

Ingvild Håvarstein Eldøy

Variation in predation and nest survival rates in the Arctic breeding Common Eider (*Somateria mollissima*)

Master's thesis in Natural Science with Teacher Education

Supervisor: Børge Moe

May 2019



Photo: Lukas Tietgen

Ingvild Håvarstein Eldøy

Variation in predation and nest survival rates in the Arctic breeding Common Eider (*Somateria mollissima*)

Master's thesis in Natural Science with Teacher Education
Supervisor: Børge Moe
May 2019

Norwegian University of Science and Technology
Faculty of Natural Sciences
Department of Biology

Abstract

Several seabird species perform breeding migrations to Arctic regions in order to utilize beneficial aspects in terms of survival or reproduction. Earlier studies have suggested decreasing predation risk with increasing latitude. In this study, nest content, nest fate and hatching success of Common Eiders (*Somateria mollissima*) were monitored to investigate nest survival rates and variation in predation. The study was conducted in a breeding colony in Kongsfjorden, Svalbard in the high Arctic, during the breeding seasons from 2007 to 2018. Variation in nest survival was evident within and between years, with the lowest survival rates in the beginning of each breeding season. Interannual variation in predation was shown as differences in egg loss rates and nest success, with overall high predation rates. Field observations suggested that the recorded interannual variation in egg predation was mainly driven by the Glaucous Gull (*Larus hyperboreus*). In recent years the Polar Bear (*Ursus maritimus*) has also posed an increasing threat to this Arctic Common Eider population.

Sammendrag

Flere migrerende sjøfuglarter hekker i arktiske områder for å kunne utnytte fordelaktige aspekter ved miljøet i form av overlevelse eller reproduksjon. Tidligere studer har antydnet minkende predasjonsrisiko med økende breddegrad. I denne studien ble reirinnhold, reirskjebne og hekkesuksess hos ærfugl (*Somateria mollissima*) overvåket for å kunne undersøke rater av reiroverlevelse og variasjon i predasjon. Studien ble utført in en hekkekoloni i Kongsfjorden, Svalbard i løpet av hekkesesongene fra 2007 til 2018. Variasjon i reiroverlevelse var synlig innad og mellom år, med de laveste overlevelseshastighetene i starten av hver hekkesesong. Variasjon i predasjon mellom år ble vist i form av forskjeller i eggtaprater og reiroverlevelse, med generelt høye predasjonsrater. Feltobservasjoner foreslår at disse årlige variasjonene i egg-predasjon i hovedsak skyldtes polarmåken (*Larus hyperboreus*). I de senere år har også isbjørn (*Ursus maritimus*) dukket opp som en økende trussel mot denne arktiske ærfugl-populasjonen.

Acknowledgement

I want to thank my supervisors, Børge Moe and Sveinn Are Hanssen for giving me access to the interesting data, and for giving me feedback on my work. A special thanks to Børge for guiding me throughout the process from data filtering, through statistical analyses and all the way to the finished product. Thanks to all who participated in gathering data during fieldwork. I also want to acknowledge Brett Sandercock for valuable guidance and help with the daily survival rate analyses. I would never have been able to run those analyses on my own, so thank you for helping me analyse and present such interesting results. I want to thank my brother and my father, Sindre and Steinar Eldøy, for comments and discussions regarding my thesis. Thanks to Lukas Tietgen for providing me with a beautiful photo for the front page. And finally, thanks to friends and family for support and for filling my spare time with memorable moments that was not related to writing a master thesis.

Contents

- Introduction 1
- Methods 3
 - Study site and species 3
 - Nest monitoring 3
 - Hatching 4
 - Data processing and criteria for selecting nests for analyses..... 4
 - Data analyses 5
 - Daily survival rates (DSR) 5
 - Nest success..... 6
 - Egg loss rates 6
- Results 7
 - Sample and population size 7
 - Daily survival rates..... 7
 - Nest success..... 9
 - Egg loss rates 11
- Discussion 13
 - Seasonal pattern in daily nest survival 13
 - Interannual variation 14
 - The Glaucous Gull: the main predator on Eider eggs 15
 - The polar bear as an increasing threat to the Eider population 15
 - Time trend 16
 - Latitudinal pattern in egg predation?..... 16
 - Data sampling and criteria use 17
 - Recommendations for future monitoring of the Common Eider..... 18
- Conclusion..... 19
- References 20
- Appendix..... 23

Introduction

Predation is a key ecological process with the potential of affecting different fitness-related traits in animals (Lecomte *et al.*, 2008). In order to avoid high predation rates and increase survival of offspring, different strategies have evolved. In migratory birds, lower nest predation risk with higher latitudes has been shown (McKinnon, 2010). Migrating long distances in order to reproduce is energy demanding, and the cost of this act must be compensated for by benefits to lifetime reproductive success (McKinnon, 2010).

Many seabirds migrate to Arctic regions to breed (Johnson and Herter, 1990). By migrating, seabirds can utilize beneficial aspects that are changing over time in different environments, in terms of survival or reproduction (Rappole, 2013). Breeding in a variable environment such as the Arctic may however result in interannual variations in the reproductive success, and an extended age schedule of reproductive effort should thus be favoured. Iteroparous species experience several reproductive events during their lifespan, which contrasts to semelparous species that only reproduce once (Begon *et al.*, 2006). Habitats with environmental variability such as the Arctic will favour iteroparity, where fewer resources should be allocated to reproduction in each reproductive event (Roff, 1992).

The Common Eider (*Somateria mollissima*) is a long-lived seaduck breeding in Arctic and Boreal zones throughout the northern hemisphere (Lydersen and Kovacs, 2006). Migration patterns in this species varies between populations, with some being resident or only migrating locally, whereas other migrate longer distances (Anker-Nilssen *et al.*, 2000). In the Svalbard archipelago, which is part of the European High Arctic, Common Eiders migrate from the Norwegian coast and Iceland in order to breed (Anker-Nilssen *et al.*, 2000). With a clutch size of 3-6 eggs (Erikstad, Bustnes and Moum, 1993), the species has a high reproductive potential considering its long lifespan. At the same time, high predation on eggs during the breeding period in Arctic Eiders has been reported (Mehlum, 1991b).

The Glaucous Gull (*Larus hyperboreus*) and the Arctic fox (*Alopex lagopus*) are the main predators on Common Eider eggs in Svalbard (Mehlum, 1991b). The Common Eider only occupies islands for breeding after ice break-up in order to prevent egg predation by the Arctic Fox (Mehlum, 1991a). Thus, Glaucous Gulls are considered to be the main predators on Eider eggs on islands free of surrounding sea ice. The Glaucous Gull is a typical generalist (Anker-Nielsen *et al.*, 2000) both categorized as a predator, a scavenger and a surface feeder (Harley and Fisher, 1936). In recent years, the population of this predator species has increased in Kongsfjorden, Svalbard (Anker-Nilssen *et al.*, 2018).

Predation causing egg loss or nesting failure is believed to play an important role in the breeding success and the population dynamic of the Common Eider, as shown from observational, experimental and modelling studies (Hanssen and Erikstad 2013; Hanssen *et al.*, 2013; Bårdsen *et al.*, 2018; Dey *et al.*, 2018). The Common Eider populations have shown strong declines in many parts of its breeding range, and at the Norwegian coast it is classified as near threatened (Kålås *et al.*, 2015). However, it is not clear whether the observed population decline is driven by limited food availability (bottom-up), or high rates of predation (top-down) causing low breeding success.

The Arctic is undergoing some of the most severe and rapid climate changes on the planet (Deschamps *et al.*, 2017). Global warming is currently changing the ecosystem and strongly affecting the habitats for Arctic species. During the last decades, sea ice cover has decreased substantially (Johannessen *et al.*, 2004; Prop *et al.*, 2015,) and temperatures

have increased (Førland *et al.*, 2011). These environmental changes have impacts on Arctic wildlife and interactions among species (Moe *et al.*, 2009; Post *et al.*, 2009; Prop *et al.*, 2015; Descamps *et al.*, 2017). As sea ice is diminishing, Polar Bears (*Ursus maritimus*) are losing their traditional hunting grounds for seals (Prop *et al.*, 2015). During the last decades, an increasing number of landlocked Polar Bears has been reported during summer, with shortening sea ice seasons and decreasing sea ice during spring being important factors for this development (Prop *et al.*, 2015). In recent years, the Polar Bear has been shown to feed on the eggs of Common Eiders nesting on islets and coastal tundra (Prop *et al.*, 2015). Melting ice is also expected to alter the predation possibilities for the Arctic Fox. As the sea ice melting starts earlier in the season within fjords, islands are made less available for feeding for this terrestrial predator.

Whether Arctic Common Eider populations are facing increased stress from its main predators due to environmental changes is unknown, and it is not known whether the Arctic breeding Common Eiders have a breeding success sufficient for maintaining a stable population size (Dey *et al.*, 2018). In particular, little is known about the variation in egg loss rates and nest survival within and between seasons, and whether this variation has changed over the last years.

The main aim of this study is to investigate variation in predation on Common Eiders eggs. Data was collected in a breeding colony in Kongsfjorden, Svalbard, during the breeding seasons from 2007 to 2018. First, variation will be investigated by estimating daily survival rates (DSR) for the first three breeding seasons (2007-2009). It is not expected that daily survival rates remain constant throughout the season, and the first aim of this study is therefore to explore whether nest survival follows any seasonal patterns and whether these patterns varies between years.

Secondly, interannual variation in egg predation will be analysed by quantifying predation as egg loss rates and nest success. Since the Glaucous Gull is a generalist, this species does not solely rely on Eider eggs as food source, but rather utilizes a combination of different food sources. Therefore, it is hypothesized significant interannual variations in predation of Common Eider eggs.

As an addition, the study seeks to clarify whether there has been a trend over time in egg loss rates and in nest success. Increased egg loss rates and reduced nest success can be expected either as a result of an increase in the population size of the Glaucous Gull, a gradual shift in their diet to become more dependent on Eider eggs, or a combination of these factors. However, trends over time are particularly expected as potential response to the increased occurrence of land-locked Polar Bears during summer and their increased interest for alternative prey.

