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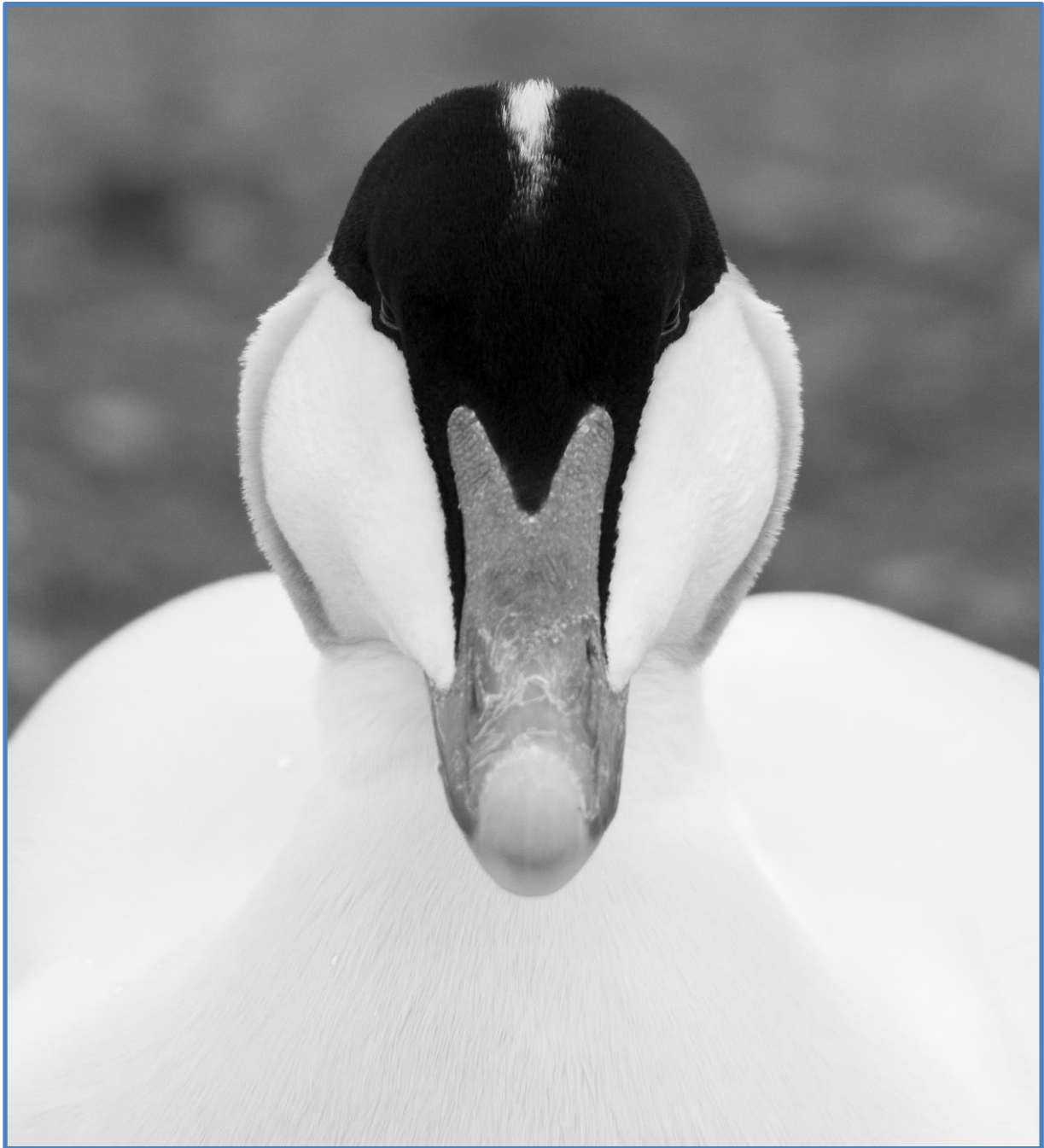
Department of Arctic and Marine Biology

The role of the male Common Eider *Somateria mollissima* as a protector against nest-predation

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BIO-3950 Master thesis in Biology

May 2017



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Northern Populations and Ecosystems
May 2017

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Cover photo of male common eider *Somateria mollissima*

Taken at the eider colony near Longyearbyen, Svalbard, by Calum Bachell, June 2016

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Abstract

Male common eiders *Somateria mollissima* in high-Arctic colonies are known to remain with females during the first weeks of incubation; a behaviour not found in eider colonies further south. Other studies have observed that, whilst adult eiders in northern latitudes experience less predation, there can be much higher levels of predation on their nests and young. The objective of this study was to investigate why males at an eider colony in Svalbard were present for longer than elsewhere in their range, and whether this was related to protection from high predation levels. Through an observational study design, this study mapped population and predator dynamics within an eider colony near Longyearbyen, Svalbard. This study found that males were present for several weeks after the first females had started incubating, and once most males left the colony there was an increase in predation. Success of predators was higher at unattended nests; however overall success of predators was not found to be significantly lower if males were present in addition to females. If males were present at the nest, females were less likely to leave their nest to respond to gulls, allowing females to conserve energy and leave nests covered. The possibility that the tendency of males to remain with females for longer has emerged from asynchronous breeding or extra-pair mating is discussed, but the findings from this study indicate that it is a direct response to high levels of predation.

Keywords:

Common eider, nest predation, predator defence, parental effort, *Somateria mollissima*, Svalbard

Introduction

Life history strategies in animals are often influenced by phenotypic adaptation to different environments. However, adaptations within a species are often unrelated to genetic and physiological processes, but are instead linked to various behavioural strategies in response to different or changing environments (Daan and Tinbergen, 1997). As survival of populations is dependent on individuals making choices that maximise fecundity and likelihood of future reproduction, there are often trade-offs between the intensity of offspring defence and parent survivability (Montgomerie and Weatherhead, 1988, Mahr et al., 2015), and differences in predation may even give rise to locally adapted behaviours within a population (Badyaev and Ghalambor, 2001). Thus, a variety of behaviours may exist within a population or species.

Breeding birds may have a strong ability to modify behaviour over time in response to nest predation, including breeding locations choice, re-nesting, nest concealment, associative nesting and formation of breeding colonies (Arnold et al., 2010, Lima, 2009, Fontaine and Martin, 2006, Quinn and Ueta, 2008). With regards to predation, there are regularly negative relationships between the time or effort spent guarding nests or young, and other types of parental care, such as provisioning (Markman et al., 1995, Ghalambor and Martin, 2001). Trade-offs between parental risk and survival of offspring may be one reason for the wide range of strategies used by breeding birds during nesting, from both parents taking active roles in nesting, to maternal raising only. Different strategies may be used by each parent depending on the species, or on the levels or type of predation encountered; often with males taking specialized roles in protection of nests, offspring, or females against predation (Weatherhead, 1990, Markman et al., 1996).

In polygynous populations, nest defence is often shared between males (Weatherhead, 1990). Even in breeding colonies where there is only some extra-pair mating, promiscuous males may have offspring within multiple nests and thus it is in their interest to increase safety of the whole colony rather than at individual nests, including through vigilance or defence against predators (Eliassen and Jørgensen, 2014). Although usually monogamous, common eiders *Somateria mollissima* have been observed to occasionally pursue extra-pair mating (Christensen, 2000), and therefore may benefit in protecting both individual nests and the wider colony from predation. Male eiders offer protection to females from predators, and from other males, during the pre-nesting period, especially during foraging (Eliassen and

Jørgensen, 2014, Hario and Hollmen, 2004). Little is known about whether such defence extends past the pre-nesting stages or towards the young.

