensen et al., 2012). In order to continue and expand this data set both ringed and non-ringed birds were chosen.



Figure 2: Illustrating the capturing of adult common guillemot using a noose pole. Photo by: Malin Kjellstadli Johansen.

Newly hatched chicks were captured using a pole with a hooked end, at ages 1-4 days (N=31), 9 chicks with known hatching date were supplemented at ages 14-15 to increase the sample size. Tarsus was measured with a sliding calliper, wing with a ruler and the weight using a Pesola spring scale. A blood sample was drawn at first capture for genetic sexing, and the blood was stored in ethanol. Individuals were marked with plastic tape around one foot, with a number representing family, to be able to identify them throughout the season. Fifteen days after first capture, chicks (N=36) if still alive, were caught and measured for a second time. Age 15 has been documented as the youngest age the chicks have been when leaving the breeding site (Nettleship and Birkhead, 1985). If chicks remained in the colony at 20 days of age (N=34) and 25 days (N=12) they were caught and measured, if their legs were big enough I attached plastic and metal ring with an individual code on the right foot and left foot, respectively.

The respective parents of the chicks were captured as soon as possible after the chicks hatched (N=61) (Figure 2). Parents without ring, got ringed with a plastic and metal ring with an individual code, biometric measurements were taken and for genetic sexing a blood sample was drawn. All adults were weighed using a Pesola spring scale. To assess the baseline stress levels in the parents, a blood sample of minimum 30  $\mu$ l was drawn within 3 minutes of

capture to prevent increased release of the stress hormone corticosterone (CORT) due to the stressful event of capture. Twelve days after the first capture, parents (N=73) were caught again to be weighed and a second blood sample was taken to analyse the baseline CORT-level at the end of the nestling period. CORT-levels in the breeding birds may give us an idea on how stressed the birds are during chick-rearing and can be used as a proxy to assess how good the food availability is throughout the period (Wingfield and Kitaysky, 2002; Doody et al., 2008; Satterthwaite et al., 2012). The chicks were thoroughly monitored on the ledge. When some of the earlier hatchers approached 20 days of age, I started to spend the evenings below the colony, and I observed that departure did not usually start before 17:00-19:00 hours. In total 7 days, and approximately 7 hours each day, were spent below the cliff, looking for marked chicks departing the nest. Under the ledge (Figure 3), I had full overview over the chicks that departed, and chicks with plastic tape or rings around their feet were caught. In many common guillemot colonies, the breeding cliffs goes straight into the ocean, making it difficult to obtain an overview of departing chicks. However, below the monitored common guillemot ledge at Hornøya, the departing chicks need to cross a vegetated and rocky area to reach the shore line. This habitat feature makes it possible to observe the departing chicks and enables catching of the marked chicks before they reach the ocean (Figure 3).



*Figure 3: Underneath the common guillemot colony. Chicks departing from the colony landed in the grass area under the cliff making it possible to catch them before they reach the ocean. Photo by: Malin Kjellstadli Johansen.*

Biometric measurements were taken, and each chick got light-weighted geolocation (Global Location Sensing or GLS) loggers attached onto their plastic ring. The GLS loggers are part of another ongoing study that will provide important and new knowledge of immature common guillemots' distribution at sea – when we retrieve them after 3-4 years when they have started to recruit as breeders. GLS loggers register ambient light to determine location. Sunrise and sunset gets estimated from thresholds in light curves; longitude is derived from the time of local midday with respect to Greenwich Mean Time and Julian day, and from the day length, latitude is derived (Wilson et al., 1992; Hill, 1994). Handling time of the chicks after they had departed was minimized as much as possible to prevent any unnecessary stress and prolonging the time from departure to reconnection with the parents.

The chick diet was also assessed in order to link any relationship between parents and chicks with any potential changes in chick diet. This was performed by observational feeding watches of the colony using binoculars (10x42) to minimize the disturbance of the birds. The observations were made not more than 10 meters away from the birds in the colony. Most of the feeding watches took place between 10:00-14:00 hours, and some from 16:00-19:00 hours, and in total 16 days were spent observing birds returning with a single prey item in their bill. Only prey items delivered to chicks were noted, and the observed prey items were capelin, herring, sandeel and small unidentified 0-group and 1-group fish, most likely gadoids, were noted as “other”. Weather data was collected from Vardø Radio, the nearest meteorological station to Hornøya. The average wind direction and speed was calculated between 17:00-01:00 hours from the 8<sup>th</sup> – 18<sup>th</sup> of July.

### Laboratory analysis

Adult and juvenile common guillemots cannot be sexed by visible characters, therefore a DNA-based sexing technique (Griffiths et al., 1998) was performed at Nord University in Bodø, Norway by Truls Moum. DNA was extracted with DNeasy Blood & Tissue kit from Qiagen. Regions on the sex-linked CHD-W, and CHD-Z genes (chromobox-helicase-DNA-binding gene) were PCR amplified using P2 and P8 primers (Griffiths et al., 1998), and the PCR products analysed by running electrophoresis on a 2% agarose gel. Different number of bands in electrophoreses gel analysis, distinguish the two sexes, where females are identified with two bands and males with a single band. This sexing-test have been proven to be robust for avian species, including the common guillemot, but with the possible exception of the

ratites (Griffiths et al., 1998; Birkhead et al., 2001). By using an enzyme immunoassay (Munro and Stabenfeldt, 1984; Munro and Lasley, 1987), plasma CORT concentration was measured in the laboratory of the Swiss Ornithological Institute in Sempach by Susanne Jenni-Eiermann. The detection limit of the assay was 1.21 ng/mL. Inter-assay variation ranged from 6.7% to 8.38%. Full details about CORT-analysis are found in Kristensen et al. (2012).

### Statistical analysis

All statistical analyses were performed using R software, version 3.3.2 (R Core Team, 2016). Body size of adult birds were calculated using a principal component analysis (PCA) on measurements of head-bill, tarsus and wing-length. Parental body condition was calculated using the residuals from a linear regression of body weight against the first axis of PCA. Body condition was estimated on females and males separately, and at two different stages during nestling period; around hatching (1-5 days after) and 12 days after the first measurement. Maternal/paternal body condition around hatching and 12 days after the first measurement will be addressed as Cond1.F, Cond2.F, Cond1.M and Cond2.M, respectively. CORT-levels were also measured twice in the nestling period; maternal/paternal stress-levels around hatching and 12 days after the first measurement. These variables will be addressed as Cort1.F, Cort2.F, Cort1.M and Cort2.M, respectively.

I examined candidate models for each response variable: juvenile wing-length, weight and age (days) at departure using the *dredge* function in the MuMIn package. The dredge function performs an automated model selection with all combinations of nested models within the supplied global model, and the models are ranked using AIC<sub>C</sub> (Barton, 2013). The explanatory variables considered were Cond1.F, Cond2.F, Cond1.M, Cond2.M, Cort1.F, Cort2.F, Cort1.M and Cort2.M, hatching date, age at departure (jumpage), juvenile wing-length (Juvwing6) and weight at departure (Juvweight6). Parental parameters were included to be used as a proxy for parental body condition and/or environmental conditions experienced by the parents during the nestling period (Wingfield and Kitaysky, 2002; Satterthwaite et al., 2012; Barrett et al., 2015). In models with juvenile wing-length, weight and age at departure as response variables, juvenile wing-length, weight and age at departure were excluded as explanatory variables, respectively.

Model selection and ranking was based on Akaike's Information Criterion corrected for small sample size  $AIC_C$  (Burnham and Anderson, 2002). Models with  $\Delta AIC_C \geq 10$  were considered improbable and failed to explain some substantial explainable variation in the data, and those where  $4 \leq \Delta AIC_C \leq 7$ , were considered less plausible than models having  $\Delta AIC_C \leq 2$  (Burnham and Anderson, 2002). Models with  $\Delta AIC_C \leq 2$  relative to the best model in the candidate set were considered strongly plausible (Burnham and Anderson, 2002), and the model with the fewest parameters having  $\Delta AIC_C \leq 2$  was chosen.