Methods

Study site and species

The study was conducted in a Common Eider colony every breeding season from 2007 to 2018 on the Storholmen island in Kongsfjorden, Svalbard (78°55'N, 12°13'E). Storholmen is relatively flat (at the highest 32 m above sea level), covered with tundra vegetation on rock- and moraine substrate (Ahlén and Andersson, 1970). The climate in the area is Arctic, with mean air temperatures around 5°C in July (Svendsen *et al.*, 2002). Earlier, it was common that the fjord froze during winter and broke up in late June or early July (Ahlén and Andersson, 1970). However, there has been a trend for less sea ice and fjord ice (Moe *et al.*, 2012; Prop *et al.*, 2015), and, if any, ice broke up around Storholmen before May in the study period (Moe *et al.*, 2012; B. Moe pers. Comm.).

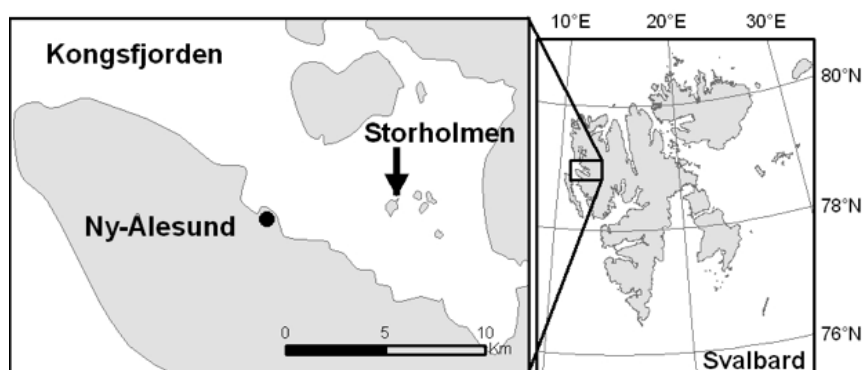


Figure 1. Location of the study area: Storholmen island in Kongsfjorden, Svalbard (78°55'N, 12°13'E).

The Common Eider is the most abundant of the three duck species breeding regularly in the Svalbard archipelago (Prestrud and Mehlum, 1991). The species is a capital breeder, relying entirely on body reserves during incubation in order to obtain a high nest attendance (Parker and Holm, 1990; Criscuolo *et al.*, 2002). During incubation the female fasts entirely, and only leave the nest for short breaks to drink or preen (Criscuolo *et al.*, 2000). The Common Eider is a precocial bird (Erikstad, Bustnes and Moum, 1993) where chicks only reside in the nest for a short time after hatching before leaving to sea with their mother (Mehlum, 1990b).

Nest monitoring

The structure of the data collection differed among the two periods 2007-2009 and 2010-2018. In the first period the main aim was to catch and sample females after incubating 5 and 20 days, respectively. In the latter, the main aim was to recapture females equipped with geolocators for tracking movements during the non-breeding season. Both approaches involved nest surveys and monitoring of nest content, nest fate and hatching success. Although it was not the main goal of the nest monitoring, the data collection allowed for extraction of information on egg loss and nest survival rates.

In 2007-2009, less than half the area of Storholmen was monitored. The nest surveys started in the end of May, in the beginning of egg laying. Thereafter, nests were followed and revisited throughout the season until hatching, with surveys ending in mid/late July. All nests were marked with a numbered nest stick along with a GPS position.

In 2010-2018, the whole area of Storholmen was monitored. In these years, nest surveys started in mid-June, when most Eiders were well into incubation. During the two first days of field work, the annual nest survey for the population count was conducted. Nests were searched for and marked with a stick, but only nests belonging to ringed females or females with geolocators were marked with a number and a GPS position. These nests were thereafter subjected to further nest visits and followed until hatching. During the period of revisits, new nests were also found and marked.

Hatching

In this study, hatching is defined as chicks in the nest or eggs with visible star fractures, indicating that hatching has started. At least one of the eggs in a nest need to be hatched in order for the nest to be termed successful. These definitions apply for all sampling years. Hatched or predated nests are hereafter referred to as nests with "known fate" (figure 2a). As all eggs in an Eider nest hatch more or less synchronous and chicks and mother leave the nest shortly after hatching, nests were in many occasions found empty during nest monitoring. These nests were determined as either hatched or predated based on the condition of the nest, the state of the egg shells and the presence or absence of egg membranes. Longer time intervals between nest visits made this determination more difficult. When in doubt, the fate of the nest was marked as uncertain, hereafter referred to as nests with "unknown fate" (figure 2a). How well this uncertainty was presented in the field notes varied. For some years, many nests were marked as uncertain, and the observed content in the empty nest was described. In other years, almost all nests were determined with known fate. The reliability of these determinations has been considered, and the criteria presented below were thus chosen.

Data processing and criteria for selecting nests for analyses

As the basis for this study, field data from all study years that had been compiled in excel files were used. Initially, the overall number of registered nests for all years was 1579 (table 1). The nest content files and the data collection in the field were, however, designed for different scientific purposes. Hence, these files were processed and filtered to obtain appropriate selections of nests for estimating egg loss rates, nest success and nest survival. As described below, two different criteria for data filtering were chosen.

With Criterion A, only nests that had seven days or fewer between the two last nest checks or had chicks in the nest on the last day were included. This criterion was made because it is expected that increasing time since last nest check results in less reliable predictions about the fate of the nest. Seven days was chosen as a balance between sample size on one side and reliability of the predictions on the other.

For criterion B, only nests that were found and marked during the nest surveying for the population count during the two first days of field work were included. These nests were considered to be suited for comparison among years as they had actively been searched for in the same area and around the same time every year. Nests that were found later in the season had survived until the point when they were found, and including these would therefore result in higher estimates of nest success. Alternatively, later found nests could possibly have been newly laid, but as this was not clarified in the data files, all such nests were excluded from further analyses. In 2018 only nests marked during the first day of field work were included due to Polar Bears visiting the island on the second day. Including nests that were found after this Polar Bear event would result in overestimation of nest success.

As nest monitoring differed among the two periods 2007-2009 and 2010-2018, the two different criteria were not suitable for all sampling years. Criterion A was used for the breeding seasons from 2007 to 2009, and criterion B was used for the remaining breeding seasons from 2010 to 2018 (table 1). Using criterion A for 2010-2018 would result in a very small sample size, since the follow up of the nests was less frequent in these years. Criterion B would not apply for the three first years (2007-2009). In these years the sampling started much earlier in the breeding season, on a time when many nests were not yet laid. Using criterion B for these years, would have given a bias towards early nests.

Table 1. Criteria for selecting nests for analyses, including study years and sample size.

Data selection	Explanation	Year	Number of nests
All nests	All Eider nests found	2007-2018	1579
Known fate	Nests determined as either hatched or failed	2007-2018	1225
Criterion A	Nests with seven days or fewer between the two last nest checks or with chicks in the nest on the last day	2007-2009	589
Criterion B	Nests found during population count the first two days of nest monitoring	2010-2018	518

Data analyses

Statistical analyses were conducted using R 3.5.2 (R Core Team, 2018). As the field work and data collection differed between 2007-2009 and 2010-2018, the data from the two periods were suited for different analyses. Daily survival rates (DSR) and calculations of true nest success (see below) could only be conducted for the three first breeding seasons. These analyses were based on a sample size of 571 nests (table 2). Apparent nest success and egg loss rates were estimated for all breeding seasons (2007-2018), with sample sizes of 949 and 1107 nests respectively (table 2).

Table 2: The different statistical analyses including the years they were applied to, number of nests included and the criteria that were used for selecting nests for these analyses.

Analysis	Year	Number of nests	Data selection
Daily survival rates (DSR)	2007-2009	571	Criterion A, known fate
True nest success	2007-2009	571	Criterion A, known fate
Apparent nest success	2007-2009	571	Criterion A, known fate
	2010-2018	378	Criterion B, known fate
Egg loss rates	2007-2009	589	Criterion A
	2010-2018	518	Criterion B

Daily survival rates (DSR)

Daily survival rates (DSR) represents the probability that a nest survives for a single day during the breeding period (Rotella, 2014). Daily survival rates for the three first breeding seasons were estimated using the package 'RMark'. Different parameters were included. Day 1 was set to the earliest date when the first egg was recorded during the three breeding seasons combined. Days are from now on therefore referred to as standardized days, with day 1 being May 20. Using this date, the age of the nest at day 1 could be calculated for all nests. Nest age was defined as lay date relative to day 1, and this was obtained by subtracting May 20 from the lay date of each nest, lay date being the date when the first egg in a clutch was laid. The fate of each nest was set to 0 or 1, where 0 is

successful and 1 is unsuccessful. In addition, the day when the nest was first found, last present and last checked was included. (If fate = 0, last present = last checked. If fate = 1, last present < last checked).

Time and year are factors assumed to affect the nest survival of Common Eiders, and these factors were therefore fitted as covariates in different models. Year was included in order to control for potential differences in nest survival among the three breeding seasons (2007-2009), and time was included to check for differences in nest survival related to the days in the breeding period, as it is expected that the vulnerability of a nest will not be constant throughout the breeding period. Both linear and quadratic effects of time were examined, in addition to interactions between time and year. Year was also tested for alone. The simplest model tested was the one where DSR was considered to be constant across all nests and all dates ($S(\sim)$). Using the Akaike's Information Criterion (AICc), the different models were compared to decide which of them best describe the daily survival rates (Burnham and Anderson, 2002). The model with the lowest AICc was chosen.

Nest success

Two methods were chosen in order to investigate the nest success of the Common Eiders in this study. If at least one egg in a nest hatched, the nest was termed successful. The apparent nest success was analyzed for all breeding season by using a Generalized Linear Model (GLM) with binomial distribution. Only nests with known fate were included ($n = 949$, table 2). The fate of the nest (hatched or failed) was fitted as the response variable and year was fitted as predictor.