Within most of their distribution, male eiders will be present in the colony during the nest-selection and egg-laying phases, and leave shortly after incubation has begun (Ashcroft, 1976, Milne, 1974, Waltho and Coulson, 2015, Swennen, 1990), however, in high-Arctic colonies the males tend to remain for the first 1-2 weeks of incubation (Prestrud and Mehlum, 1991, Ahlén and Andersson, 1970, Kristjansson and Jónsson, 2015). The role played by the male during this time has not yet been studied in these colonies. While female eiders often rely on cryptic camouflage to avoid detection from predators, letting predators get much closer than other duck species before being flushed (Ahlén and Andersson, 1970, Forbes et al., 1994), the males bold black and white plumage would seem to negate this. Most successful predations occur when females are away from the nest (Götmark and Åhlund, 1988, Mehlum, 1991b), defending against other predators or getting water. Therefore, nest security should be increased if males can respond to predators instead, or watch while females are away. It is possible that eiders in Svalbard have adopted a different strategy, relying more on aggressive defence from males, to withstand these high predation levels during early-incubation. Such behaviour has been noted in other large species of wildfowl, such as male Whistling Swans (Hawkins, 1986) and Canada Geese (Raveling, 1981), which remain with the female for the primary purpose of predator detection and defence.

Predators often choose their prey accounting for the capture times, handling times and prey size (Halsey et al., 2007, Ydenberg, 2007). Not only do predators risk energetic loss with inefficient hunting, but some are also at risk of injury or even death when attempting to capture their prey, perhaps from defensive weaponry of prey species such as the quills on a porcupine, or the vomit of a petrel (Sweitzer and Berger, 1992, Warham, 1977, Brown and Kotler, 2007), or from aggressive attacks against recognised predators, like the mobbing of raptors by passerines or the defence of young by parental lapwings (Dutour et al., 2016, Kis et al., 2000). Thus, it seems possible, or even likely, that nest predators would select prey based on how well guarded they are by parental birds. Perhaps, just by being passively near to a nest, eiders can indirectly protect against predation by making nests appear too large a risk to predators.

By looking at sex-specific behavioural responses to predators at a colony in Svalbard, this study investigated the potential role of male common eider in defence against nest-predation. The first aim was to better quantify the presence of males within high-Arctic colonies, as existing literature has only anecdotal information on the length of time spent in the colony during incubation, especially with regard to Arctic colonies. I also aimed to understand the predator dynamics, assessing the impact that they have on the colony and how the intensity of predation varies over time, perhaps in relation to male eider presence. I predicted that males remain in the colony with the purpose of nest guarding against predation, and I expected that the intensity of predation would decrease as more males were present within the colony. I also predicted that the success of predators would be lower at individual nests if there was a male present. If the role of the male was indeed predator protection I would expect that they would react readily to predators, removing the need for females to leave the nest and increasing safety of offspring. I predicted that females would react to predators less often if there was a male present at the nest. Conversely, I expected males to respond less often to predators if they were not with a female, but instead might only be in the colony looking for extra-pair mating or simply resting, rather than defending a nest.

Materials and methods

Study population

The common eider *Somateria mollissima* (henceforth referred to as “eiders”) is a ground-nesting sea duck that has a breeding range extending from relatively temperate climates, such as Scotland and Fennoscandia into Arctic regions including northern Alaska, Greenland and Svalbard. Throughout its breeding range eiders may employ several different nesting strategies to minimise the risk of predation. In Svalbard, eiders are the most numerous breeding duck and often are an important food source for several predatory species; notably the arctic fox *Vulpes lagopus* and glaucous gull *Larus hyperboreus* as well as being subject to occasional predation from arctic skua *Stercorarius parasiticus* and polar bear *Ursus Maritimus* (Prop et al., 2015, Frafjord, 1993, Mehlum, 1991b, Prestrud and Mehlum, 1991, Ahlén and Andersson, 1970). Most predation is directed towards eggs and newly hatched young during the nesting period. Predation on eggs and young is more intense during this time here than in more southern populations (Ahlén and Andersson, 1970), and so the nesting location is of particular importance to the Svalbard eiders. Most therefore tend to nest in dense colonies on islands out of reach from predatory arctic foxes (Mehlum, 1991b, Parker and Mehlum, 1991). Eiders have been observed to occasionally nest successfully in association with predatory gull species in some more southern populations (Olsson, 1951, Götmark and Åhlund, 1988) and, in Svalbard, with arctic tern *Sterna paradisaea* colonies (Ahlén and Andersson, 1970, Pratte et al., 2016) where it has been thought that the eiders may benefit from the “protector” species’ more aggressive nest defence. Other species of waterfowl have also been known to forgo their usual nesting location in order to nest close to species exhibiting aggressive nest defence (Blomqvist and Elander, 1988, Tremblay et al., 1997) including king eider *Somateria spectabilis* nesting in association with long-tailed skua *Stercorarius longicaudus*.

Study site

The study took place at an eider colony close to the town of Longyearbyen, Svalbard. This colony was used not just because male eiders are known to stay for the first part of incubation, but also for easy accessibility allowing daily observations. The eider colony is located on the main island of Spitsbergen, unlike colonies elsewhere in Svalbard, and thus is readily accessible to most predators in the area. However, the colony is partially surrounded

by dog kennels and is close to the only road out of the town on the east side. Whilst the dogs could be a legitimate threat to any birds that get too close, other predators may be less likely to enter the colony due to the dogs' presence (Meltofte, 1978). The owners of the western dog kennels frequently placed 1-2 dogs on chains outside of the fence to prevent fox predation. This seems to have not been completely successful as a deterrent, as the colony is still frequently visited by foxes, although perhaps to a lesser extent.

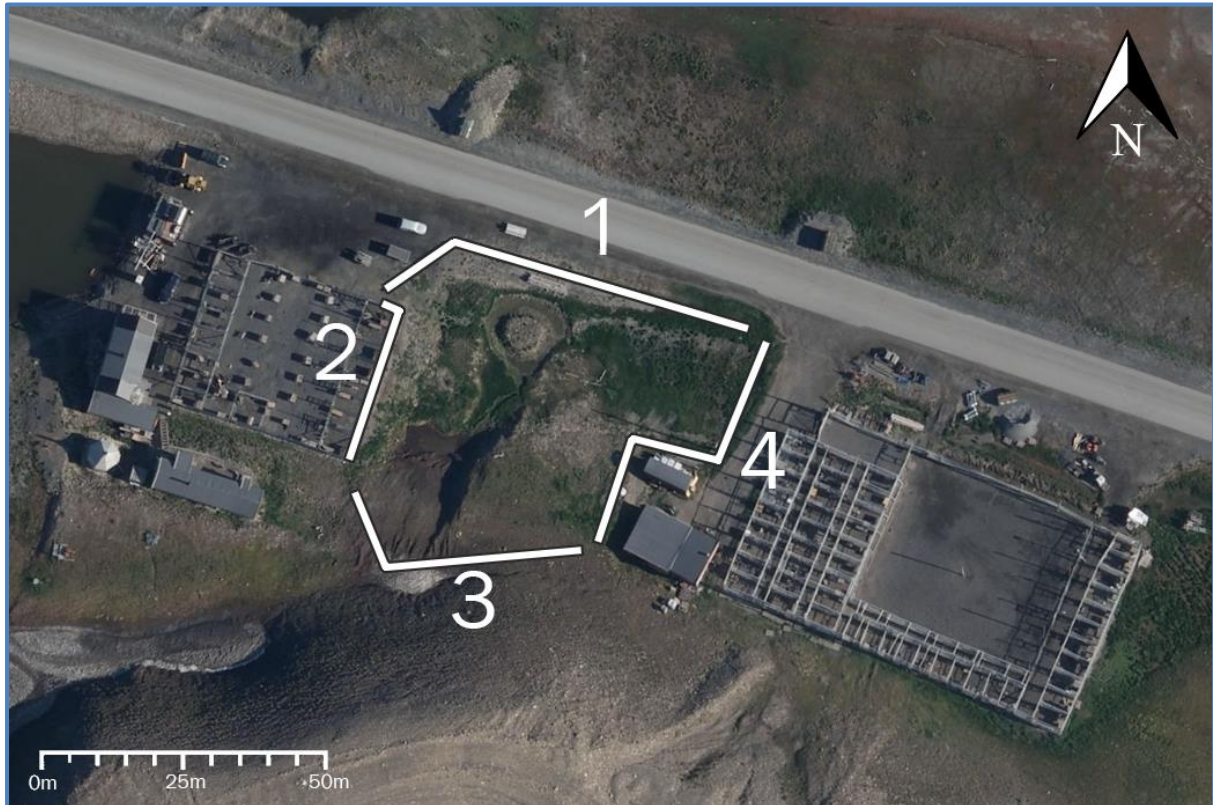


Figure 1 - Boundaries of the eider colony, different boundaries are explained in the main text – adapted from Norsk Polarinstitutt (<http://toposvalbard.npolar.no/>).