The coefficients of determination for the selected models ( $r^2$ ) and partial  $r^2$  were calculated, as were the estimates and levels of significance (p-values) for variables included in the selected models. Means are given in  $\pm SE$  (standard error). The differences between the explanatory variables were investigated using Pearson's correlation coefficient (Appendix D), to assess whether the variables were highly correlated or not. I also looked at the variance inflation factor (VIF) High correlation between predictors is not wanted, as it can increase the variance of the regression coefficients. When predictors are not correlated the  $VIF = 1$ , when  $1 < VIF < 5$  they are moderately correlated and  $VIF > 5$  to 10 they are highly correlated.

## Results

### Juvenile wing-length at departure

All candidate models had  $\Delta AIC_C \leq 7$ , hence none of them were considered improbable (Appendix A). The best model included four predictor variables (Cort1.M, Cort2.F, Cond2.M and Cond2.F) with an explained variance of 95 % (Table 1). Maternal body condition (Cond2.F) was the most important single variable included in all the best ranked models.

*Table 1: Estimated slopes with SE, explained variance (partial  $r^2$  and model  $r^2$ ), t-value, p-value and variance inflation factor (VIF) for the paternal CORT-levels around hatching (Cort1.M) and maternal CORT-levels at day 12 (Cort2.F) and paternal and maternal body condition at day 12 (Cond2.M and Cond2.F) that best explained the variation in juvenile wing-length at departure.*

Parameter	Estimate ( $\pm$ SE)	t	P	Partial $r^2$	Model $r^2$	VIF
<b>Intercept</b>	81.45 (1.47)	55.40				
<b>Cort1.M</b>	-0.57 (0.19)	-2.90	0.014	0.43	0.95	1.88
<b>Cort2.F</b>	-0.36 (0.09)	-3.961	0.002	0.59	0.95	1.04
<b>Cond2.M</b>	-0.04 (0.01)	-4.08	0.002	0.64	0.95	1.25
<b>Cond2.F</b>	0.09 (0.01)	7.40	<0.0001	0.83	0.95	1.67

Paternal stress-levels early in the season and maternal stress-levels late in the season both led to juveniles with shorter wings at departure, compared to less stressed parents (Figure 4B and 4D). Additionally, the parents differed in the relationship between their body condition and the juvenile wing-length. Females in good body condition late in the season had juveniles with longer wings at departure compared to females with poorer body condition (Figure 4A). However, males with good body condition late in the season had juveniles with shorter wings at departure, compared to males with poorer body condition (Figure 4C).

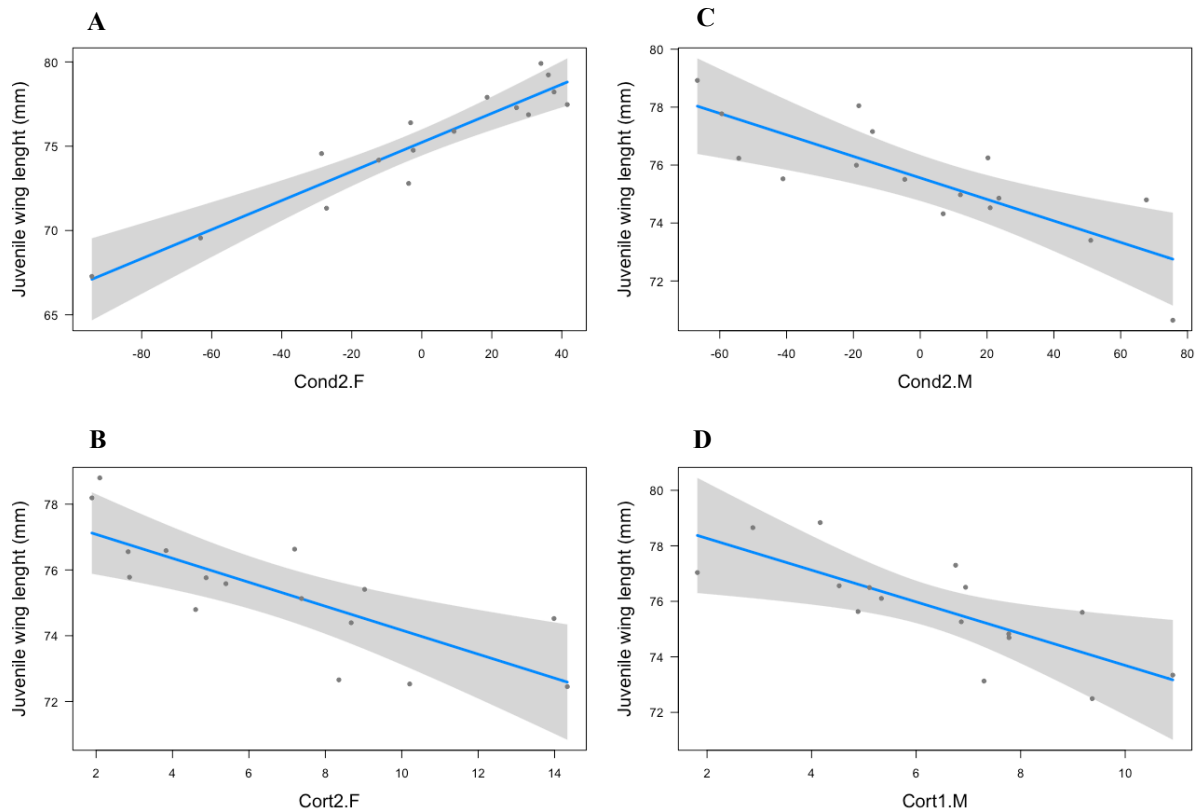


Figure 4: The relationship between juvenile wing-length at departure and A) maternal body condition at day 12 of the chick-rearing period ( $Cond2.F$ ,  $r^2=0.83$ ), B) maternal CORT-levels at day 12 in the chick-rearing period ( $Cort2.F$ ,  $r^2=0.59$ ), C) paternal body condition at day 12 in the chick-rearing period ( $Cond2.M$ ,  $r^2=0.64$ ) and D) paternal CORT-levels around hatching ( $Cort1.M$ ,  $r^2=0.43$ ).

### Juvenile weight at departure

None of the candidate models were interpreted as improbable as all  $\Delta AIC_C \leq 5$  (Appendix B). Three of the candidate models had  $\Delta AIC_C \leq 2$ . The best model describing the juvenile weight at departure contained two predictor variables, maternal and paternal stress-levels ( $Cort2.F$  and  $Cort1.M$ ). The model gave an explained variance of 61 % (Table 2).

Table 2: Estimated slopes with SE, explained variance (partial  $r^2$  and model  $r^2$ ),  $t$ -value,  $p$ -value and variance inflation factor (VIF), for paternal CORT-levels at hatching and maternal CORT-levels at day 12 ( $Cort1.M$  and  $Cort2.F$ ) that best explains the variation in juvenile weight at departure.

Parameter	Estimate ( $\pm$ SE)	t	P	Partial $r^2$	Model $r^2$	VIF
<b>Intercept</b>	311.21 (17.06)	18.25				
<b>Cort1.M</b>	-7.61 (2.09)	-3.63	0.003	0.50	0.61	1.00
<b>Cort2.F</b>	-3.64 (1.31)	-2.78	0.016	0.37	0.61	1.00