The probability of surviving from initiation to hatching could be estimated by calculating the length of the breeding period of the Common Eiders and by using the mean values of daily survival rates for each year. For simplicity, these mean values were obtained by using the model only testing variations in DSR with year ($\text{year}(S)$). The probability is hereafter referred to as the true nest success. To estimate the true nest success, the estimated DSR values for the three years were raised to the number of days from nest initiation to nest completion.

Egg loss rates

Egg loss rates were examined for all breeding seasons and included both nests with known and unknown fate (2007-2018, $n = 1107$, table 2). The proportion of lost eggs was divided by the total amount of eggs in the nest, and these egg loss rates were then investigated using Generalized Linear Models (GLM) with binomial distribution. Lost eggs along with eggs that were not lost were fitted as a two-column response variable, and year was fitted as a factor in order to examine whether egg loss rates differed among years. In order to explore trends in egg loss rates over time, year was fitted as covariate in the model. The best model was chosen by comparing AICc-values.

Results

Sample and population size

The number of monitored nests with known and unknown fate are presented in figure 2a. From a total of 974 monitored nests, 25 (2.57%) had unknown fate, with some years having a higher proportion than others. As the structure of the data collection differed between 2007-2009 and 2010-2018, the number of monitored nests between the two periods also varies. The sample size was largest for the first three years, when nest monitoring started early in the breeding season and nests were followed up frequently.

The total number of Eider nests on Storholmen declined during the study period, from 858 nests in 2007 to 358 nests in 2018 (figure 2b). Still, the number of monitored nests is not necessarily reflecting the population size. This is especially evident for 2010, when 888 nests were registered during population count but only 15 monitored nests were included in further analyses.

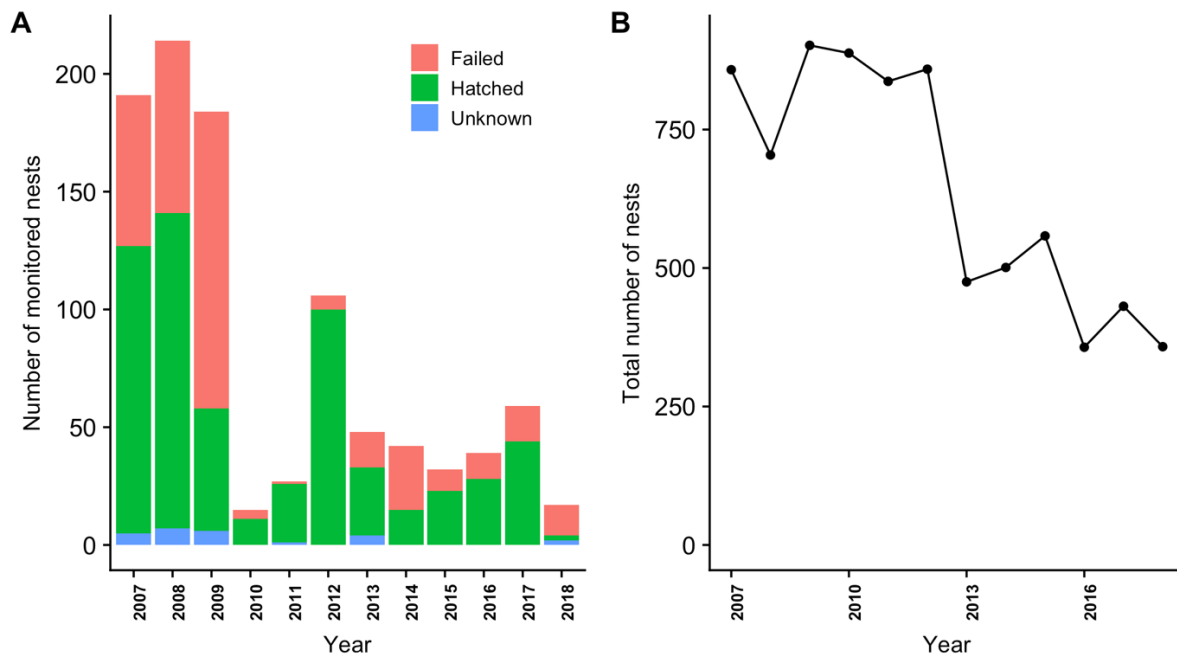


Figure 2. **A** Number of monitored Common Eider nests in the breeding seasons 2007-2018. Red = failed, green = hatched (red and green = known fate) and blue = unknown fate. 2007-2009; nest selected under criterion A, and 2010-2018; nests selected under criterion B. **B** Total number of Common Eider nests on Storholmen for the breeding seasons 2007-2018. The annual nest survey for the population count was conducted during the two first days of field work each year.

Daily survival rates

Daily survival rates (DSR) were estimated using nest survival models with the package 'RMark'. The model that best described the DSR according to the ΔAIC_c was the one which included both year, quadratic effects of day of season and interactions between these two variables ($w_i = 1$, table 3). All other models had $\Delta AIC_c > 182$, showing little support in the analyses compared to the best model.

Table 3. Model selection results for daily nest survival rates (DSR) for Common Eiders. The models are sorted after increasing ΔAIC_c values and is shown with the corresponding number of model parameters (K), the model deviance, the difference between the AIC_c value for each model and the model with the lowest AIC_c (ΔAIC_c) and the model weight (w_i).

Model	K	Deviance	ΔAIC_c	w_i
$S(\text{year} * (\text{day of season} + (\text{day of season})^2))$	9	1499.5	0.00	1
$S(\text{year})$	3	1694.1	182.57	0
$S(\text{day of season} + (\text{day of season})^2)$	3	1756.4	244.94	0
$S(\text{day of season})$	2	1760.8	247.28	0
$S(1)$	1	1815.2	299.70	0

The chosen model showed both variations in daily survival rates within the breeding season as well as differences among years (figure 3). The daily survival rates were lowest in the beginning of the breeding season with increasing trends as the season progressed. Curved lines suggest that nests were least vulnerable in the middle of the breeding season, with a slight increase in vulnerability towards the end of the season. DSR estimates for each time step (day of season) for each year is specified in the appendix (table S1).

The estimates of daily survival rates for 2007 and 2008 were similar, but 2009 differed from the two first years both in having a later start of the breeding season, and a lower overall DSR. This was also evident when comparing the lower and upper confidence limits of the estimates (Appendix, table S1). In addition, median lay date for 2007 and 2008 was closer to the peak of the DSR-curves compared to 2009, indicating higher survival rates around egg laying for the two first years.

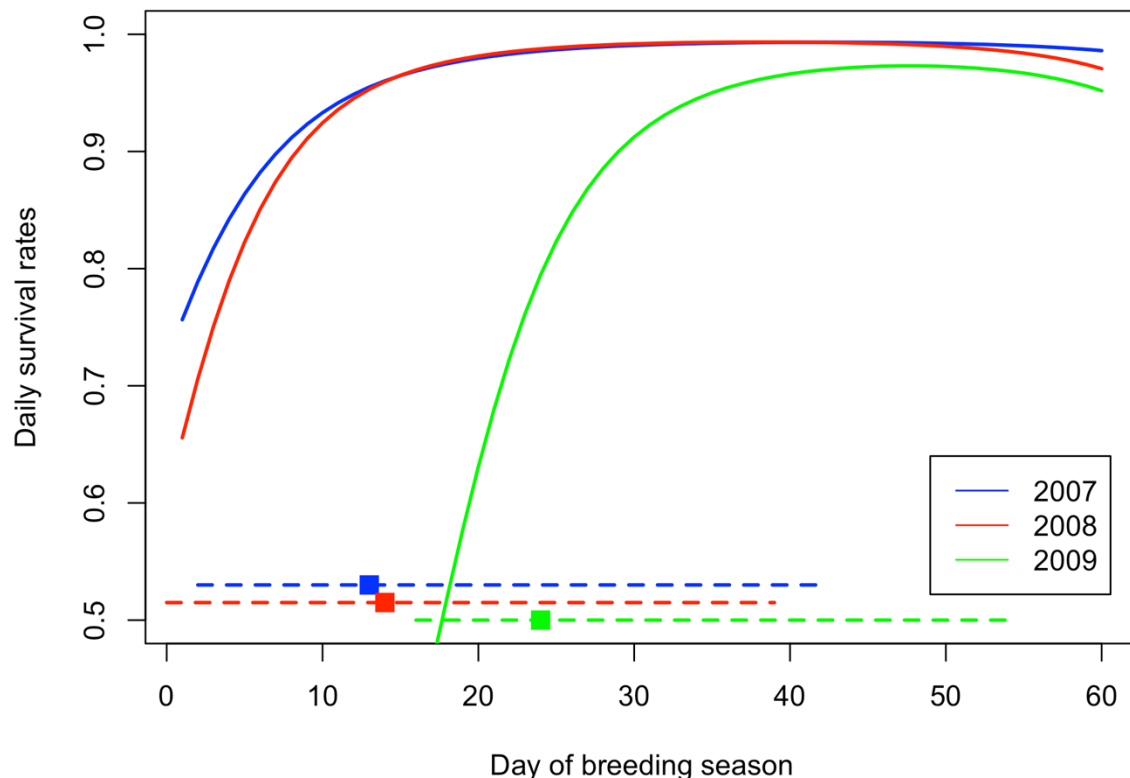


Figure 3. Estimated daily survival rates (DSR) of Common Eider nests across the three breeding seasons 2007-2009 in relation to day of season (day 1 = May 20). DSR is here shown as a function of year, day of season, and the interaction between these two covariates. Dashed lines represent lay date based on observed values, with median lay date indicated with a square.

To obtain mean values for daily survival rates for each year independent from day of breeding season, the model only testing variations in DSR with year was used (year(S), $\Delta AIC_c = 182.5727$, table 3). According to this model the daily survival rates ranged from 0.93 to 0.98 for the different years, with an overall DSR of 0.97 for the three breeding seasons (table 4).

Table 4. Mean daily survival rates (DSR) for Common Eider nests across the three breeding seasons 2007-2009 and for the three years combined, including the standard error (SE) and 95% confidence intervals.