The limits of the main colony (Figure 1) were: (1) the logs on the north side separating the colony from the main road and people; (2) the fence of the dog kennel on the west side, as this was a physical barrier preventing eiders nesting any further; (3) the base of the steep slope on the south side, as birds did not to move any further up for nesting, and; (4) the driveway and buildings on the east side where eiders did not nest due to foot traffic. Some birds did nest outside of these boundaries (notably a small sub-colony of 100-200 females on the other side of the western dog kennel), but these nesters were not considered to be part of the main colony and were not counted, and predation directed towards them was not monitored either.

Observations

Observations took place from the 24th May when eiders were still arriving to the colony, until the 7th July once almost all birds had left the colony. Data were collected from all times of day to capture any circadian differences in predation regimes. Days were split into 2-hour blocks (starting on each even hour), with an average of two 2-hour observations taking place each day. The start time for each observation was decided randomly for each day, with slight adjustments being made when it was not feasible to visit the colony. On one occasion an observation was stopped one hour early due to heavy rain and wind. The date and time of each observation can be found in the Appendix (Table 5).

Before each observation started, the male and female eiders within the main colony were counted for colony population size. Population size data were available from the 16th May until observations began via the results of another concurrent study. In addition, all predators were counted every 15 minutes to estimate predator activity. An avian predator was counted if they were in areas considered to be vantage points overlooking the colony or within the colony itself. The vantage points were surrounding perches overlooking the colony (lampposts and wooden poles extending above the fence) and on the hilltop. Foxes were counted if they were in the main colony itself, on the hill, or on the road immediately next to the colony. While predator counts were done, the number of people next to the colony and the number of barnacle geese within the colony were counted also, as they had potential to disturb the birds and impact predation.

Predation and behavioural responses

Any predator simply entering the colony was not necessarily considered a predation event. Something would be considered a predation event if a predator was willingly getting within 1 metre of an eider in the colony or, when predating in the absence of any eider, actively searching for unoccupied nest sites in the colony. A predator was assumed to be searching for eggs or ducklings if they were pecking at the ground and moving foliage or feathers within the colony. Exceptions that were not considered predation events included kleptoparasitism between predators (e.g. gulls stealing eggs from each other or from foxes) and when taking eider carcasses.

For each predation event the following was recorded: species of predator, the direction from which they entered the colony, the time (to nearest minute) that predation started, the number of predators involved, the number of prey taken and whether prey taken were eggs or ducklings.

When each predation event occurred, the presence of males or females at the nest was recorded, and the nature of their responses. As it is often difficult to say which nest a bird is associated with (especially for males and at the start of nesting), it cannot be assumed that the bird responding was necessarily the nest owner, therefore an eider was considered present if a predator had to get within 1 metre to access prey. The behaviours were grouped into 6 response types: pecking at the predator without leaving the nest, chasing the predator, preventing birds landing near nest, walking away, flying away or not reacting at all. Originally chase responses were to be split into long and short chases, but eiders only pursued predators for short distances during this study.

Statistical methods

Statistical analysis was conducted using R version 3.2.4 (R Core Team, 2016).

Predation intensity was measured as the number of predations within each observation period, and thus a Poisson regression was used to test for a relationship between number of males present in the colony, observation number (time) and number of predations. The Akaike information criterion (AIC) values indicated overdispersion of the data, so a quasi-Poisson regression was found to be most suitable. A Pearson's correlation test was then used for number of males and observation number to test how strongly these factors might conflate.

Predation events were always analysed separately for each species of predator, as eiders responded differently to each, and predation events were considered independent. Binomial regressions were used to model the responses of females in the presence or absence of males. The predictor variable was male presence/absence at the nest, with the response variable being female response (responded/did not respond). Binomial regressions were used again to model the responses of males in the presence or absence of females. The predictor variable was female presence/absence at the nest, with the response variable being male response

(responded/did not respond). The results from these models of female and male responses to predators are presented with odds-ratios and 95% confidence intervals.

Binomial regressions were used for analysing the success of predators in relation to presence or absence of females and males. This was done in one model for each predator species, where predator success (yes or no) was the response variable, and the predictor variables were female presence, male presence, observation number and the interaction of male and female presence. A Binomial Regression was again used for the analysis of success of predators and whether males and females responded aggressively towards the predator. Predator success (yes or no) was the response variable, and the predictor variables were female response or male response, and observation number. The results for these models of predator success are presented with estimates and standard errors.

Results

Colony population dynamics and phenology

The first nesting female was seen on the 13th May. At this time there were already 3 eggs in her nest, so it can be assumed that she had been present since at least the 11th May. At the start of the first observation (24th May), 109 females and 118 males (227 total) were counted within the colony boundaries (Figure 2). The total population increased until the 9th June, where there were 498 eiders within the colony, however the peak number of 345 females was 5 days later (14th June), after which they left at an average rate of 14.7 females/day. The first males were seen in the colony on the evening of the 15th May. The greatest number of males observed was 198 on the 7th June, however number of males had been regularly within 25 of their peak number since the 29th May. Male numbers declined rapidly between the 11th and 12th June (104 to 36 males), and did not rise above 10 individuals after the 17th June. There were regularly 0 males in the colony from the 21st June, and never more than 2 afterwards. The last males seen in the colony during population counts were on the 1st July (2 individuals). The first hatched ducklings were observed on the 11th June, and the first ducklings were seen leaving the colony the following day (12th June). A total of 120 ducklings were seen leaving the colony with adult females during the 2-hour observations from this date until the end of the study.

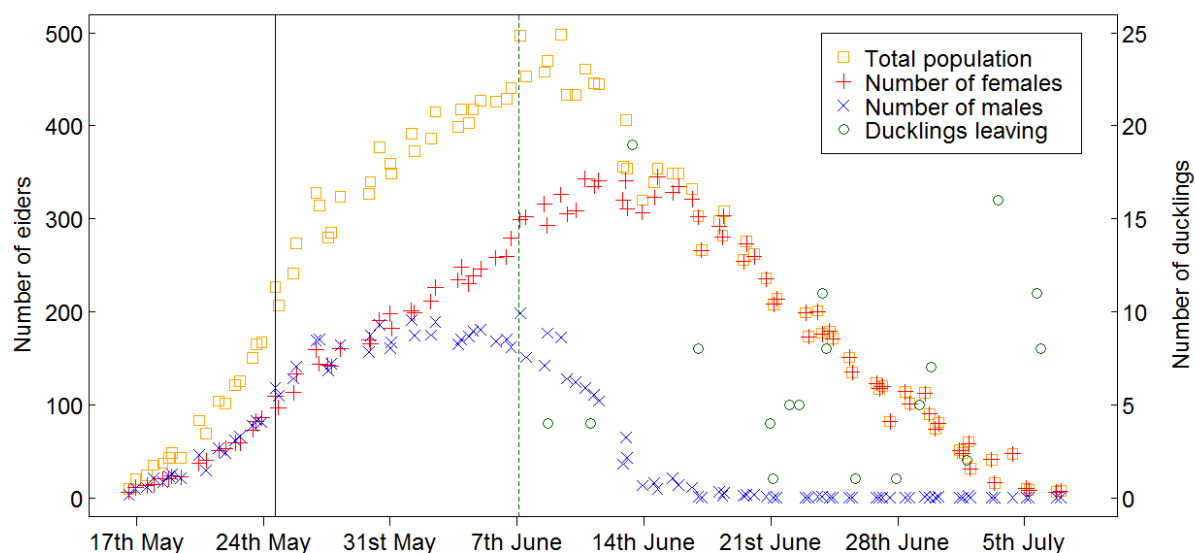


Figure 2 – Common eider numbers within the Longyearbyen colony in 2016. Solid line indicates the first 2-hour observation. Dashed line indicates the first sighting of chicks in the colony.