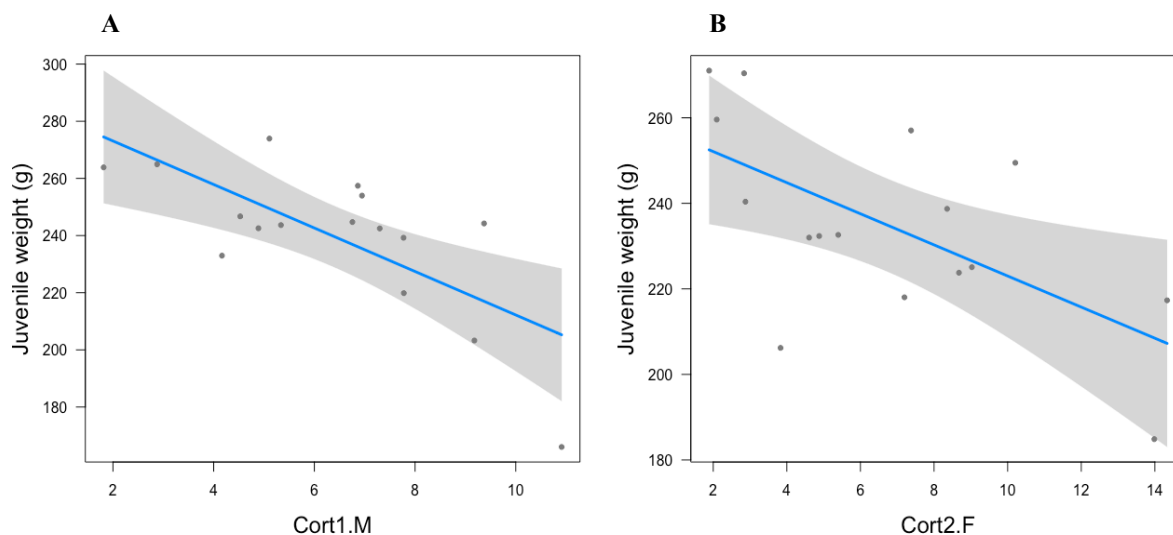


Figure 5: The relationship between juvenile weight at departure and A) paternal CORT-levels around hatching (Cort1.M,  $r^2=0.50$ ) and B) maternal CORT-levels at day 12 in the chick-rearing period (Cort2.F,  $r^2=0.37$ ).

Both paternal and maternal stress-levels had an impact on the juvenile weight at departure. Juvenile weight at departure decreased with both paternal and maternal stress-levels. Hence, heavier juveniles had parents with lowest levels of CORT in their blood plasma (Figure 5A and 5B)

### Growth rates in chicks

Wing-length continued to increase throughout the nestling period, with its highest average at departure (Table 3, Figure 6). However, body weight increased rapidly up to day 15 and then in average decreased up until departure (Table 3, Figure 6). The juvenile wing-length and weight at departure were strongly positively correlated ( $r = 0.66$ ,  $p = 0.005$ , Appendix D)

Table 3: Juvenile mean body weight (g) and wing-length (mm) at different stages in their nestling period. Including only chicks ( $N=17$ ) that were measured at every sample day (hatching, day 15, day 20 and after departure).

Age	Weight ( $\pm$ SE)	Wing ( $\pm$ SE)
<b>Hatch</b>	97.1 (3.3)	30.3 (0.8)
<b>Day 15</b>	249.1 (7.1)	58.4 (1.7)
<b>Day 20</b>	247.9 (6.6)	68.2 (1.5)
<b>Departure</b>	240 (6.4)	74.6 (0.8)

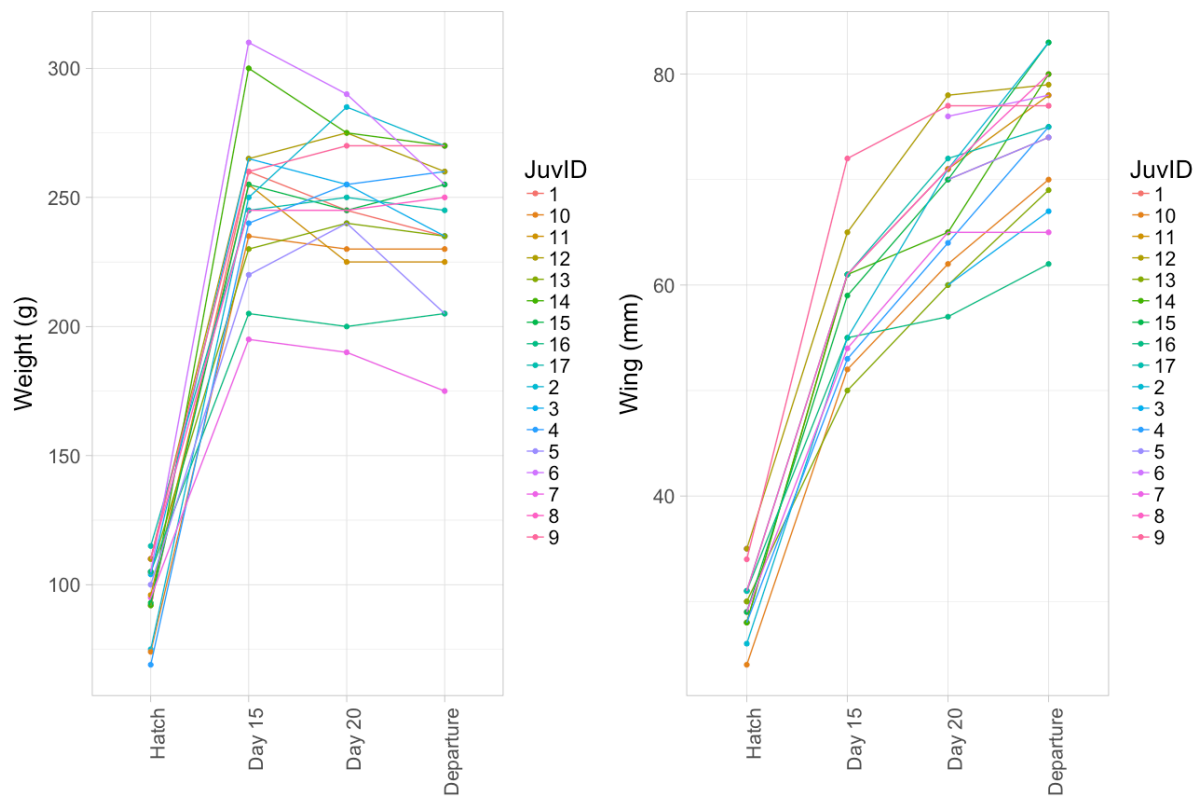


Figure 6: Juvenile weight (g) and wing-length (mm) at 1-4 days after hatching, day 15, day 20 and when they had departed the nest ( $N=17$ ). Including only chicks that were measured at every sample day (hatching, day 15, day 20 and after departure).

## Juvenile age at departure

All candidate models had  $\Delta AIC_C \leq 4$ , and therefore considered plausible (Appendix C). The best model estimating the relationship between juvenile age at departure and parental parameters, included only one parameter (Cond1.F), this variable explained 44 % of the variance (Table 4). Hence, juveniles were older when departing if the maternal body condition was greater around hatching (Figure 7).

Table 4: Estimated slopes with SE, explained variance (model  $r^2$ ), t-value and p-value for the maternal body condition (Cond1.F) that best explains the variation in juvenile age at departure.

Parameter	Estimate ( $\pm$ SE)	t	P	Model $r^2$
<b>Intercept</b>	22.19 (0.43)	51.32		
<b>Cond1.F</b>	0.03 (0.01)	3.30	0.005	0.44

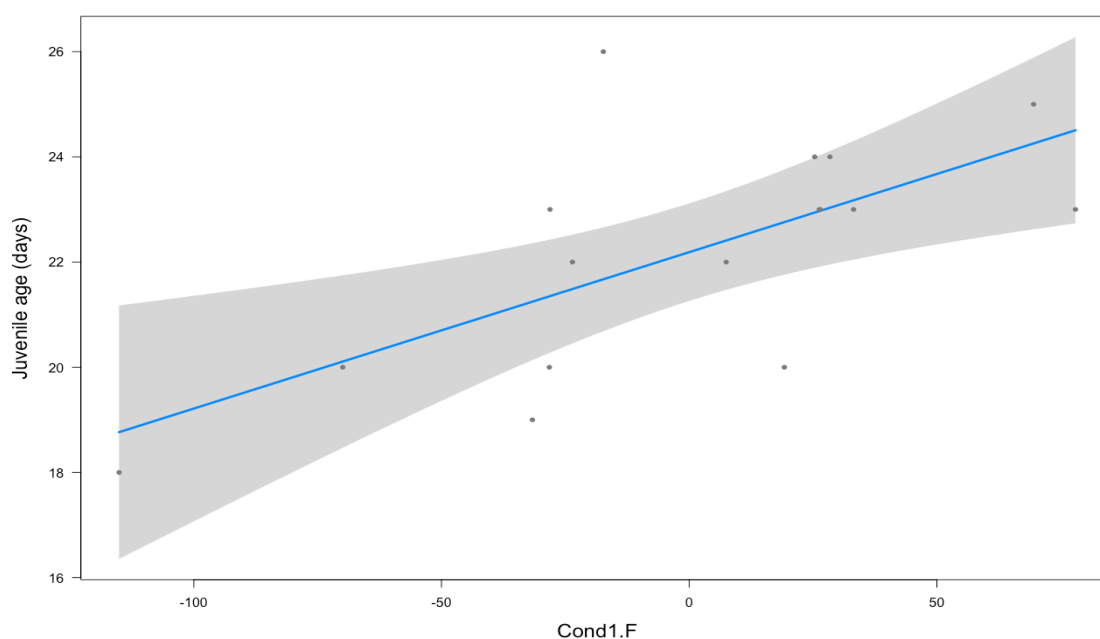


Figure 7: Relationship between juvenile age (days) at departure and maternal body condition around hatching and ( $r^2=0.44$ ).