Year	DSR	SE	Confidence interval	
			Lower 95%	Upper 95%
2007	0.982	0.002	0.977	0.986
2008	0.981	0.002	0.976	0.985
2009	0.925	0.007	0.911	0.936
All years	0.971	0.002	0.967	0.974

Nest success

Nest success was analyzed for all breeding seasons. For a particular nest to be termed successful, at least one of the eggs in the nest needed to be hatched. The success of the Eider nests for each year was explored by calculating true and apparent nest success. The apparent nest success was investigated using a Generalized Linear Model (GLM) with binomial distribution and with the fate of the nest (hatched or failed) as response variable and year as predictor variable. The apparent nest success varied between years (figure 4).

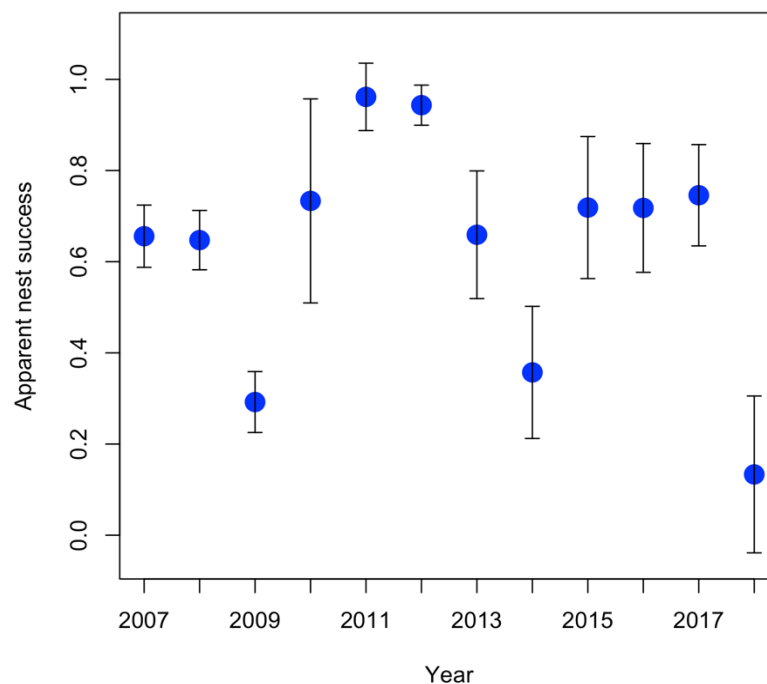


Figure 4. Apparent nest success of Common Eider nests for the breeding seasons 2007-2018, obtained from a Generalized Linear Model (GLM) with binomial distribution with nest fate as response variable and year as predictor variable. 95% confidence intervals are included.

The mean DSR values (table 4) were used to calculate the true nest success, where the DSR-values for each year was raised to the number corresponding to the average time from laying to hatching ($DSR^{26.88}$, table 5). The mean length of the breeding period in 2007-2009 was 26.88 days, calculated from nests with hatching success, known lay date and known hatching date ($n = 309$). Values for true nest success were lower for all years compared to the apparent nest success, with the biggest differences observed for 2009 (table 5, figure 5). As for the apparent nest success, true nest success also revealed interannual variation in nest success.

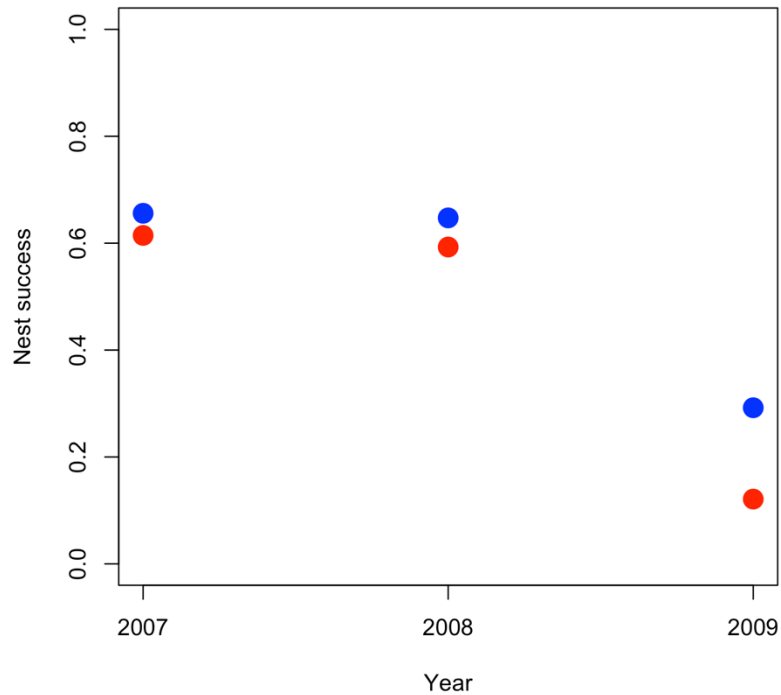


Figure 5: Apparent nest success (blue) and true nest success (red) for the three breeding seasons 2007-2009. Apparent nest success was obtained from a Generalized Linear Model (GLM) with binomial distribution. True nest success was calculated from estimated daily nest survival rates (DSR) and the mean length of the breeding season (26.88).

Table 5. Apparent nest success obtained from a Generalized Linear Model (GLM) with binomial distribution with nest fate as response variable and year as predictor variable, and true nest success calculated from DSR raised to the power of 26.88 for Common Eider nests at Storholmen.

Year	True nest success	Apparent nest success	Confidence interval	
			Lower 95%	Upper 95%
2007	0.62	0.66	0.59	0.72
2008	0.59	0.65	0.58	0.71
2009	0.12	0.29	0.23	0.36
2010	-	0.73	0.51	0.96
2011	-	0.96	0.89	1.04
2012	-	0.94	0.90	0.99
2013	-	0.66	0.52	0.80
2014	-	0.36	0.21	0.50
2015	-	0.72	0.56	0.88
2016	-	0.72	0.58	0.86
2017	-	0.75	0.64	0.86
2018	-	0.13	-0.04	0.31
All years	0.45	0.63	-	-

Egg loss rates

Egg loss rates were calculated for all breeding seasons (2007-2018). The model that best described these egg loss rates according to the ΔAIC_c was the one where year was entered as factor, thus showing variations among years ($w_i = 1$, table 6). The highest egg loss rates were found in 2009, 2014 and 2018 (0.65, 0.53, 0.87), whereas the lowest rates and thus the most successful years were 2010, 2011 and 2012 (0.13, 0.11, 0.09) (table 7, figure 6). The model where year was entered as covariate showed little support in the analyses compared to the best model (table 6, $\Delta AIC_c = 377.95$, $w_i = 0$). The slope estimate was negative, but since the estimate was not significantly different from zero, there was no decreasing trend in egg loss rates over time ($\beta = -0.016$, $SE = 0.011$, $p = 0.17$).

Table 6. Model selection results for daily nest survival rates (DSR) for Common Eiders. The models are sorted after increasing ΔAIC_c values and is shown with the corresponding number of model parameters (K), the model deviance, the difference between the AIC_c value for each model and the model with the lowest AIC_c (ΔAIC_c) and the model weight (w_i).

Model	K	Deviance	ΔAIC_c	w_i
Year (factor)	12	2675.5	0.00	1
Year (covariate)	2	3095.1	399.27	0

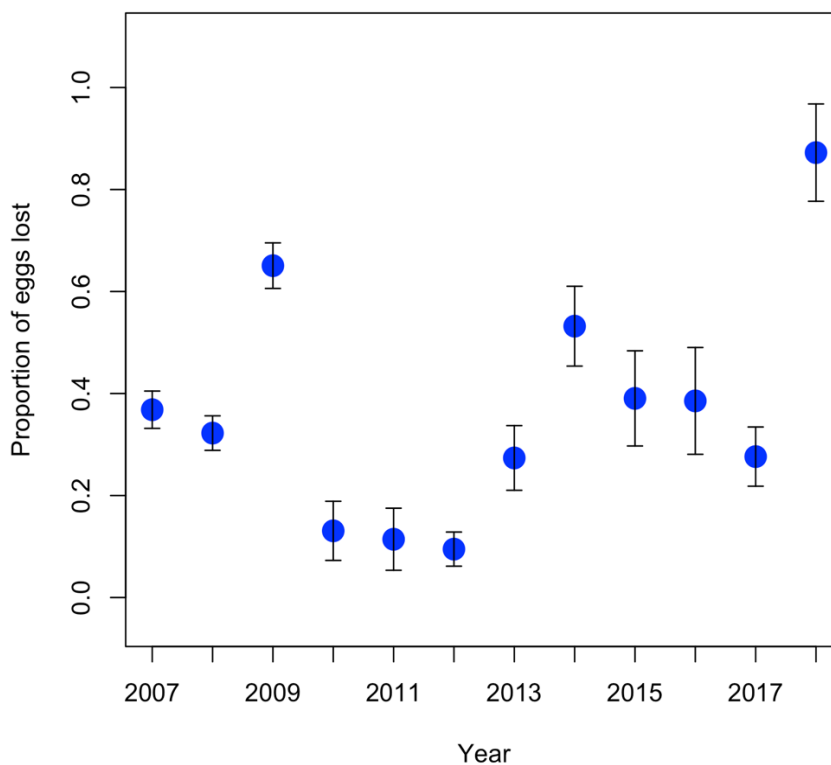


Figure 6. The proportion of lost eggs of Common Eiders for each breeding season, 2007-2018, including 95% confidence intervals. Egg loss rates were calculated as the proportion of lost eggs divided by the total amount of eggs in the nest and thereafter investigated using a Generalized Linear Model (GLM) with binomial distribution.

Table 7. Egg loss rates of Common Eiders for the breeding seasons 2007-2018 obtained using Generalized Linear Models (GLM) with binomial distribution, including 95% confidence intervals.