Predator dynamics and predation intensity

There were three main species of predator seen in the colony throughout the study; arctic fox, glaucous gull and arctic skua. Throughout the study there were 388 total predation attempts observed (Figure.3). By far, the most frequent predator was the glaucous gull, with 270 predation attempts during this period, followed by arctic fox, with 89 observed predation efforts, and skuas which made 27 predation attempts. Gulls were active throughout the entire study period, and at all times of day (Figure 4). Foxes tended to be active only between midnight and 10am, but were also present throughout the study. Skuas were only occasionally seen in the colony for the first 45 observations, and their last predation was on the 21st June (observation 56). In addition to these predators there were two predation-attempts from ivory gull *Pagophila eburnea*. Ivory gull was not expected to be a predator, and thus were not counted in 15 minute counts, although they were an infrequent visitor and there was never more than one in the colony at a given time.

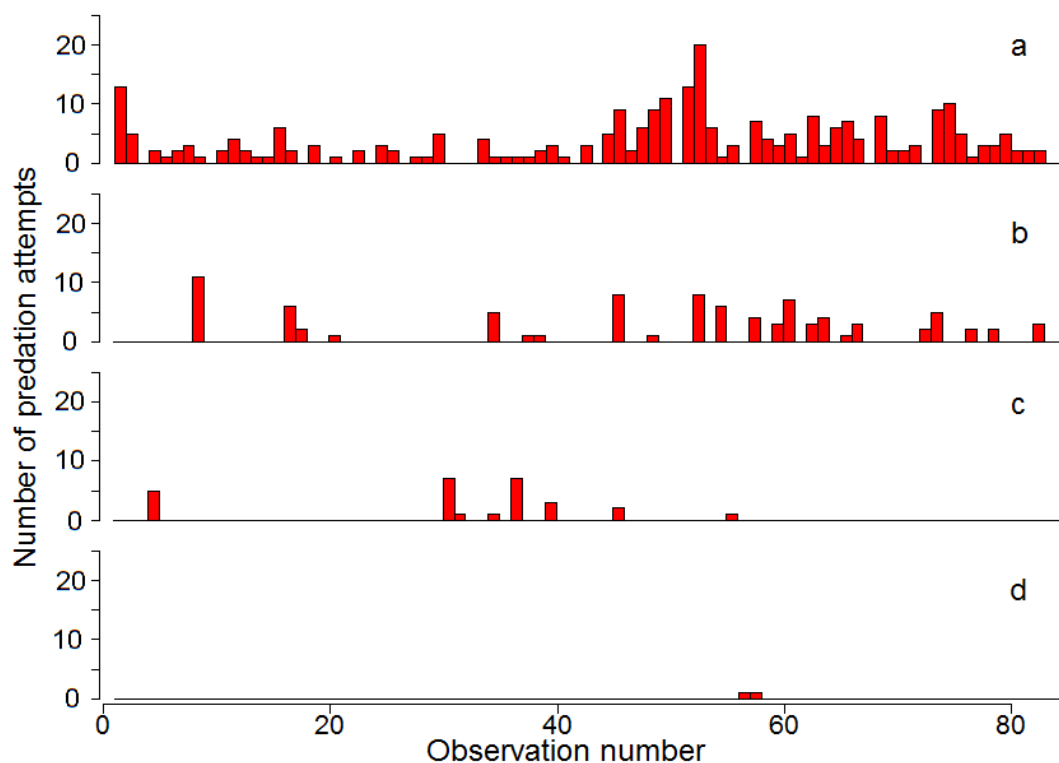


Figure 3 – Number of predations attempts by each predator within 2-hour observations.

a = glaucous gull, b = arctic fox, c = arctic skua, d = ivory gull.

Whilst glaucous gulls were the most numerous predator, and present at the colony a substantial amount of time, the arctic fox appeared to have the largest impact on eiders within the colony. Foxes successfully took 78 eggs and 27 ducklings, whereas glaucous gulls took 52 eggs and 7 ducklings. Skuas had comparatively little impact, taking only 6 eggs and 0

ducklings. In the 2 predation attempts from ivory gull, it was successful once, managing to take one egg from an undefended nest. Whilst adult eiders may make up part of the diet of arctic foxes, no adults were seen to be killed by any of these predators. A chained dog was observed killing an adult female, and dogs from outside the kennels were seen chasing birds within the colony twice during observations. On at least 5 occasions, dead adult eiders, male and female, were found in the colony and subsequently eaten by gulls and foxes.

In total, 137 eggs and 34 ducklings were seen taken by predators within the colony boundaries, and more ducklings were observed taken on route to the water after leaving the colony (although these predations were not counted). As 120 ducklings were seen to leave, it can be estimated that roughly 41% of ducklings successfully left the colony ($n \text{ ducklings seen leaving} / (\text{total number predated eggs} + \text{ducklings} + n \text{ ducklings seen leaving}) * 100$), however, this is likely an overestimate as it does not consider predations before the 24th May. Of the ducklings that did hatch, an estimated 22% were predated before leaving the colony ($n \text{ predated ducklings} / (n \text{ ducklings seen leaving} + n \text{ predated ducklings}) * 100$). The number of predations between the colony and reaching the water is unknown, but anecdotal observations include instances of fox and glaucous gulls taking ducklings from the road next to the colony.

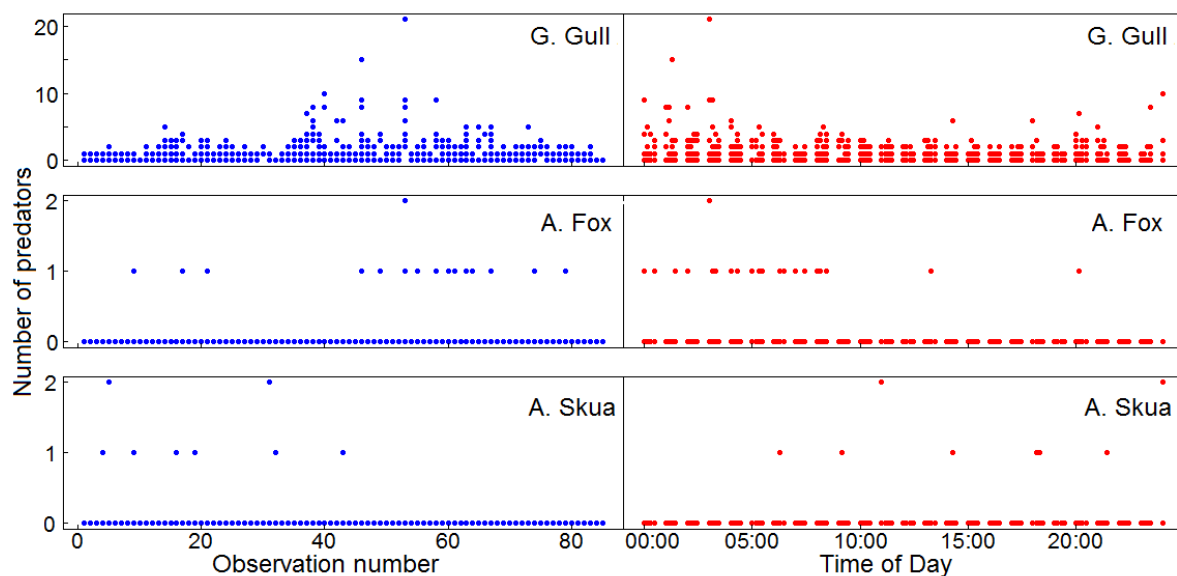


Figure 4 - Predator activity from 15 minute counts at each 2-hour observation (blue, left) and over time of day (red, right).