No significant correlation was found between juvenile wing-length and age at departure ( $r = 0.41$ ,  $p = 0.11$ , Appendix D), and weight and age at departure ( $r = -0.07$ ,  $p = 0.79$ , Appendix D).

### Synchronized departure

Common guillemot chicks hatched over a period of 10 days (16<sup>th</sup>-25<sup>th</sup> of June), whereas the same chicks departed from the colony over a 7-day period (10<sup>th</sup>-16<sup>th</sup> of July) (Figure 8).

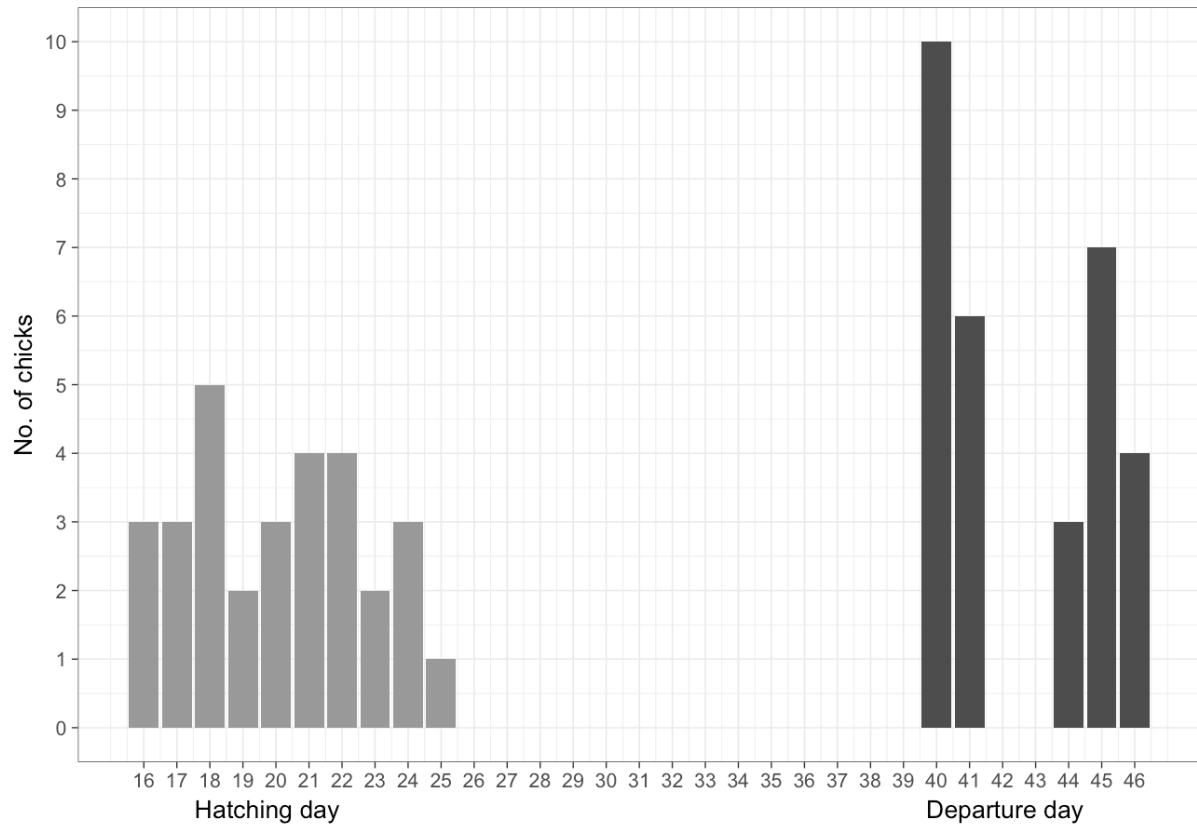


Figure 8: Overview of hatching day (16<sup>th</sup> – 25<sup>th</sup> of June, N=30) and number of chicks departing the colony (10<sup>th</sup> - 16<sup>th</sup> of July, N=30). Days are given from 1<sup>st</sup> of June.

These results show some synchronization in departure time, from what should be expected from their hatching date. All the chicks departed the colony between 19:00-00:00 hours, showing a preferred time frame during the day of departing. Out of the 41 families, 30 chicks were recaptured under the cliff after departure. Eight chicks died or departed the colony in a time window I was not present under the cliff. Three chicks were still observed in the colony when I left the field (19<sup>th</sup> of July), they were 21, 27 and 31 days of age. None of the chicks from this sample was observed preyed upon before they reached the sea.

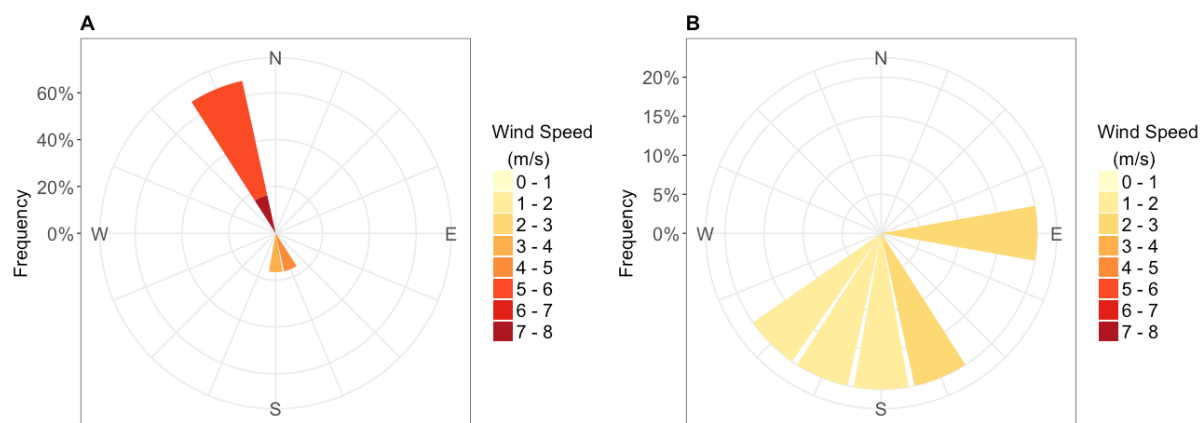


Figure 9: Mean wind direction and speed in in the time-period 17:00-01:00 hours from 8th-18th of July. A) When none of the marked birds departed and B) when the marked birds departed.