Year	Egg loss rates	Confidence interval	
		Lower 95%	Upper 95%
2007	0.37	0.33	0.41
2008	0.32	0.29	0.36
2009	0.65	0.61	0.70
2010	0.13	0.07	0.19
2011	0.11	0.05	0.18
2012	0.10	0.06	0.13
2013	0.27	0.21	0.34
2014	0.53	0.45	0.61
2015	0.39	0.30	0.48
2016	0.39	0.28	0.49
2017	0.28	0.22	0.33
2018	0.87	0.78	0.97
All years	0.37	-	-

Discussion

This study documented variability in nest survival within and between breeding seasons of the Common Eider. Egg loss rates ranged from 0.09 to 0.87, showing large variations with occasional years of near absolute nest failure, and with an overall high egg loss in this Arctic breeding colony (mean egg loss rate = 0.37 for all years). Based on observations in the field, predation is of major importance for the reported differences in egg loss and nest survival of the Common Eiders in this study. With the Glaucous Gull as the main avian predator (Mehlum, 1991b) and an increasing degree of visits from the Polar Bear into Eider colonies (Prop *et al.*, 2015), a great proportion of lost eggs are taken by these predators.

Seasonal pattern in daily nest survival

A relationship between daily survival rates (DSR) and time of nesting was demonstrated for the three first breeding seasons (2007-2009), with DSR increasing as the nesting season progressed, and with a slight decrease towards the end of the season (figure 3). Overall, the middle of the breeding season had the highest DSR.

The estimated lower survival rates around egg laying and incubation start in this study is consistent with similar studies conducted in Svalbard. Mehlum (1991b) reported higher probability of predation in the first part of the breeding season in 1983 and 1984. Previous studies have documented that the first egg laid by the Common Eider is covered up by moss, other plant material or dead vegetation, and left unattended until the female is ready to lay the next egg (Mehlum, 1991b; Hanssen, Engebretsen and Erikstad, 2002). Low survival rates in the beginning of the breeding season might partly be related to high predation rates of such unattended eggs. In a study conducted by Hanssen, Engebretsen and Erikstad (2002), predation rates decreased from 48.7% on first eggs to 3.43% on average after laying of the second egg. This increased nest survival is probably closely related to nest attendance. Time spent on the nest increase as the Eider lay more eggs, until the female remains constantly on the nest until hatching (Hanssen, Engebretsen and Erikstad, 2002), only interrupted by short breaks (Criscuolo *et al.*, 2000). The strategy to constantly reside on the nest and fast during incubation may have evolved as an anti-predator strategy, as most predation occurs in unattended nests (Erikstad and Tveraa, 1995).

Higher survival in the middle of the breeding season might be related to a higher abundance of breeding females in the colony. When a female Eider take short breaks to drink or preen (Criscuolo *et al.*, 2000), neighboring birds have been observed to attack Glaucous Gulls trying to take eggs from the unattended nest. Mehlum (1991b) reported significantly lower predation rates for high density nests with evenly surrounded close neighbors compared to low density nests, supporting the hypothesis that it might be more beneficial to breed when everyone else is doing the same. The probability of egg predation in one specific nest may also decrease when the number of nests increases due to dilution effects (Hamer, Schreiber and Burger, 2002). Nevertheless, an increasing number of nesting birds might also attract more predators, making the effect of protection by numbers smaller or even negligible.

As the Common Eider is a precocial species where the chicks leave to shore with their mothers shortly after hatching, breeding when the nest abundance is high might be beneficial due to synchronized hatching. When larger groups of female Eiders and their

chicks gather along the outer coasts, this is likely to result in better protection of young with lower predation risk (Mehlum, 1991b). As the female Eiders fast entirely during incubation and lose a considerable amount of their body weight (Parker and Holm 1990), some females abandon their chicks to the care of other Eiders in such groups in order to reduce the reproductive cost (Hanssen, Folstad and Erikstad, 2003). Thus, hatching around the same time is crucial.

The longer into breeding the female Eider is, the more energy she has invested in the clutch. Possibly, the female is less likely to give up her clutch the more she has invested in it. Bourgeon *et al.* (2006) found that Eiders were most likely to abandon their nest in the beginning of the incubation period and when initial clutch size was small. In the high Arctic the summer is short and the time window for breeding is accordingly narrow (Martin and Wiebe, 2004). Therefore, relaying a second clutch might not be possible, unless the clutch is lost very early in a breeding attempt. As the breeding commences, the possibility of relaying vanishes, and completing the current clutch thus becomes the only way to obtain reproductive success that year.

To be able to exert a high nest attendance during incubation, the Common Eider needs to build up good fat reserves before incubation commences (Parker and Holm, 1990). In a bird species that rely on endogenous reserves during incubation, nest success is related to the nutrient reserve levels (Blums, Mednis and Clark, 1997). Starvation during incubation is costly, with a loss of total body weight around 40% during the period from initiation of incubation to hatching (Parker and Holm, 1990). As Common Eiders are long lived birds with many years to reproduce (Lydersen and Kovacs, 2006), Eiders with insufficient body reserves might benefit from abandoning the nest or the chicks in order to secure survival and future reproduction (Kilpi *et al.*, 2001). Kilpi *et al.* (2001) found that the rate of abandonment of Common Eiders was highest in years when the average female condition was poorest, supporting the idea that current reproduction might be sacrificed for the benefit of future reproduction. If female Eiders give up easier when their body condition is poor, an overall worse body condition of female Eiders in the colony is expected to lead to less successful years. Thus, an insufficient body condition can both lead to lower survival rates in the beginning of each breeding season, and in differences in nest success among years.

Interannual variation

Egg loss rates and apparent nest success differed among all study years 2007-2018, and daily survival rates and true nest success varied between the three first years. Apparent nest success was the calculated proportion of successful nests, whereas true nest success took the average time from egg laying to hatching into account and was thus calculated as daily survival rate raised to the power of 26.88. Out of the three first breeding seasons, the daily survival rates reviled lowest overall DSR for 2009, where the mean lay date also had a lower DSR compared to the two first years.

Egg loss rates varied substantially between years during the study period, with some years having high nest success (2011, egg loss = 0.11) whereas other years almost failed completely (2018, egg loss = 0.87). The differences among years did not follow any clear time trend, and good years followed worse years and vice versa.

Interannual variation with occasionally high egg loss rates in Common Eiders has also been reported in other studies conducted in Kongsfjorden, Svalbard. Mehlum (1991b) registered the amount of eggs subjected to predation during three consecutive breeding

seasons (1982-1984), with an egg loss of 29.2%, 59.4% and 58.1% respectively. The values were obtained by dividing the number of successful nests by the total number of monitored nests for each year and are thus comparable to the egg loss rates in this study. As Mehlum (1991b) started nest monitoring in the beginning of egg-laying and proceeded until hatching, the study method and the obtained values are most comparable to the egg loss rates for the three first breeding seasons in this study (2007-2009). Mehlum (1991b) also estimated the probability of egg predation during the incubation period by extrapolating mean daily predation rates for a set period of days. The risk of predation was 41.5% in 1982 and 77.9% in the following two years. As nest monitoring was conducted throughout the breeding season from initiation to hatching, these estimates are comparable to the estimated daily survival rates in this study. Still, it is important to notice that Mehlum (1991b) reported the probability of eggs being predated, whereas the estimates in this study present the probability of nest survival. Nevertheless, interannual variation was evident in both studies.

The Glaucous Gull: the main predator on Eider eggs

The main avian predator on Common Eider eggs in Kongsfjorden is the Glaucous Gull (Mehlum, 1991b), and a large portion of the lost eggs in this study was caused by this predator. Wildlife cameras have not been used to prove this statement, still field observations underpin the Glaucous Gull as the main predator. During the study period (2007-2018) no Arctic Foxes were seen on the island, and the few events of Polar Bears visiting the island were well monitored as this large predator is easy to spot. The Arctic Skua (*Stercorarius parasiticus*) may take some Eider eggs, but few individuals were observed, and therefore there is little reason to believe that this species accounts for egg loss of importance.

During field work the Glaucous Gull was observed to take eggs, both from attended and unattended nests. When the Eiders took short breaks away from the nest during incubation, eggs were especially vulnerable. In addition, Gulls were observed to harass females on their nests forcing them to leave their eggs, and in many occasions, Gulls cooperated in groups to make egg predation easier. As a large portion of Eider eggs were lost to this species, it is hypothesized that predation by the Glaucous Gull is the main reason for the demonstrated interannual variations in egg loss rates and nest success.

The Glaucous Gull is considered to be a generalist. In addition to Eider eggs, common food sources for this species are birds, chicks, fish, molluscs, crustaceans and offal (Anker-Nilsen *et al.*, 2000). Thus, the differences in egg loss among years might be related to the availability of alternative food sources in the Arctic ecosystem. Years with high egg loss rates show that the Glaucous Gulls are able to exert a considerable predation pressure on Eider eggs. At the same time, years with low egg loss rates suggests that this predator may prefer other food sources if they are available. The abundance of alternative prey might also vary throughout the season, and therefore possibly influencing the observed differences in survival rates throughout the breeding season.

The polar bear as an increasing threat to the Eider population

In addition to the Glaucous Gull, the Polar Bear has been shown to feed on Eider eggs (Prop *et al.*, 2015). During the study period from 2007-2018, Polar Bears were observed on Storholmen at several occasions (2010, 2013, 2014, 2017 and 2018). The earliest and most devastating visit was observed in 2018, when a female with her cub stayed on the island for 4 days (June 17 – June 20). Polar Bears were also observed on the island at a later occasion this year. When such events occur, many eggs are eaten by the Polar Bear,

and in addition, observations show that the presence of this predator scares the Eiders, causing them to leave their nests for some time. Consequently, egg predation increases even further as the Glaucous Gull gets easy access to unprotected eggs. The result is high egg loss rates with few successful nests. In 2018 egg loss rate was higher than in any other year covered by this study (0.87, table 7), with an apparent nest success of only 13% (table 5, figure 4).

For now, there are few Polar Bears remaining on land during summer. Nevertheless, a visit from one single Polar Bear into a bird colony can be devastating, especially if residing in the colony for several days. The presence of Polar Bears during summer has increased significantly the last decades, with a tendency to visit bird colonies earlier each year (Prop *et al.*, 2015). Such early visits when the Eiders are in the beginning of the breeding season may be especially devastating. As sea ice is decreasing, an increasing predation pressure from the Polar Bear on Common Eider eggs is expected to threaten the reproductive success of the Common Eider. The variation in nest success between years suggests that the Common Eider tolerate some years with low nest success, but if Polar Bears continue to visit the breeding colony every year, the Eiders will not be able to retain the current population size.