Predation intensity and presence of males

The number of predations in each observation was found to increase with a decrease in number of males (Table 1), with predation intensity decreasing with an increase in the

number of males. Number of females and 2-hour observation number were not found to have a statistically significant effect on predation intensity. There was a large correlation between observation number and number of males (Table 2), with number of males decreasing over time. Thus, it cannot be said with confidence that the increase in predation is a result of decreased male presence and not another factor that corresponded with time.

Table 1 - Quasi-Poisson Regression of predation intensity in relation to male and female common eider presence and the 2-hour observation number (Obs. n.).

	β	Std. err.	<i>t</i>	<i>df</i>	<i>p</i>
Male eider	-0.009	0.003	-3.09	81	0.003*
Female eider	-0.0002	0.001	-0.15	81	0.88
Obs. n.	-0.017	0.009	-1.77	81	0.08

Table 2 - Pearson's product moment correlation of number of male eiders present in the colony and the 2-hour observation number with 95% confidence intervals (CI).

	Corr.	2.5% CI	97.5% CI	<i>t</i>	<i>df</i>	<i>p</i>
Male eiders and observation n.	-0.87	-0.91	-0.80	-15.8	83	<0.001*

Responses of females in the presence or absence of males

When female eiders reacted to predation attempts from glaucous gull and arctic skua, the responses were always aggressive; usually attempting to chase or peck at the predator, or prevent them from landing. Conversely, when foxes were predating, the response was always evasive; they flew or walked away from the fox. Male presence had a significant effect on the likelihood a female responds to glaucous gull predation attempts (Table 3). Females responded to 74.1% of glaucous gull predation attempts when there was no male, but to only 37.5% of glaucous gull predation attempts if there was a male present (Figure 5). The effect of male presence for arctic fox predations could not be tested with a model as there were no observations of 'no response' from females. However, as females responded to 100% of fox predations with or without males, there is no evidence to suggest that male presence influences the response of females to arctic fox predation. The effect of male presence could not be well tested with arctic skuas due to a small sample size. When males were present, females responded to arctic skuas 100% of the time and, in the absence of males, females

responded to 84.6% of skua predations. When the ivory gull predated, females responded aggressively both times, and there were no males present on either occasion. Ivory gull predations were not modelled as there were only two predation attempts observed.

Table 3 - Results from binomial regressions of female (♀) common eider responses to predators in relation to male presence at the nest (m. pres.), and male (♂) common eider responses to predators in relation to female presence at the nest (f. pres.), presented as odds-ratios (OR) with 95% confidence intervals (CI). N/A values where there is insufficient data in one or more comparison groups to run model.

	OR	2.5% CI	97.5% CI	z	p
♀ resp. to G.Gull ~ m. pres.	0.21	0.09	0.46	-3.85	<0.001*
♀ resp. to A.Fox ~ m. pres.	N/A	-	-	-	1
♀ resp. to A.Skua ~ m. pres.	N/A	-	-	-	>0.9
♂ resp. to G.Gull ~ f. pres.	1.32	0.23	6.52	0.34	0.7
♂ resp. to A.Fox ~ f. pres.	N/A	-	-	-	-
♂ resp. to A.Skua ~ f. pres.	N/A	-	-	-	>0.9

Responses of males in the presence or absence of females

Males, like the females, only responded to the avian predators with aggression or did not respond at all, and tried to escape when foxes were present. Unlike females, males were never observed walking away from foxes, only flying. It seemed that males were quicker to respond to foxes, flying away before females, however this was not measured. Males responded to 68.8% of predations from glaucous gulls when females were present, and 62.5% when females were not present (Figure 6). The slight difference was not found to be significant, and thus there is no evidence to suggest that males respond differently to gull predation whether there is a female present or not. Male responses to arctic fox predations could not be modelled as there were no observations of males without females, but they responded to 100% of fox predations when females were present. Due to small sample size, responses of males to arctic skua predation could not be modelled. Males did not respond to the 1 predation event where females were not present, and responded to 2 out of 5 predations when females were present. Males were not present for either predation attempt from ivory gulls.

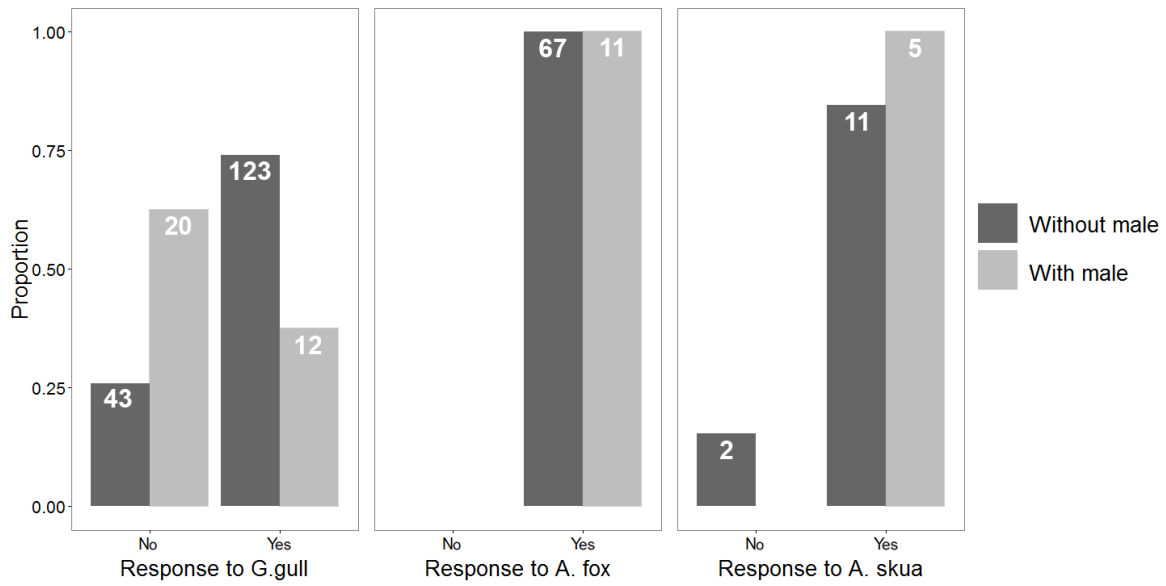


Figure 5 - Response proportions of female eiders to predation events for different predator species. Numbers on columns indicate frequency of each observed response.