During days with strong northerly wind none of the chicks followed in this study departed the colony. Wind conditions therefore seem to influence the day of departure and may synchronize departure time even further. Wind from the north hits the colony straight on, making conditions non-favourable for departure (Figure 9). When the wind direction shifted and wind speed decreased, all our marked chicks (N=30) jumped (Figure 9, Figure 10)

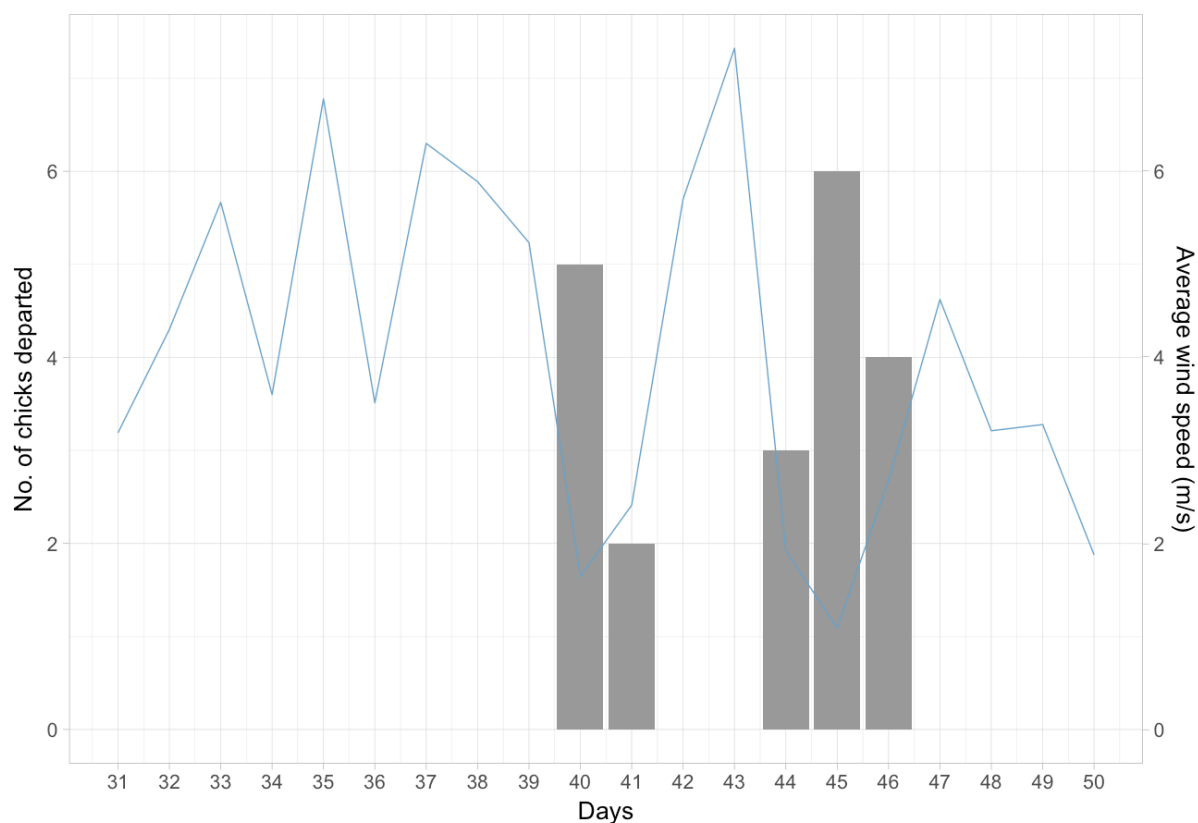


Figure 10: Number of chicks departed (bars) and the average wind speed (line) at Vardø radio in the time-period (17:00-01:00 hours) from 1st-30th of July. "Days" are given from 1<sup>st</sup> of June.

### Chick diet

The chicks' diet during the nestling period consisted mainly of capelin, sandeel and herring, and made up 50.3, 30.1 and 10.5% of the diet, respectively. In addition, a smaller fraction (8.9 %) of the diet consisted of unidentified fish (mainly gadoids) (Figure 11).

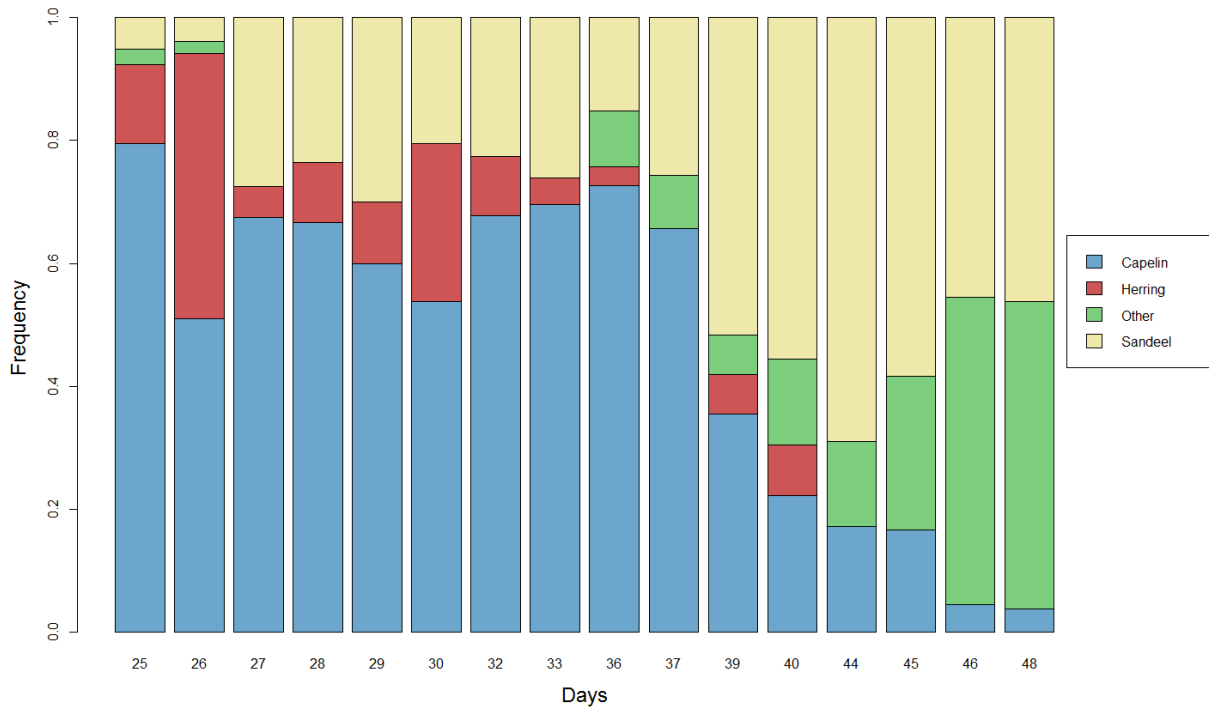


Figure 11: Proportion of capelin, herring, sandeel and unidentified small fish (other) in chicks' diet ( $N=550$ ) during nestling period. "Days" are given from the 1<sup>st</sup> of June.

The composition of the diet varied significantly during the 16 days of observation ( $\chi^2 = 325.51$ ,  $df = 45$ ,  $p < 0.001$ ) (Figure 11). A clear change in the diet was observed during the time-period when the first chick departed (day 40) (Figure 11). As a decrease of especially capelin, and herring in the chicks' diet was observed, an increase of smaller sandeels and small-unidentified fish (most likely gadoids) was observed in the chicks' diet.

## Discussion

In this study, I did not find strong support for my hypothesis that both parental stress-levels and body condition are the drivers behind the common guillemot intermediate nest departure. The only support for this hypothesis, was that maternal body condition around hatching had a positive impact on the juveniles' age at departure. This indicates that mothers in good body condition around hatching can afford to have chicks staying longer at the nest-site. However, the results showed as predicted that both parental stress-levels and body condition had impact on juvenile wing-length and weight at departure. I also observed that the nest departure is highly synchronized and weather dependent, which might support the hypothesis that chicks should depart more synchronously to avoid predation through a swamping effect.

Additionally, indications of differential allocation towards longer wings and lower mass of departing chicks and that parents seemed to have differential compensating chick providing strategies during the chick-rearing period were found.

### Parental stress and body condition affecting juveniles at departure

To assess whether environmental conditions had any impact on the timing of nest departure, parental blood CORT-levels, indicating stress-levels, were used as a proxy for short-term changes in food abundance and energy available during the breeding season (Barrett et al., 2015). I predicted that if resources would be a determining factor for timing of nest departure I would find a negative relationship between stress-levels and age at departure. Though, neither paternal nor maternal stress-levels had any effects on juvenile age at departure, suggesting other factors to be more important in determining the age at departure.