Time trend

The variation in egg loss among years was evident, but no significant trends over time were found when fitting year as covariate in the Generalized Linear Model. Nevertheless, the population size of the Common Eider has decreased during the study period (figure 2b). As discussed, the nest success in this population was especially low in some years, but more successful years also occurred. As the Common Eider is a long-lived species that breed multiple times throughout its lifetime, the species is expected to cope well with occasional years with low nest survival. Being an iteroparous species gives the opportunity to spread the reproductive risk over many breeding attempts, which is a good strategy when conditions are changing a lot between years, as is the case for the Eiders in Kongsfjorden. However, the observed population decline in the study population may indicate that overall egg loss rates during the study period has exceeded the limit required to maintain a stable population size. Possibly, there have not been enough good seasons, or the best seasons have not been good enough.

Unlike the Common Eiders, the population size of the Glaucous Gull has increased in Kongsfjorden during the study period (Anker-Nilssen *et al.*, 2018). Since the Glaucous Gull is the main avian predator on Eider eggs, a higher number of this predator may therefor also have contributed to the declining population of the Common Eider, as a bigger population may lead to a higher competition for food. At the same time, the presence of Polar Bears during summer has increased significantly the last decades (Prop *et al.*, 2015), thus applying additional predation pressure on the Eider eggs.

Latitudinal pattern in egg predation?

McKinnon (2010) proposed that bird migration to higher latitudes could result in reproductive benefits due to lower nest predation risk. Accordingly, one would expect lower egg predation in the Common Eider population on Svalbard compared to populations further south. In this study, mean values for the egg loss rates was 0.37 for the breeding seasons from 2007-2018, with values ranging from 0.10 to 0.87. Thus, egg predation is occasionally very high in this Arctic breeding population. When comparing with other studies, the highest egg predation is in fact reported from Eider colonies on Svalbard. From

studies conducted in Kongsfjorden in 1964 and 1967, an average egg loss of 0.73 was reported (Ahlén and Andersson 1970), and as already mentioned, Mehlum (1991b) reported egg loss rates of 0.29, 0.59 and 0.58 during three breeding seasons in the same fjord (1982-1984). In comparison, reported egg predation rates from Northern Canada was 0.19 and 0.13 (1955-1956), and in a study conducted in Scotland, mean calculated egg predation rates was 0.21 with values ranging from 0.04 to 0.27 (1961-1967, 1969) (Bårdsen, Hanssen and Bustnes, 2018 Appendix S1 pp. 7). These populations further south thus experienced lower egg predation rates compared to the Arctic populations. However, it is important to keep in mind that the different studies were not conducted in the same study years, and that the methods also may have varied to some extent. In addition, other environmental factors may have contributed to the observed differences. For example, Eiders breeding in Svalbard nest openly on flat islands while populations further south to a larger degree hide their nest in the vegetation (Bustnes, Erikstad and Bjørn, 2002). Therefore, differences in predation pressure does not solely reflect differences in latitude. In addition, it must be emphasized that differences in predation pressure is not necessarily the only reason for migrating to higher latitudes. It is reasonable to believe that some bird species might actually migrate to Arctic areas to breed despite a higher predation pressure, due to other favorable aspects such as resource availability, parasite load or adult survival.

Data sampling and criteria use

Both apparent and true nest success was presented in this study, since the collected data only allowed for calculations of true nest success for the three first breeding seasons (2007-2009). The years from 2007 to 2009 had in common that the nest monitoring started early in the breeding season, when egg laying had only just begun. Most of the nests were found before the clutch was fully laid, with only one, two or three eggs in the nest. The frequency of nest visits was high in these years, with the second visit often occurring already after three days. In 2009, many of the nests were registered with only one egg in the nest on the first visit, indicating that nest monitoring started in the very beginning of egg laying. Alternatively, some nests were already subjected to predation causing egg loss and thereby containing only one egg when monitoring began. During the first three years, the highest egg loss was indeed registered in 2009 (figure 6). In this year, many of the eggs that were registered on the first day were already gone on the next nest visit. Therefore, it is reasonable to believe that some eggs had also been lost before they were registered for the first time. Estimates of daily survival rates for 2007, 2008 and 2009 revealed lower DSR in the beginning of the breeding season in 2009 compared to the two first years (figure 3). When comparing true and apparent nest success, 2009 also vary from the other years in that the difference between true and apparent nest success was largest this year (figure 5). This lower true nest success compared to the apparent nest success is probably related to the lower daily survival rates in the beginning of the season in 2009. Even though the frequency of nest visit was high, the probability of eggs already being lost between the visits was higher in this year when the probability of surviving from one day to the next was lower. This might indicate that the difference between true and apparent nest success is related to nest survival rates, assuming that the nest monitoring has started in the beginning of egg laying. In years with little predation (2007 and 2008) the differences are relatively small, whereas the differences increase when predation pressure is higher (2009).

In 2010-2018, field work started later in the season, when most Eiders were well into incubation. Many nests had therefore already survived for some time when they were observed for the first time. Some nests had probably also disappeared before they were

found, thus resulting in a higher proportion of successful nest than unsuccessful nests being found and included in the analyses (Mayfield, 1961; Mayfield, 1975). The apparent nest success for these years will therefore be well overestimated towards nest success compared to the estimates obtained for 2007-2009 and from other studies that have monitored the nests from egg-laying to hatching. Still, the estimates can tell something about the variation among years within the study period, as the study was conducted more or less the same way for all these years (2010-2018). In addition, only nests that were found during population count the first two days of nest monitoring (criterion B) was included in the analyses in order to reduce the bias towards overestimation.

Recommendations for future monitoring of the Common Eider

To be able to compare predation pressure or nest success among years, consistent monitoring is crucial. Established criteria for how data sampling should be carried out would make comparison easier, both within and between studies. A proposal is to have a defined onset time for nest monitoring, and to visit a number of nests with a certain time interval between each nest visit. The same monitoring regime should thereafter be conducted annually. Ideally, every nest should be found when the first egg is laid, and the nest should thereafter be followed frequently throughout the incubation period until all eggs are hatched.

During the three first breeding seasons included in this study (2007-2009), early onset of nest monitoring and frequent nest visits were carried out. This data collection method made it possible to calculate daily survival rates that could both be used to show variations within and between breeding seasons. When nest monitoring is frequent, egg loss and the reason for eggs disappearing can more easily be detected. Proving the right predator species might not necessarily be simple, but if there are no signs of Polar Bears or Arctic Foxes in the nest or on the island, the predator is most likely the Glaucous Gull. Using wildlife cameras is possible if predator determination is desirable.

Realistically, early and frequent nest monitoring might be difficult to carry out. First of all, the monitoring would be time consuming, with field work starting early in the season and with more people possibly being necessary to be able to find and follow all nests. More frequent nest visits would also lead to more disturbance of the Eiders, which might affect the hatching success negatively. The estimated daily survival rates in this study showed the lowest nest survival rates in the beginning of the breeding season, thus suggesting that nests are especially vulnerable to disturbance during this time of breeding. If monitoring is initiated later on in order to reduce disturbance during this susceptible period, calculations of daily survival rates would not be possible due to the lack of information about lay date and initial clutch size. This was the case for the monitored breeding season from 2010 to 2018, where calculated apparent nest success was shown to be overestimated due to the later onset.

In the study years from 2010 to 2018, less frequent nest visits in the end of the breeding season led to many nests being found after hatching. Predation could also be the reason for empty nests and determining the fate of these nest was often difficult. When monitoring is infrequent, placing temperature loggers in the nest could be a possible solution for making determination easier, as this could provide information about when the nest was emptied. If the nest was emptied at a time when incubation had just begun, this could indicate predation as hatching would not be possible. In addition, the loggers could provide valuable information about the timing and frequency of recess behavior. Still, the disadvantages of placing such loggers in the nest should be considered. Nest temperature loggers are often formed as an egg. Placing one extra egg in the nest would lead to an

extra incubation cost for the female Eider, while replacing one egg with the logger would result in altered reproductive success.

When a specific study is carried out, several research questions might be studied at the same time. Sampling methods therefore often need to be suited for several research goals. Finding the balance between sampling size, time and disturbance is therefore necessary in order to get comparable estimates of egg predation or hatching success, in addition to being consequent with these sampling methods.

Conclusion

This study has presented variations in egg loss and nest success within and between breeding seasons in a colony of Common Eiders in Kongsfjorden, Svalbard. Overall high egg loss rates were evident for this Arctic breeding population, with some years having especially low nest success. These high rates and the fluctuations among years appear to be highly related to predation. Still, other contributing factors have been emphasized. The general condition of the female Eiders and their breeding strategies may affect the nest success and the degree of predation. Breeding in the high Arctic also poses challenges, with times of harsh weather, a short time window for breeding, and fluctuations in food availability for Eiders and predators.

The Glaucous Gull is the main avian predator of Eider eggs, and a large portion of the observed egg loss in this study is due to this predator. As the egg loss varies a lot between years, it seems like Eider eggs are not the main food source of the Glaucous Gull, which is a generalist that can rely on a number of different food sources. The Glaucous Gull population has increased the last decade, and future population development and the availability of alternative food sources for this predator will probably have a major impact on the survival and population size of this Common Eider population. In recent years, Polar Bear visits to the Eider colony has also been an increasing challenge. If egg predation is consistently high over several years it may result in recruiting failure and population declines in this colony. The observed high frequency of years with high egg loss rates, combined with a declining population size throughout the study period, suggests that the overall egg predation in this study period have been too high to maintain a stable population size.