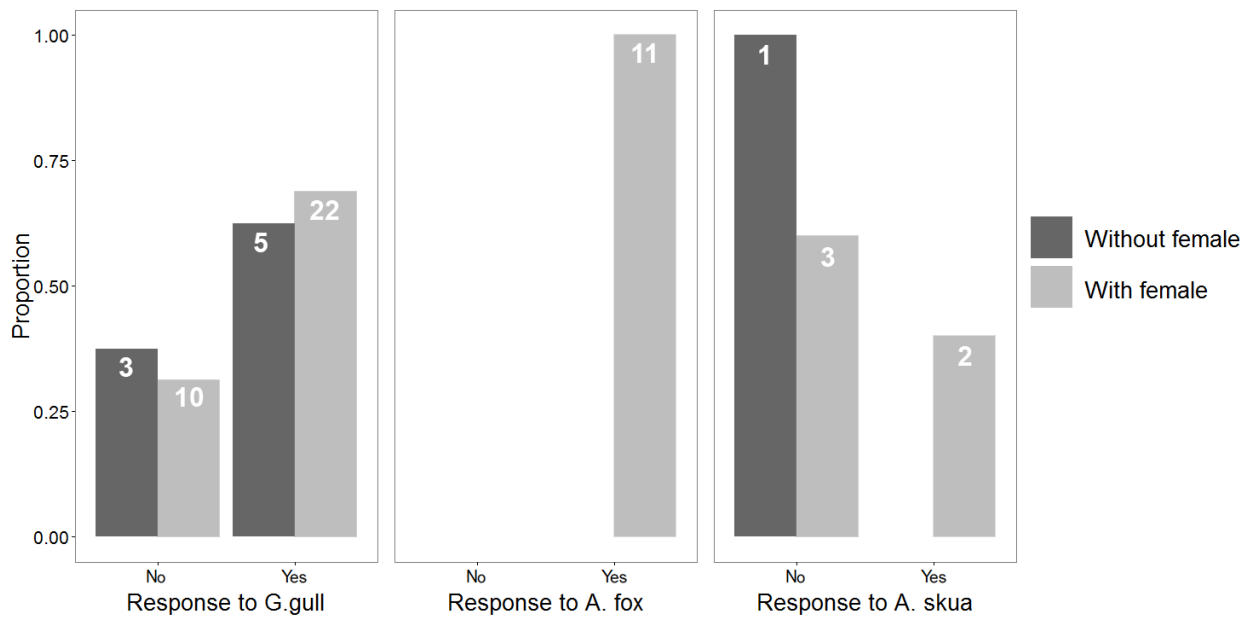


Figure 6 - Response proportions of male eiders to predation events for different predator species. Numbers on columns indicate frequency of each observed response.

Predator success and presence of females and males

The success rate of glaucous gulls was lower when males were present and, if modelled independently of female presence, the effect appeared significant. However, as males were more likely to be present when there are also females, male presence was then analysed with

female presence and was not found to have a statistically significant effect on glaucous gull success (Table 4a). Glaucous gull success was lower when females were present at the nest (13% vs 33%) and this difference was found to be statistically significant when modelled with male presence. Arctic foxes were successful in all but 3 of 89 attempts. There was no evidence to suggest that presence of either males or females at the nest prevent predation from foxes (Table 4b). On the occasions that they were unsuccessful, it is unlikely to be related to presence or absence of eiders at the nest, as the birds always reacted by moving away. The success rate of arctic skuas was not found to be lower in the presence of either males or females at the nest (Table 4c). However, there were relatively few predation attempts from skuas, especially when there were males present. It is possible that, with an increased sample size, the success rate of skuas would be found to decrease with the presence of males or females at the nest, as with the glaucous gulls.

Predator success and the response of eiders

Female eiders responded aggressively to glaucous gull predations 135 times, of which the gulls were successful in 18 attempts (13.3%). When females did not respond aggressively, gulls were successful 8 of 63 attempts (12.7%). This minor difference was not found to be statistically significant (Table 4a), and so there was no evidence that gulls had lower predation success if females responded aggressively. When males responded aggressively, gulls were successful 2 of 27 attempts (7.4%), and when males did not respond aggressively gulls were successful on 1 of 13 occasions (7.7%). There was no evidence to suggest that an aggressive response from males reduced gull success (Table 4a). Eiders always responded to fox predations by trying to escape, so fox success could not be modelled with response of either males or females. Predation success of arctic skua was lower when females responded, but the relation was not found to be statistically significant. Skua success could not be well modelled with male response due to sample size. Ivory gull predations were not modelled in relation to eider responses, also due to small sample sizes.

Table 4 – Results from binomial regression of: predator success in relation to female (♀) presence, male (♂) presence, observation number and ♀:♂ presence interaction; predator success in relation to female response and male response. a = glaucous gull predation, b = arctic fox predation, c = arctic skua predation. NA values where there was insufficient data in comparison group.

a	β	Std. err.	z	p
♀ presence	-1.01	0.38	-2.68	0.007*
♂ presence	0.25	0.80	0.32	0.75
Observation n.	0.002	0.009	0.28	0.78
♀ ♂ interaction	-17	1153	-0.015	>0.9
♀ response	-0.26	0.48	-0.55	0.58
♂ response	0.22	1.32	0.17	0.87

b	β	Std. err.	z	p
♀ presence	2.17	1.44	1.51	0.13
♂ presence	13.67	3161	0.004	>0.9
Observation n.	-0.06	0.04	-1.50	0.13
♀ ♂ interaction	N/A	N/A	N/A	N/A
♀ response	N/A	N/A	N/A	N/A
♂ response	N/A	N/A	N/A	N/A

c	β	Std. err.	z	p
♀ presence	-1.36	1.11	-1.22	0.22
♂ presence	-18.18	6522	-0.003	>0.9
Observation n.	-0.03	0.04	-0.96	0.34
♀ ♂ interaction	0.94	7110	0.00	1
♀ response	-2.66	1.79	-1.48	0.14
♂ response	6e-16	4e+3	0	1

Discussion

Population dynamics and phenology

Arrival of eiders to the colony was not synchronised, with females arriving over the span of a month, from early-May until mid-June. The lack of synchrony was further evidenced by the time difference between the first and last ducklings leaving the colony. Incubation period in common eiders is between 24 and 27 days (Waltho and Coulson, 2015). Assuming the first ducklings seen were from the first nesters, then incubation of the first eggs started mid-May. The last nesters must have started incubating in mid-June, as it was not until early July before almost all females had left their nest. Males were arriving to the colony until the start of June, and it was another week before they began to decrease in number. In Iceland Kristjansson and Jónsson (2015) noted that males remained in a dense colony until mid-June, after incubation had started in late May; much like the situation in Svalbard, as observed by this study, and noted anecdotally by Ahlén and Andersson (1970) in Kongsjorden. Elsewhere, male eiders rarely stay this long near the nest. Swennen (1990) notes that paired males in The Netherlands roosted close to the nesting area at high tide during breeding, and start to leave the coastal roosts a week before the first eggs hatched. In Scotland, Milne (1974) observed that males would accompany females searching for nesting site, but did not take an active role in searching themselves and remained in the estuary during incubation.

Whilst it certainly appears that males are present near the nest for considerably longer than observed in 'southern' colonies, without individual marking of males it is impossible to say for certain how long each individual male remains. Due to the asynchronous arrival of eiders to the colony, an arrival of males at a similar rate to those leaving could give the impression that males remain for a long period of time, when in reality each male stays for only a few days after their paired female starts incubation. Parker and Mehlum (1991) and Mehlum (1991a) observed that eiders had higher breeding synchronization in years with late establishment of colonies, as a result of late break-up of sea-ice and snow-cover melt. Sea-ice is not a factor for the Longyearbyen colony, and snow-cover at the colony site had mostly melted by early May, allowing early establishment of the colony relative to breeding dates from other studies in Svalbard (Campbell, 1975, Mehlum, 1991a, Parker and Mehlum, 1991, Ahlén and Andersson, 1970). Yet, despite variation in breeding time and synchrony between

these studies, the lingering of males is still reported. So, it would seem the behaviour of males in Arctic colonies is not entirely due to the presence of asynchronous breeding.

There were no observations of copulation in the colony, or in the small freshwater pond next to the colony. Mating in eiders generally takes place on the water, rather than on land (Waltho and Coulson, 2015), so males looking for extra-pair mating would logically have more success in the fjord rather than in the colony. Whilst extra-pair mating is not widely reported in eiders (Christensen, 2000), there seems to be little reason why it would happen here to a greater degree than in colonies further south.

Predator activity

Long daylight periods mean that predators can be active throughout the entire day, probably contributing to the higher nest predation intensity discussed by Ahlén and Andersson (1970), Campbell (1975) and Mehlum (1991b) in the Arctic colonies. In fact, the highest predator activity occurred during late night/early morning, when activities of people were at a minimum. As expected, the two main predators were glaucous gulls and arctic foxes. As shown by previous eider studies in Svalbard (Prestrud and Mehlum, 1991, Ahlén and Andersson, 1970), when eiders in Svalbard nest on the mainland (or on islands connected by ice) they are extremely susceptible to predation from foxes. So, it was not unexpected that the predator with the largest impact on eggs and ducklings in the Longyearbyen colony was the arctic fox, taking more than other predators combined. There are also likely high energetic costs to adult birds with these predations, as they are flushed from the nest when the fox enters the colony.