Maternal body condition around hatching was shown to have a positive effect on the age at departure. This supported part of my prediction, that chicks with mothers in better body condition stayed longer at the nest site. Good body condition might indicate a higher ability to feed the chicks for a prolonged time at the nest – and the urge of getting the chicks out to sea would not be as great as if mothers were in poorer body condition. However, no other parental parameters showed any relationship with the timing of juvenile departure. A large variation in juvenile age at departure was observed, varying from 18 - 26 days of age, suggesting no preferred age at departure, and other factors might play a more important role in the timing of departure than age.

The results did however provide evidence of the importance of resource availability in potential chick growth. Negative relationship was found between parental stress-levels and the juvenile wing-length, indicating that more stressed parents, possibly due to lower food availability, have chicks with lower growth. The results showed a difference in parental stress-levels at different time of the rearing-period which had an impact on the chicks' wing-length at departure. Paternal stress-levels had an impact around hatching, while maternal stress-levels showed an impact later in the chick-rearing period. The results also showed differential effects of parental body condition on juveniles' wing-length. While there was a positive relationship between maternal body condition late in the season and juvenile wing-length at departure, there was a negative relationship with the same parameter and paternal body condition late in the nestling period. Thus, it indicates that male parents may allocate more of the resources to their own maintenance late in the season instead of putting it into the growth of the chick. This could indicate sex-specific parental effort at different parts of the breeding season, as they might compensate between each other – as they will have differing responsibilities after nest departure. A greater impact of paternal stress-levels around hatching may suggest that males have a higher rate of parental care early in the nestling period. And the negative impact of higher paternal body condition may be a result of decreased provisioning effort towards the chick later in the nestling period. It might also indicate that males in lower body condition are less selfish than those in good condition. The chicks are predominantly followed by the males at sea (Gaston and Jones, 1998), and in anticipation of the increased parental effort after nest departure they might allocate more foraging effort to their own needs (Thaxter et al., 2009). This can be supported by a higher rate of provision effort towards the chick by the female as the males are observed to take longer foraging trips both in duration and time most likely to self-foraging (Wanless and Harris, 1986; Thaxter et al., 2009). The common guillemot has high site-fidelity and are monogamous. Females stay behind after nest departure to defend the nest site, and will then have an earlier opportunity than males to refill nutritional reserves (Wanless and Harris, 1986) (pers. obs.). This might support why higher maternal stress-levels late in the nestling period have a large impact on the juvenile wing-length and weight. The positive impact of higher maternal body condition late in the breeding season – might indicate higher ability to provide chicks with enough food to grow larger wings during the nestling period. Parental stress-levels and body condition are not necessarily mutually exclusive parameters. A good body condition may reflect the ability to minimize stress by optimizing foraging. However, adult stress-levels reflects short-term changes in food availability and body condition reflects more the overall condition of the bird.



The composition of chicks' diet throughout the nestling period may indicate if there are any changes in the food availability and within the marine ecosystem during the season. For the common guillemots breeding at Hornøya; capelin, 1-group herring and sandeels are the most important fish species in the chicks' diet (Barrett et al., 1997; Barrett, 2002; Barrett and Erikstad, 2013). All of these fish species are highly calorific and easily digested (Hilton et al., 2000). The observed dominance of capelin, herring and sandeel in our data corroborates these earlier studies on the importance of these species. Capelin was the predominant fish species in the chicks' diet, making up 50 % of the diet. As the breeding season progressed the composition of prey items shifted, from mainly capelin to a higher intake of sandeel and unidentified fish (most likely gadoid larvae) (Figure 11). There was also a decrease in the sandeels' body size late in the nestling period (pers. obs). The change in the chicks' diet during the nestling period, might suggest a spatial shift in capelin distribution and availability. This has also been observed in the kittiwake *Rissa tridactyla* diet during their breeding season (Ponchon et al., 2014). Capelin – is a cold-water fish species with a near-coast distribution in spring and early summer – making it perfect prey item for the breeding seabirds at Hornøya. Late in the summer their distribution shifts and their main feeding area moves northwards (Gjøsæter, 1998). This might be one of the factors triggering the timing of nest departure. If the capelin moves further away from the colony, the parents will not be able to provision the chicks with enough food as their energy demand increases. This may support the theory that as the chicks' energy demand rises it becomes more profitable for the parents to bring the chick out at sea. However, that adult diet during chick-rearing period differs from the chicks' diet (Bugge et al., 2011). Adults are observed to forage on poorer quality fish than fish fed to their chicks, with a higher portion of 0-group cod in their diet (Bugge et al., 2011). Stress-levels may provide us with a proxy for relative forage-stress in parents due to short-term changes in food availability. Whereas, observed chicks diet may give us a better understanding to how prey availability affects the timing of departure. If there is a shift in the capelin distribution as the nestling period goes on, this might have an impact on the timing of departure.

### Juvenile growth at nest-site

The juvenile weight has been shown to reach a plateau at around 250 gram, and some studies have shown a decrease in body weight at the end of their nestling period (Birkhead, 1977). On the other hand, the wing grows continuously (Harris et al., 1991; Barrett and Erikstad, 2013). This is supported by my results - juveniles' wings grew continuously and rapidly throughout the nestling period and weight was observed to level off and decreased after day 15 (Figure 6). Wing-length is thought to be an important factor in when the juveniles leave the nest to increase the gliding distance from the cliff, which could decrease predation risk (Birkhead, 1977; Hedgren, 1981). Contrary to Ydenberg's model, it has been suggested that it is not only the juvenile weight as a measurement of development that influences timing of departure, but that wing-length should also be included (Birkhead, 1977; Hedgren, 1981; Hatch, 1983). Studies done on the Brünnich's guillemot *Uria lomvia* showed that departure age declined significantly with 14-day wing-length (Hipfner and Gaston, 1999). No such correlation was found between wing-length and age at departure in our study.

The decrease in body weight may be a result of lesser food provisioning by the parents (Sealy, 1973; Birkhead, 1977). The energy demand of the juvenile increases during the nestling period, and a trade-off in allocation of growth may shift to increase the energy input in wing growth. To increase the glide length from cliff to ocean, juveniles benefit from lighter weight and longer wings. My results showed a positive relationship between juvenile weight and wing-length, indicating that heavier chicks had longer wings. However, I observed that juveniles' weight decreased from day-15 until departure (Figure 6). This decline in body weight, might be a parental cue to the chicks that departure needs to occur. Declined feeding rate of chicks at the end of nestling period can support a parent-offspring conflict. This was however not tested in our study. Parents take advantage of shorter nestling period, whereas juveniles prefer a longer nestling period. A parental decrease of feeding rate towards the chick might force the chick to depart from the colony earlier than they would prefer. As mentioned earlier a significant shift in the diet composition occurs during the nestling period. However, this shift is observed after the weight is detected to level off and decrease. I believe that the most likely explanation behind the weight levelling off is a change in allocation of growth to increasing wing-length and the possible decreased feeding rate.

### Synchronized departure

The juveniles hatched over a longer period (10 days), compared to the departure (5 days) (Figure 8). This suggests a stronger synchronization in departure. However, the results also showed that weather conditions with strong northerly winds prevented chicks from jumping, and could potentially affect the nest departure timing. The effect of weather conditions on timing of departure may lead to a larger synchronization than would occur without unfavourable wind speed and direction. This could potentially influence the impact parental parameters have on the age at departure, and the age of departure itself. The synchronizing pattern of departure supports the prediction that chicks should depart more synchronized in order to avoid being predated through a swamping effect (Williams, 1975). As the common guillemot is a colonial seabird, the dense colony increases the defence against avian and terrestrial predators. However, when departing the colony the predation risk will increase (Greenwood, 1964). At Hornøya, the main predators on common guillemot chicks are the great black-backed gull and herring gull. I did not observe any predation on the chicks I followed when departing. This might be due to my presence in the area or reduced foraging motivation by high numbers of departing chicks or the declining gull population at Hornøya (Barrett et al., 2012). The high synchronicity in nest departure might also be influenced by the timing of food availability at feeding areas outside the colony.

## Conclusion and recommendations

In conclusion, except for the positive relationship between maternal body condition around hatching and juveniles' age at departure, I did not find strong support for that parental body condition or short-term changes in food supply during the nestling period have an impact on chicks' age at departure. Juveniles with mothers in better body condition around hatching stayed longer at the nest-site. Strong correlation between parental body condition and stress-levels on the juveniles' weight and wing-length at departure was found.