The interannual variability in nest success suggests that the predation pressure of Common Eider eggs is not constant. The Common Eider is long-lived with many possible breeding attempts and is thus expected to withstand some breeding seasons with high egg loss rates. Still, they need some successful seasons in order to sustain their population. During the study period the population size of the Common Eider has decreased. The reason for this decline might be that there have been too few breeding seasons with high nest success, or that the good seasons have not been good enough. The last study year almost completely failed due to Polar Bears, and how such events with unsuccessful breeding affect the population will be interesting to monitor in the coming years. Further monitoring should be consistent in order to obtain comparable results regarding predation pressure or nest success among years. Long term surveys are necessary in order to monitor population dynamics and species interactions in the rapid changing environment of the High Arctic.

References

- Ahlén, I. and Andersson, Å. (1970) Breeding ecology of an eider population on Spitsbergen. *Scandinavian Journal of Ornithology*, 1(2), pp. 83-106. doi:10.2307/3676027
- Anker-Nilssen, T., Bakken, V., Strøm, H., Golovkin, A. N., Bianki, V. V. and Tatarinkova, I. P. (2000) *The status of marine birds breeding in the Barents Sea region*. Vol. Nr. 113. Tromsø: Norsk polarinstitutt
- Anker-Nilssen, T., Barrett, R. T., Christensen-Dalsgaard, S., Descamps, S., Erikstad, K. E., Hanssen, S.A., Lorentsen, S.-H., Moe, B., Reiertsen, T. K., Strøm, H., Systad, G. H. (2018) *Sjøfugl i Norge 2017. Resultater fra SEAPOP-programmet*. Available at: <http://www.seapop.no/no/publikasjoner/publisert-seapop/2018/index.html>
- Begon, M., Harper, J. L., and Townsend, C. R. (2006). *Ecology : From individuals to ecosystems*. 4th edn. Oxford: Blackwell
- Blums, P., Mednis, A. and Clark, R. G. (1997) Effect of incubation body mass on reproductive success and survival of two European diving ducks: A test of the nutrient limitation hypothesis, *The Condor*, 99(4), pp. 916-925. Available at: <https://www.jstor.org/stable/1370142>
- Bourgeon, S., Criscuolo, F., Bertile, F., Raclot, T., Gabrielsen, G. W. and Massemin, S. (2006) Effects of clutch sizes and incubation stage on nest desertion in the female Common Eider *Somateria mollissima* nesting in the high Arctic, *Polar Biology*, 29(5), pp. 358-363. doi: 10.1007/s00300-005-0064-7
- Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multimodel interference: A practical information-theoretic approach*. 2nd edn. New York: Springer
- Bustnes, J. O., Erikstad, K. E. and Bjørn, T. H. (2002) Body condition and brood abandonment in Common Eiders breeding in the High Arctic, *Waterbirds*, 25(1), pp. 63-66. doi: 10.1675/1524-4695(2002)025[0063:BCABAI]2.0.CO;2
- Bårdsen, B. J., Hanssen, S. A. and Bustnes, J. O. (2018) Multiple stressors: modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird, *Ecosphere*, 9(7), e02342. doi:10.1002/ecs2.2342
- Criscuolo, F., Gabrielsen, G. W., Gendner, J. P. and Le Maho, Y. (2002) Body mass regulation during incubation in female common eiders *Somateria mollissima*, *Journal of Avian Biology*, 33(1), pp. 83-88. doi: 10.1034/j.1600-048X.2002.330113.x
- Criscuolo, F., Gauthier-Clerc, M., Gabrielsen, G. W. and Le Maho, Y. (2000) Recess behaviour of the incubating Common Eider *Somateria mollissima*, *Polar Biology*, 23(8), pp. 571-574. doi:10.1007/s003000000123
- Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., Lydersen, C., Pavlova, O., Pedersen, Å. Ø., Ravolainen, V. and Strøm, H. (2017) Climate change impacts on wildlife in a High Arctic archipelago - Svalbard, Norway. *Global Change Biology*, 23(2), pp. 490-502. doi:10.1111/gcb.13381
- Dey, C. J., Semeniuk, C. A., Iverson, S. A., Richardson, E., McGeachy, D. and Gilchrist, H. G. (2018) Forecasting the outcome of multiple effects of climate change on northern common eiders, *Biological Conservation*, 220, pp. 94-103. doi:10.1016/j.biocon.2018.02.007
- Erikstad, K. E., Bustnes, J. O. and Moum, T. (1993) Clutch-size determination in precocial birds: a study of the common eider, *The Auk: Ornithological Advances*, 110(3), pp. 623-628. doi:10.2307/4088426
- Erikstad, K. E. and Tveraa, T. (1995) Does the cost of incubation set limits to clutch size in Common Eiders *Somateria mollissima*?, *Oecologia*, 103(3), pp. 270-274. doi:10.1007/BF00328614
- Førland, E. J., Benestad, R., Hanssen-Bauer, I., Haugen, J. E. and Skaugen, T. E. (2011) Temperature and precipitation development at Svalbard 1900–2100, *Advances in Meteorology*, 2011. doi:10.1155/2011/893790
- Hamer, K. C., Schreiber, E., and Burger, J. (2002) Breeding biology, life histories, and

- life history-environment interactions in seabirds, in Schreiber, E., and Burger, J. (ed.) *Biology of marine birds*. Boca Raton, Florida: CRC Press
- Hanssen, S., Engebretsen, H. and Erikstad, K. (2002) Incubation start and egg size in relation to body reserves in the common eider, *Behavioral Ecology and Sociobiology*, 52(4), pp. 282-288. doi:10.1007/s00265-002-0523-x
- Hanssen, S. A. and Erikstad, K. E. (2013) The long-term consequences of egg predation. *Behavioral Ecology*, 24(2), pp. 564-569. doi:10.1093/beheco/ars198
- Hanssen, S. A., Folstad, I. and Erikstad, K. E. (2003) Reduced immunocompetence and cost of reproduction in common eiders. *Oecologia*, 136(3), pp. 457-464. doi: 10.1007/s00442-003-1282-8
- Hanssen, S. A., Moe, B., Bårdsen, B. J., Hanssen, F. and Gabrielsen, G. W. (2013) A natural antipredation experiment: predator control and reduced sea ice increases colony size in a long-lived duck, *Ecology and Evolution*, 3(10), pp. 3554-3564. doi:10.1002/ece3.735
- Johannessen, O. M., Bengtsson, L., Miles, M. W., Kuzmina, S. I., Semenov, V. A., Alekseev, G. V., Nagurnyi, A. P., Zakharov, V. F., Bobylev, L. P., Pettersson, L. H., Hasselmann, K. and Cattle, H. P. (2004) Arctic climate change: observed and modelled temperature and sea-ice variability. *Tellus A: Dynamic Meteorology and Oceanography*, 56(4), pp. 328-341. doi:10.3402/tellusa.v56i4.14418
- Johnson S. R. and Herter D. R. (1990) Bird migration in the Arctic: A review. In Gwinner, E. (eds) *Bird migration*. Springer, Berlin, Heidelberg
- Kilpi, M., Öst, M., Lindström, K. and Rita, H. (2001) Female characteristics and parental care mode in the creching system of eiders, *Somateria mollissima*. *Animal Behaviour*, 62(3), pp. 527-534. doi:10.1006/anbe.2001.1784
- Kålås, J. A., Lislevatn, T., Gjershaug, J. O., Strann, K.-B., Husby, M., Dahle, S. and Strøm, H. (2015) Fugler - Aves, in Henriksen, S. and Hilmo, O. (ed.) *Norsk rødliste for arter 2015*. Artsdatabanken, Norge
- Lecomte, N., Careau, V., Gauthier, G. and Giroux, J. F. (2008) Predator behaviour and predation risk in the heterogeneous Arctic environment, *Journal of Animal Ecology*, 77(3), pp. 439-447. doi:10.1111/j.1365-2656.2008.01354.x
- Lydersen, C., and Kovacs, K. (ed.) (2006). *Svalbards fugler og pattedyr*. Vol. Nr. 13. Tromsø: Norsk polarinstitutt
- Martin, K. and Wiebe, K. L. (2004) Coping mechanisms of Alpine and Arctic breeding birds: Extreme weather and limitations to reproductive resilience, *Integrative and Comparative Biology*, 44(2), pp. 177-185. doi: 10.1093/icb/44.2.177
- Mayfield, H. F. (1961) Nesting success calculated from exposure, *The Wilson Bulletin*, 73(3), pp. 255-261. Available at: <http://www.jstor.org/stable/4158936>
- Mayfield, H. F. (1975) Suggestions for calculating nest success, *The Wilson Bulletin*, 87(4), pp. 456-466. Available at: <http://www.jstor.org/stable/4160682>
- McKinnon, L., Smith, P. A., Nol, E., Martin, J. L., Doyle, F. I., Abraham, K. F., Gilchrist, H. G., Morrison, R. I. G. and Bêty, J. (2010) Lower predation risk for migratory birds at high latitudes, *Science*, 327(5963), pp. 326-327. doi:10.1126/science.1183010
- Mehlum, F. (1991a) Breeding population size of the Common Eider *Somateria mollissima* in Kongsfjorden, Svalbard, *Norsk Polarinstitutt Skrifter*, 195, pp. 21-29
- Mehlum, F. (1991b) Egg predation in a breeding colony of the common eider *Somateria mollissima* in Kongsfjorden, Svalbard, *Norsk Polarinstitutt Skrifter*, 195, pp. 37-45
- Moe, B., Stempniewicz, L., Jakubas, D., Angelier, F., Chastel, O., Dinessen, F., Gabrielsen, G. W., Hanssen, F., Karnovsky, N. J., Rønning, B., Welcker, J., Wojczulanis-Jakubas, K. and Bech, C. (2009) Climate change and phenological responses of two seabird species breeding in the high-Arctic. *Marine Ecology Progress Series*, 393, pp. 235-246. doi:10.3354/meps08222
- Moe, B., Hanssen, S. A., Bårdsen, B.-J., Hanssen, F., Bourgeon, S., Pavlova, O., Nielsen, C. P., Gerland, S. and Gabrielsen, G. W. (2012) Effekter av predator kontroll og klima på bestandsforhold hos ærfugl på Svalbard. Sluttrapport for Svalbards Miljøvernfond - NINA Rapport 868
- Parker, H. and Holm, H. (1990) Patterns of nutrient and energy expenditure in female