The main avian predators were glaucous gulls, which were almost always present at, or at least near to, the colony. Glaucous gulls are opportunistic feeders, whose diet can vary substantially between individuals (Barry and Barry, 1990, Samelius and Alisauskas, 1999) and the eider colony likely provides a substantial part of the diet to many of the gulls in the area. During this study gulls were often present within the eider colony, usually on poles overlooking the nesting eiders. They do not always predate during this time, but wait for opportunities to steal eggs or ducklings. Mehlum (1991b) observed that glaucous gull predation almost only occurred when females were away from their nest, with a success rate of 50%. The results from this study are quite different, as gulls regularly attempted to predate

occupied nests, but with a much lower success rate. Food availability, or specialization of specific gulls may account for this difference between studies.

Arctic skuas were seen less frequently in the colony from mid-June, around the same time that predation from glaucous gulls and foxes increased. The skuas may have stopped predated the colony to avoid competition or disturbance from the increased gull presence, however, as skuas usual feeding strategy involves stealing food from other seabirds (Arnason and Grant, 1978, Davis et al., 2005), the colony probably comprises only a small portion of their diet. Thus, the skuas may have switched diet once their preferred food became more available on the arrival of greater numbers of arctic terns and foraging kittiwakes *Rissa tridactyla*. The handling of more developed eggs or ducklings may also be more challenging for skuas, contributing to this diet switch. The predation from ivory gull was not expected, and to this study's knowledge is the first recorded predation of ivory gull on active eider nests.

The estimated losses of 58.8% of young to predation from this study is within the range of numbers from Mehlum (1991b), where he observed losses of 29.2%, 58.1% and 59.4% in successive years. Mehlum notes that the year with lowest percentage losses was also the year with highest synchrony and greatest number of eggs. Ahlén and Andersson (1970) thought 10 to 20% of ducklings was a likely loss due to predation on land, which is comparable to the estimated loss of 22% of ducklings after hatching from this study. This does not include predation between the colony and the water, which from anecdotal observations could be quite large, however, the colony from Ahlén and Andersson's study did not suffer from the same high numbers of fox predations. Perhaps then, the survival rate at the colony near Longyearbyen is comparable to the colonies in Kongsfjorden despite being situated on land.

Predation activity appeared to increase within a few days of most males leaving, however, this occurred around the same time as the appearance of the first ducklings. Thus, the exact reason for the predation increase is difficult to determine, but it could be attributed to three potential factors. First; the presence of males may have acted as a deterrent for many opportunistic gulls, and their leaving opened new opportunities for these predators. The increased risk of feather damage or injury from the additional eider at the nest could outweigh the benefits from predated male-guarded nests, and by being at the nest males may act as a visual deterrent to the gulls. Second; the ducklings are a much more obvious and

perhaps easy to catch prey than covered eggs, especially when they are not underneath the female. In this study ducklings were frequently seen running outside the nest shortly before they were ready to leave the colony. Campbell (1975) observed that predation from glaucous gulls was more frequent, and had greater success, on nests with hatched ducklings, so it is likely that ducklings are more vulnerable to predation from gulls than the hidden eggs. Third; the timing of the males leaving and chicks appearing could coincide with the hatching of some glaucous gull chicks, which can start as early as mid-June (Norderhaug, 1989, Descamps, NPI, unpubl. data). The new chicks would require adult gulls to bring them food, and predation intensity could increase accordingly. A combination of these factors may be a reasonable explanation for the increase in predation.

Eider responses to predators

Females were less likely to respond to glaucous gulls if there were males present. This could be important for conservation of energy for the females. As capital breeders, they rely on stored energy to survive the nesting period, rarely leaving the nest for food. Incubating the eggs requires a large amount of energy expenditure, with females losing 40% of their body mass during this period (Gabrielsen et al., 1991). Frequently leaving the nest to defend would take a greater energetic toll on females, and the presence of males alleviates this to a degree. As glaucous gulls were by far the most frequent predator in the colony, the energetic savings of females not having to respond could be quite substantial. Therefore, even if the primary purpose of males accompanying females at the nest is not directly as a predator defence, their presence may be quite beneficial to the female.

When foxes entered the colony, it was usual that all the birds in the colony would leave, especially at the start of incubation, most likely to protect themselves against direct predation. Although not quantified, the males were almost always the first to leave. Such a response suggests that they are not willing to accept as great a risk as females who were more reluctant to abandon nests, especially if they were with ducklings rather than just eggs. Females often opted to walk away from the fox, rather than flying, until the fox got close, particularly once their ducklings had hatched.

Whilst males readily respond to gulls harassing feeding females on the water (Hario and Hollmen, 2004, Eliassen and Jørgensen, 2014), it was unknown whether this defence

extended past the pre-nesting period. In this study males responded readily to predators near the nest, regardless of whether there was a female present or not. Whether this is males continuing to defend the female is not known, but as they respond just as readily when there is no female, they may be responding for reasons of self-defence or to protect the nearby nest. Prevention of other males harassing females did seem to extend to the colony, as males were regularly seen fighting off other males that approached too close to their female. There were no instances of extra-pair mating observed within the colony itself, but females were frequently seen followed by numerous males at the start of nesting. Perhaps then, unpaired males in the colony are still looking for potential to breed, whilst paired males accompany their mate in the colony to prevent other eiders successfully extra-pair mating.

Predator success

The success of predating gulls was lower when there were female eiders at the nest. This is not surprising, as they are usually covering eggs and will readily chase off gulls. Although male presence may have decreased predation success, they almost always accompanied females. Therefore, any impacts that male presence had on success were difficult to determine, but it is probable that the presence of any eider at the nest will reduce gull success. Gulls did not have lower success when either female or male eiders responded aggressively vs not responding at all. With females, responding aggressively often required getting off their nest leaving the eggs or ducklings exposed. So, the increased likelihood of chasing off the gull is offset by the increased risk to the nest by briefly exposing it. By responding to predators, males did not reduce the success of gulls either. This is more surprising than the females, as by responding males did not leave the nest at additional risk.

Foxes were not put off by the presence of males or females at the nest, as there were no attempts from eiders to defend against them. Foxes sometimes seemed a bit tentative when approaching eiders, but as they always flew or walked away the foxes could access the prey without risk. If anything, the movement of eiders alerted the fox to where a nest was located. Perhaps then, the presence of males could be detrimental in this circumstance, and may account for why they left earlier than the more-camouflaged females, that could easier go unnoticed.

Concluding remarks

Males were found to be present within the eider colony for a period extending past the start of incubation, until some of the first ducklings appeared. There was often a small number of males in the colony until very near the end of incubation. This study found that by being present in the colony, males provide some protection against certain predators. By responding to avian predators, the males reduce the need for females to leave their nest, conserving the female's energy, critical for surviving through the incubation period, and allowing nests to remain covered.

While I did not see that the success rate of gulls was affected by the presence of males, it is likely that by sitting near the nest males reduce the number of easy predation opportunities for gulls. If this is the case, the males act as a visual deterrent against predators to the benefit of paired females, and potentially their neighbours. Protection of nests and females in the colony may not be the only reason for males to remain longer during incubation in northern colonies. However, the results of this study suggest that in doing so, the males contribute to the successful breeding of eiders in these areas, despite high levels of predation.

There was no evidence from this study to suggest that male presence in the colony is primarily driven by extra-pair mating, or even protection of females from other males. I propose then, an increase in paternal effort has emerged as a direct response to the high predation pressures faced in the Arctic colonies, rather than through extra-pair mating or asynchronous breeding.

Acknowledgements

I would first like to thank both of my supervisors, Øystein Varpe and Rolf Anker Ims, for this project opportunity and the experience gained from it, as well as for their guidance and enthusiasm throughout. Special thanks also to Anna Ejsmond, who helped with advice and encouragement during my stay in Svalbard, especially during fieldwork. Thanks also to my friends and especially my family for their support throughout my education. Lastly, I would like to thank the eiders, who kept me company during the many hours of fieldwork.