Synchronized departure is thought to reduce predation risk and increase juvenile survival, and this study does support that there is a strong degree of synchronized departure occurring within the common guillemot. However, a strong relationship was found between the departure date of marked chicks and weather conditions. Juveniles would if possible prolong their stay at the nest when weather was not favourable – resulting in older age at departure and even higher synchronization.

New research has shown that there is no higher rate of mortality at sea than at nest site (Elliott et al., 2017). Elliott et al. (2017) concluded that the duration of nestling period was more associated with differences in energy intake between the nest site and at sea. This contradicts Ydenberg's model, where he predicted that higher mortality rate at sea was an important factor in intermediate nest departure (Ydenberg, 1989). This opens up to focus more on the available resources both during the nestling period and after nest departure and the effect of prey availability on the mechanisms behind the timing of nest departure.

There is little knowledge about the life at sea of immature common guillemots. GLS-loggers were deployed on the chicks after they had departed the colony. Even though the precision of GLS loggers are not nearly perfect, it might when and if retrieved provide us with important knowledge about juvenile distribution and ecology at sea after nest departure.

And important questions to look further into in future studies, are whether the timing of nest departure are more controlled by the conditions at sea – and whether the common guillemots try to time an optimized foraging window when departing from the nest site.

The Norwegian common guillemot population is critically endangered, and is on the Norwegian red list (Henriksen and Hilmo, 2015), and new knowledge, about a part of the common guillemots life that is little known, is important to future monitoring and conservation approaches. And further investigation on the effect of changing food availability as the climate is warming may provide us with greater understanding of how vulnerable the common guillemot is to climate change and to human activities in this highly vulnerable phase of the common guillemots' life-cycle.

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# Appendix

## Appendix A

Contains candidate model with juvenile wing-length at departure as response variable. And the R output from using the dredge function.

Table A: Candidate models conducted from model selection using the dredge function. Juvenile wing-length at departure is used as the response variable. Significant code in parentheses 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 '.' 1

Rank	Model	AICc	$\Delta$ AICc	r <sup>2</sup>
<b>1</b>	<b>Cort1.M(*)+Cort2.F(**)+Cond2.M(**)+Cond2.F(***)</b>	<b>70.5</b>	<b>0.00</b>	<b>0.95</b>
2	Cort1.F(.) + Cort2.F(**) + Cond2.M(***) + Cond2.F(***)	74.2	3.68	0.93
3	Cort1.M(*) + Cort2.F(**) + Cond1.M + Cond2.M(*) + Cond2.F(***)	74.2	3.70	0.95
4	Cort2.F(*) + Cond2.M(***) + Cond2.F(***)	74.3	3.74	0.90
5	Cort1.F + Cort2.F(**) + Cort1.M(.) + Cond2.M(**) + Cond2.F(***)	74.9	4.38	0.95
6	Cort1.F(*) + Cort2.F(***) + Cond1.M(.) + Cond2.M(*) + Cond2.F(***)	75.4	4.91	0.95
7	Cort2.F(**) + Cort1.M(*) + Cond2.F(***) + Cond2.M(**) + Juvweight6	76.1	5.54	0.95
8	Cort1.M(*) + Cort1.F(.) + Cort2.F(***) + Cond1.M(*) + Cond2.M(*) + Cond2.F(***)	76.2	5.65	0.97
9	Cort1.M(**) + Cort2.F(**) + Cond1.M(*) + Cond2.F(***)	76.6	6.10	0.92
10	Cort1.M(*) + Cort2.F(**) + +Cond2.M(**) + Cond2.F(***) + Cond1.F	76.6	6.11	0.95

R-output from model selection using the MuMIn- package. Includes chosen parameters, AICc,  $\Delta$ AICc and the Akaike weights. Chosen model in bold

```
Global model call: lm(formula = Juvwing6 ~ Cort1.M + Cort2.M + Cort1.F + Cort2.F +
  Cond1.M + Cond2.M + Cond1.F + Cond2.F + Hatching.date + Jumpage +
  Juvweight6, data = malinhopp, na.action = "na.fail")
---
Model selection table
      (Int)  Cn1.F  Cn1.M  Cn2.F  Cn2.M  Cr1.F  Cr1.M  Cr2.F  Jv6 df logLik AICc delta weight
109 81.46          0.08616 -0.03710 -0.5720 -0.3642      6 -24.599 70.5 0.00 0.530
93 76.81          0.10860 -0.04451 0.2632 -0.4287      6 -26.438 74.2 3.68 0.084
111 81.72        -0.01087 0.08764 -0.02883 -0.5973 -0.3803      7 -23.115 74.2 3.70 0.083
77 77.72          0.10710 -0.04818 -0.3484      5 -29.133 74.3 3.74 0.082
125 80.18          0.09129 -0.03725 0.1505 -0.4558 -0.4069      7 -23.453 74.9 4.38 0.059
95 76.69        -0.01682 0.11280 -0.03136 0.3430 -0.4767      7 -23.719 75.4 4.91 0.046
1133 86.59          0.08841 -0.03896 -0.6695 -0.4272 -0.01716      7 -24.037 76.1 5.54 0.033
127 79.88        -0.01578 0.09622 -0.02533 0.2318 -0.4298 -0.4532      8 -19.798 76.2 5.64 0.032
103 82.99        -0.02253 0.08349 -0.8070 -0.3698      6 -27.648 76.6 6.10 0.025
110 81.53 -0.006436          0.09150 -0.03614 -0.5920 -0.3563      7 -24.321 76.6 6.11 0.025
Models ranked by AICc(x)
```

## Appendix B

Contains candidate model with juvenile wing-length as response variable. And the R output from using the dredge function.

Table B: Candidate models conducted from model selection using the dredge function. Juvenile weight at departure is used as the response variable. Significant code in parentheses 0 '\*\*\*\*' 0.001 '\*\*\*' 0.01 '\*\*' 0.05 '.' 0.1 '.' 1

Rank	Model	AICc	$\Delta$ AICc	$r^2$
1	Cort1.M(**)+Cort2.F(*)+Hatching.date(.)	148.9	0.00	0.70
2	<b>Cort1.M(**)+Cort2.F(*)</b>	<b>149.2</b>	<b>0.24</b>	<b>0.61</b>
3	Jumpage(.)+Juvwing6(**)	150.2	1.23	0.58
4	Cort1.M(**)+Cort2.F(**)+Cort2.M	151.2	2.22	0.66
5	Juvwing6(**)	151.2	2.31	0.42
6	Cort1.M(**)+Cort2.F(*)+Jumpage	151.8	2.84	0.65
7	Cort2.F+Juvwing6(*)	152.4	3.44	0.52
8	Hatching.date+Juvwing6(**)	152.4	3.51	0.51
9	Cort2.F+Jumpage(.)+Juvwing6(**)	152.6	3.64	0.62
10	Cort1.M(**)+Hatching.date(.)	152.7	3.77	0.51

R-output from model selection using the MuMIn- package. Includes chosen parameters, AICc,  $\Delta$ AICc and the Akaike weights. Chosen model in bold.

```
Global model call: lm(formula = Juvweight6 ~ Cort1.M + Cort2.M + Cort1.F + Cort2.F +
  Cond1.M + Cond2.M + Cond1.F + Cond2.F + Hatching.date + Jumpage +
  Juvwing6, data = malinhopp, na.action = "na.fail")
---
Model selection table
      (Int) Cr1.M Cr2.F Cr2.M Htc.dat   Jmp   Jv6 df  logLik  AICc delta weight
353  208.900 -8.222 -3.352      5.054      5 -66.467 148.9  0.00  0.251
97   311.200 -7.611 -3.637          -5.472 4.755 4 -69.266 150.2  1.23  0.136
225  296.900 -7.818 -4.369 4.091      5 -67.577 151.2  2.22  0.083
1025 -45.710                3.770 3 -71.621 151.2  2.31  0.079
609  375.400 -8.198 -3.577      -2.745      5 -67.887 151.8  2.84  0.061
1089   3.355         -2.226                3.317 4 -70.370 152.4  3.44  0.045
1281 -140.500                4.443      3.812 4 -70.406 152.4  3.51  0.043
1601  34.730         -1.742      -4.879 4.294 5 -68.288 152.6  3.64  0.041
289  167.700 -8.052                5.909      4 -70.532 152.7  3.77  0.038
Models ranked by AICc(x)
```

## Appendix C

Contains candidate model with juvenile age at departure as response variable. And the R output from using the dredge function.