- common eiders nesting in the high arctic. *The Auk: Ornithological Advances*, 107(4), pp. 660-668. doi:10.2307/4087996
- Post, E., Forchhammer, M. C., Bret-Harte, M. S., Callaghan, T. V., Christensen, T. R., Elberling, B., Fox, A. D., Gilg, O., Hik, D. S., Høye, T. T., Ims, R. A., Jeppesen, E., Klein, D. R., Madsen, J., McGuire, A. D., Rysgaard, S., Schindler, D. E., Stirling, I., Tamstorf, M. P., Tyler, N. J. C., van der Wal, R., Welker, J., Wookey, P. A., Schmidt, N. M. and Aastrup, P. (2009) Ecological dynamics across the Arctic associated with recent climate change, *Science*, 325(5946), pp. 1355-1358. doi:10.1126/science.1173113
- Prestrud, P. and Mehlum, F. (1991) Population size and summer distribution of the Common Eider *Somateria mollissima* in Svalbard, 1981-1985, *Norsk Polarinstitutt Skrifter*, 195, pp. 9-20
- Prop, J., Aars, J., Bårdsen, B. J., Hanssen, S. A., Bech, C., Bourgeon, S., de Fouw, J., Gabrielsen, G. W., Lang, J., Noreen, E., Oudman, T., Sittler, B., Stempniewicz, L., Tombre, I., Wolters, E. and Moe, B. (2015) Climate change and the increasing impact of polar bears on bird populations, *Frontiers in Ecology and Evolution*, 3(33). doi:10.3389/fevo.2015.00033
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>
- Rappole, J. H. (2013) *The avian migrant : The biology of bird migration*. New York: Columbia University Press
- Roff, D. A. (1992) *The evolution of life histories : Theory and analysis*. New York: Chapman and Hall
- Rotella, J. (2014). Nest survival models, in Cooch, E. and White, G. (ed.) *Program Mark: a gentle introduction*. 13th edn. Available at: <http://www.phidot.org/software/mark/docs/book/>
- Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbæk, J. B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O. and Wiencke, C. (2002) The physical environment of Kongsfjorden–Krossfjorden, an Arctic fjord system in Svalbard, *Polar research*, 21(1), pp. 133-166. doi:10.3402/polar.v21i1.6479

Appendix

Table S1. Estimates of daily survival rates (DSR) for each day of season in the three years from the model $S(\text{year} * (\text{day of season} + \text{day of season}^2))$ which was the highest ranked model among the set of candidate models. lcl and ucl refer to lower (2.5%) and upper (97.5%) confidence limits. The model estimates DSR as a quadratic function of day of season, and since there is an interaction with 'year'- the relationship between day of season and DSR depends on year. See figure 3 in the main text to visualize the relationships. The estimates of DSR for 2007 and 2008 are very similar, but 2009 differs from the two. This is evident when comparing the lower and upper confidence limits of the estimates in this table.

Day	2007			2008			2009		
	estimate	lcl	ucl	estimate	lcl	ucl	estimate	lcl	ucl
1	0.7564	0.5097	0.9027	0.6557	0.4800	0.7971	0.0061	0.0003	0.1200
2	0.7889	0.5792	0.9103	0.7060	0.5537	0.8229	0.0088	0.0005	0.1404
3	0.8174	0.6436	0.9173	0.7506	0.6228	0.8458	0.0126	0.0008	0.1632
4	0.8422	0.7012	0.9239	0.7893	0.6850	0.8659	0.0178	0.0014	0.1886
5	0.8637	0.7513	0.9300	0.8226	0.7391	0.8836	0.0249	0.0024	0.2165
6	0.8822	0.7938	0.9357	0.8508	0.7850	0.8990	0.0345	0.0039	0.2469
7	0.8980	0.8292	0.9411	0.8745	0.8232	0.9125	0.0473	0.0063	0.2796
8	0.9116	0.8584	0.9461	0.8943	0.8543	0.9242	0.0640	0.0101	0.3143
9	0.9232	0.8821	0.9507	0.9107	0.8795	0.9345	0.0854	0.0159	0.3507
10	0.9331	0.9013	0.9551	0.9244	0.8997	0.9434	0.1123	0.0246	0.3884
11	0.9415	0.9167	0.9593	0.9358	0.9159	0.9512	0.1454	0.0374	0.4270
12	0.9488	0.9291	0.9632	0.9452	0.9288	0.9580	0.1850	0.0558	0.4659
13	0.9549	0.9390	0.9668	0.9530	0.9392	0.9638	0.2310	0.0814	0.5047
14	0.9602	0.9470	0.9703	0.9595	0.9476	0.9688	0.2828	0.1158	0.5430
15	0.9648	0.9534	0.9735	0.9650	0.9544	0.9731	0.3394	0.1603	0.5802
16	0.9687	0.9586	0.9764	0.9695	0.9601	0.9768	0.3990	0.2154	0.6162
17	0.9720	0.9629	0.9790	0.9733	0.9647	0.9798	0.4597	0.2801	0.6505
18	0.9749	0.9664	0.9813	0.9765	0.9686	0.9824	0.5197	0.3522	0.6829
19	0.9774	0.9695	0.9833	0.9792	0.9719	0.9846	0.5772	0.4282	0.7134
20	0.9796	0.9721	0.9851	0.9815	0.9747	0.9864	0.6308	0.5040	0.7419
21	0.9815	0.9744	0.9866	0.9834	0.9772	0.9879	0.6797	0.5758	0.7683
22	0.9831	0.9764	0.9880	0.9850	0.9792	0.9892	0.7233	0.6409	0.7929
23	0.9845	0.9781	0.9891	0.9864	0.9810	0.9903	0.7616	0.6976	0.8156
24	0.9858	0.9797	0.9900	0.9876	0.9825	0.9912	0.7948	0.7453	0.8367
25	0.9869	0.9811	0.9909	0.9886	0.9839	0.9920	0.8233	0.7845	0.8563
26	0.9878	0.9824	0.9916	0.9895	0.9850	0.9926	0.8475	0.8160	0.8745
27	0.9886	0.9835	0.9922	0.9902	0.9860	0.9932	0.8681	0.8411	0.8911
28	0.9894	0.9844	0.9927	0.9909	0.9868	0.9937	0.8854	0.8612	0.9059
29	0.9900	0.9853	0.9932	0.9914	0.9876	0.9941	0.9000	0.8775	0.9188
30	0.9905	0.9861	0.9936	0.9919	0.9882	0.9944	0.9123	0.8910	0.9298
31	0.9910	0.9867	0.9940	0.9922	0.9887	0.9947	0.9227	0.9024	0.9391
32	0.9915	0.9872	0.9943	0.9925	0.9891	0.9949	0.9314	0.9120	0.9467
33	0.9918	0.9876	0.9946	0.9928	0.9894	0.9951	0.9387	0.9204	0.9531

34	0.9921	0.9880	0.9949	0.9930	0.9896	0.9953	0.9449	0.9276	0.9583
35	0.9924	0.9882	0.9951	0.9932	0.9897	0.9955	0.9501	0.9338	0.9626
36	0.9926	0.9882	0.9954	0.9933	0.9898	0.9956	0.9545	0.9393	0.9661
37	0.9928	0.9882	0.9956	0.9934	0.9897	0.9957	0.9582	0.9439	0.9690
38	0.9930	0.9881	0.9958	0.9934	0.9895	0.9958	0.9614	0.9479	0.9715
39	0.9931	0.9878	0.9961	0.9934	0.9893	0.9959	0.9640	0.9513	0.9735
40	0.9932	0.9874	0.9963	0.9933	0.9889	0.9960	0.9662	0.9540	0.9752
41	0.9932	0.9868	0.9965	0.9932	0.9883	0.9961	0.9680	0.9562	0.9767
42	0.9932	0.9861	0.9967	0.9931	0.9877	0.9961	0.9695	0.9579	0.9780
43	0.9932	0.9852	0.9969	0.9929	0.9868	0.9962	0.9707	0.9589	0.9792
44	0.9932	0.9841	0.9971	0.9926	0.9857	0.9962	0.9716	0.9593	0.9803
45	0.9931	0.9827	0.9973	0.9923	0.9844	0.9962	0.9723	0.9592	0.9813
46	0.9930	0.9810	0.9974	0.9920	0.9828	0.9963	0.9728	0.9584	0.9823
47	0.9929	0.9789	0.9976	0.9915	0.9808	0.9963	0.9730	0.9569	0.9833
48	0.9927	0.9764	0.9978	0.9910	0.9784	0.9963	0.9731	0.9546	0.9842
49	0.9925	0.9734	0.9979	0.9904	0.9755	0.9963	0.9729	0.9515	0.9850
50	0.9922	0.9697	0.9980	0.9897	0.9719	0.9963	0.9725	0.9474	0.9858
51	0.9919	0.9652	0.9982	0.9889	0.9675	0.9963	0.9719	0.9422	0.9866
52	0.9916	0.9597	0.9983	0.9879	0.9620	0.9962	0.9711	0.9356	0.9873
53	0.9912	0.9530	0.9984	0.9868	0.9553	0.9962	0.9700	0.9272	0.9879
54	0.9907	0.9447	0.9985	0.9855	0.9469	0.9961	0.9686	0.9168	0.9886
55	0.9902	0.9345	0.9986	0.9839	0.9366	0.9961	0.9669	0.9038	0.9891
56	0.9896	0.9220	0.9987	0.9821	0.9236	0.9960	0.9649	0.8875	0.9896
57	0.9889	0.9065	0.9988	0.9799	0.9075	0.9959	0.9624	0.8673	0.9901
58	0.9881	0.8874	0.9989	0.9773	0.8874	0.9958	0.9595	0.8421	0.9906
59	0.9871	0.8639	0.9989	0.9743	0.8625	0.9956	0.9560	0.8111	0.9910
60	0.9861	0.8352	0.9990	0.9707	0.8318	0.9955	0.9519	0.7732	0.9914