Table C: Candidate models conducted from model selection using the dredge function. Juvenile age at departure is used as the response variable. Significant code in parentheses 0 '\*\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1

Rank	Model	AICc	$\Delta$ AICc	$r^2$
<b>1</b>	<b>Cond1.F(**)</b>	<b>68.8</b>	<b>0.00</b>	<b>0.44</b>
2	Cond1.F(**)+Cond2.M	70.6	1.77	0.50
3	Cond1.F(**)+Juvweight6	70.9	2.08	0.49
4	Cond1.F(*)+Hatching.date	71.1	2.28	0.48
5	Cond1.F(**)+Cort2.M	71.4	2.63	0.47
6	Cond1.F(**)+Cond1.M	71.5	2.68	0.47
7	Cond1.F(**)+Cond2.M+Juvweight6	71.6	2.77	0.59
8	Cond1.F(**)+Cort1.M	72.1	3.35	0.45
9	Cond1.F(*)+Juvwing6	72.3	3.55	0.44
10	Cond1.F(**)+Juvwing6	72.4	3.60	0.44

R-output from model selection using the MuMIn- package. Includes chosen parameters, AICc,  $\Delta$ AICc and the Akaike weights. Chosen model in bold.

```
Global model call: lm(formula = Jumpage ~ Cort1.M + Cort2.M + Cort1.F + Cort2.F +
  Cond1.M + Cond2.M + Cond1.F + Cond2.F + Hatching.date + Juvwing6 +
  Juvweight6, data = malinhopp, na.action = "na.fail")
---
Model selection table
  (Int)  Cn1.F  Cn1.M  Cn2.M  Cr1.M  Cr2.F  Cr2.M  Htc.dat  Jvng6  Jvwn6  df  logLik  AICc  delta  weight
2   22.19 0.02973          -0.01284          -0.01788          -0.263          -0.02500
10  22.19 0.03012          -0.01284          -0.01788          -0.263          -0.02500
514 26.45 0.03213          -0.01284          -0.01788          -0.263          -0.02500
258 27.61 0.02759          -0.01284          -0.01788          -0.263          -0.02500
130 23.34 0.03083          -0.01284          -0.01788          -0.263          -0.02500
4   22.19 0.03173 -0.007485          -0.01731          -0.263          -0.02500
522 28.15 0.03362          -0.01731          -0.01788          -0.263          -0.02500
34  21.53 0.03222          -0.01731          -0.01788          -0.263          -0.02500
1026 19.97 0.02804          -0.01731          -0.01788          -0.263          -0.02500
66  22.05 0.02969          -0.01731          -0.01788          -0.263          -0.02500
Models ranked by AICc(x)
```

## Appendix D

Includes Pearson's correlation matrix

	Cort1.M	Cort2.M	Cort1.F	Cort2.F	Wing.M	Wing.F	Cond1.M	Cond2.M	Cond1.F	Cond2.F	Hatching.date	Fledgedate	Jumpage	Juvweight6	Juvwing6
Cort1.M	1	0.04831	-0.33263	-0.05173	-0.21059	0.32976	0.06726	0.37096	-0.48786	-0.58664	0.16487	-0.09376	-0.23614	-0.60898	-0.75453
		0.85896	0.20809	0.84909	0.43369	0.21228	0.80451	0.15720	0.05522	<b>0.01690</b>	0.54172	0.72980	0.37858	<b>0.01228</b>	<b>0.00073</b>
Cort2.M		1	-0.11070	<b>0.38129</b>	<b>0.07108</b>	<b>-0.20254</b>	<b>-0.14420</b>	<b>0.00257</b>	<b>0.13184</b>	<b>-0.08373</b>	<b>0.21998</b>	<b>0.08309</b>	<b>-0.09597</b>	<b>0.00009</b>	<b>-0.16209</b>
			0.68318	0.14507	0.79365	0.45187	0.59416	0.99248	0.62645	0.75785	0.41299	0.75965	0.72366	0.99974	0.54866
Cort1.F			1	<b>0.38005</b>	-0.45787	<b>-0.53083</b>	<b>0.06249</b>	<b>-0.23212</b>	<b>-0.10296</b>	<b>-0.09087</b>	<b>-0.53131</b>	<b>-0.47270</b>	<b>-0.05445</b>	<b>-0.05337</b>	<b>0.06654</b>
				0.14649	0.07452	<b>0.03438</b>	0.81818	0.38701	0.70436	0.73786	<b>0.03418</b>	0.06445	0.84127	0.84439	0.80659
Cort2.F				1	<b>-0.04599</b>	<b>-0.14771</b>	<b>-0.21100</b>	<b>-0.17482</b>	<b>0.02360</b>	<b>-0.09072</b>	<b>-0.12667</b>	<b>-0.05219</b>	<b>0.05069</b>	<b>-0.45185</b>	<b>-0.26716</b>
					0.86570	0.58511	0.43278	0.51727	0.93086	0.73828	0.64016	0.84777	0.85209	0.07891	0.31716
Wing.M					1	<b>0.33550</b>	<b>-0.10967</b>	<b>-0.22045</b>	<b>0.55377</b>	<b>0.54236</b>	<b>0.28330</b>	<b>0.70287</b>	<b>0.50346</b>	<b>0.37854</b>	<b>0.48466</b>
						0.20396	0.68599	0.41197	<b>0.02604</b>	<b>0.02997</b>	0.28766	<b>0.00239</b>	<b>0.04680</b>	0.14823	0.05709
Wing.F						1	<b>-0.30726</b>	<b>-0.07018</b>	<b>0.00613</b>	<b>0.16143</b>	<b>0.35670</b>	<b>0.36740</b>	<b>0.08922</b>	<b>0.00741</b>	<b>0.02003</b>
							0.24702	0.79619	0.98204	0.55031	0.17505	0.16154	0.74246	0.97828	0.94131
Cond1.M							1	<b>0.57100</b>	<b>0.23885</b>	<b>0.14458</b>	<b>-0.11707</b>	<b>-0.10932</b>	<b>-0.01744</b>	<b>0.11532</b>	<b>-0.11904</b>
								<b>0.02088</b>	0.37299	0.59317	0.66590	0.68692	0.94890	0.67062	0.66058
Cond2.M								1	<b>0.03526</b>	<b>-0.03398</b>	<b>0.09093</b>	<b>-0.14231</b>	<b>-0.22558</b>	<b>-0.25593</b>	<b>-0.38766</b>
									0.89686	0.90057	0.73769	0.59906	0.40089	0.33870	0.13791
Cond1.F									1	<b>0.72166</b>	<b>-0.21694</b>	<b>0.45672</b>	<b>0.66152</b>	<b>0.22772</b>	<b>0.55520</b>
										<b>0.00160</b>	0.41963	0.07534	<b>0.00526</b>	0.39632	<b>0.02558</b>
Cond2.F										1	<b>0.05153</b>	<b>0.48163</b>	<b>0.46389</b>	<b>0.50062</b>	<b>0.84424</b>
											0.84969	0.05889	0.07030	<b>0.04826</b>	<b>0.00004</b>
Hatching.date											1	<b>0.45739</b>	<b>-0.35245</b>	<b>0.26456</b>	<b>-0.02627</b>
												0.07486	0.18061	0.32207	0.92307
Fledgedate												1	<b>0.67099</b>	<b>0.14126</b>	<b>0.37257</b>
													<b>0.00443</b>	0.60178	0.15526
Jumpage													1	<b>-0.07193</b>	<b>0.41399</b>
														0.79122	0.11091
Juvweight6														1	<b>0.66027</b>
															<b>0.00537</b>
Juvwing6															1

Figure A: Pearson's correlation matrix (N=16). Black numbers indicating r-values and green numbers indicates p-value. Values in bold and underlined are significant p-values indicating significant correlation.