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Appendix I



Figure 7 - View of the common eider colony near Longyearbyen.



Figure 8 - Ivory gull with common eider egg, chased away by nesting female eider.

Appendix II

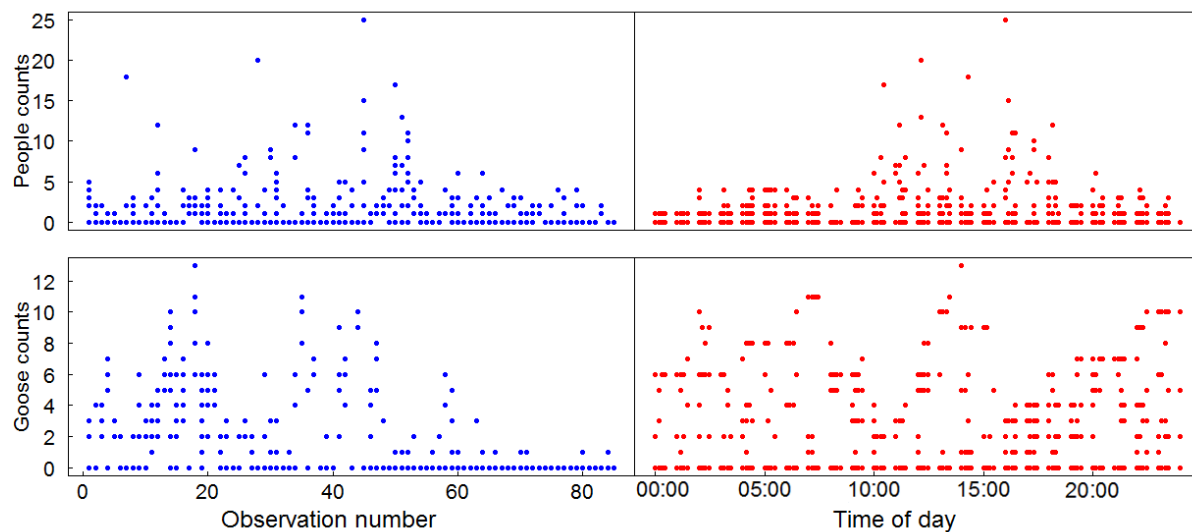


Figure 9 – Human and barnacle goose activity from 15 minute counts at each 2-hour observation (blue, left) and over time of day (red, right).

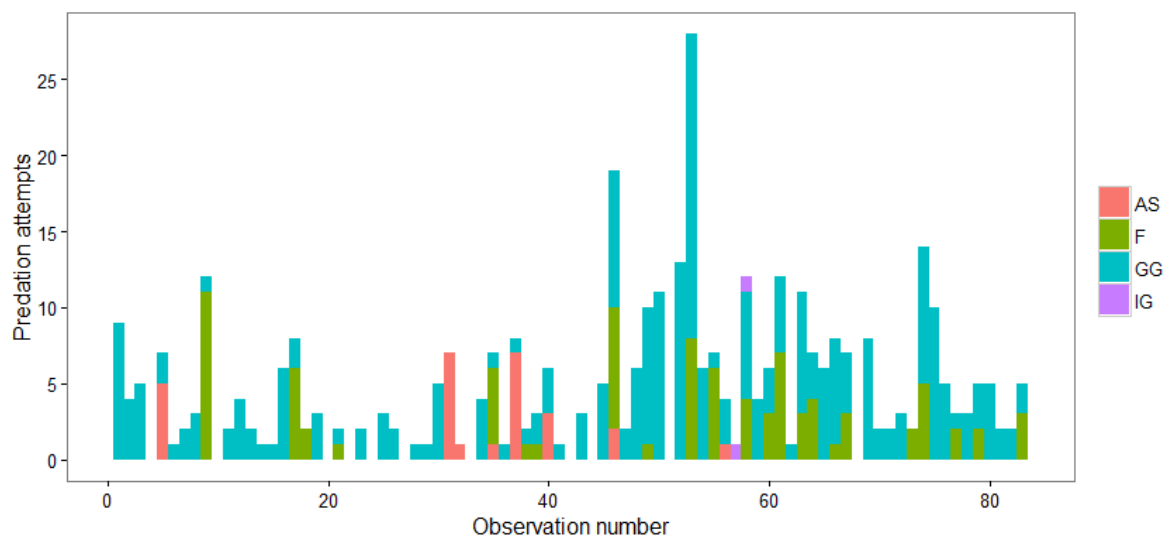


Figure 10 – Total predation intensity on common eider over time in the eider colony.

AS = Artic Skua predations, F = Arctic Fox predations, GG = Glaucous Gull predations, IG = Ivory Gull predations.

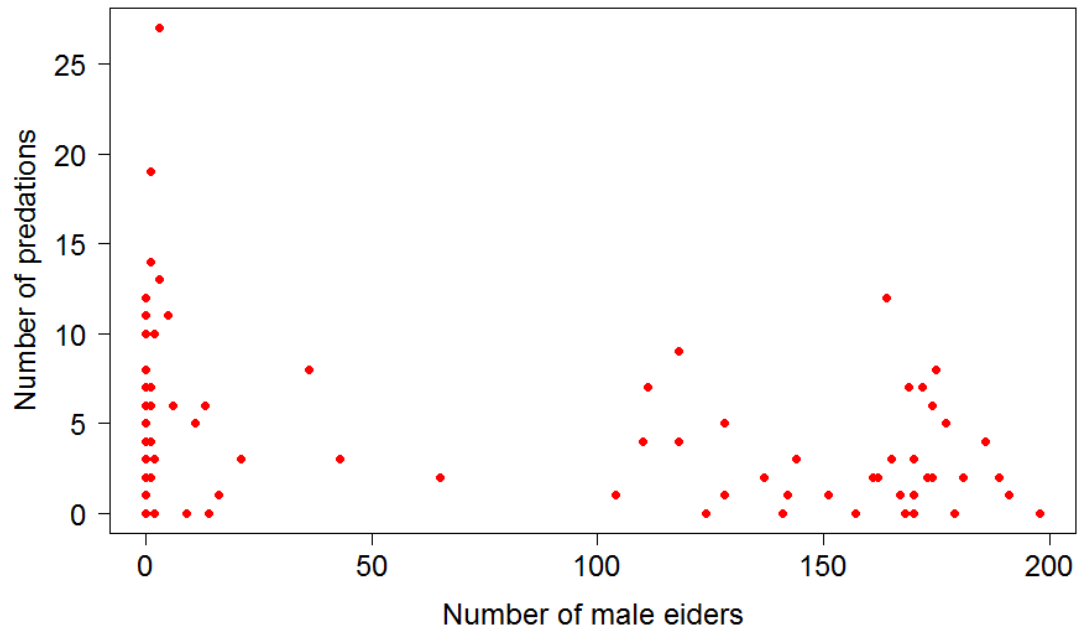


Figure 11 - Predation intensity in the common eider colony in relation to the number of males present within the colony.

Appendix III

Table 5 - Date and time of each observation. *Observation lasted only one hour.

Observation	Date	Time
1	24/05/2016	1600-1800
2	24/05/2016	2000-2200
3	25/05/2016	1600-1800
4	25/05/2016	2000-2200
5	26/05/2016	2200-0000
6	27/05/2016	0200-0400
7	27/05/2016	1400-1600
8	27/05/2016	1800-2000
9	28/05/2016	0600-0800
10	29/05/2016	2000-2200
11	29/05/2016	2200-0000
12	30/05/2016	1000-1200
13	31/05/2016	0000-0200
14	31/05/2016	0200-0400
15	01/06/2016	0400-0600
16	01/06/2016	0800-1000
17	02/06/2016	0600-0800
18	02/06/2016	1200-1400
19	03/06/2016	1800-2000
20	03/06/2016	2200-0000
21	04/06/2016	0800-1000
22	04/06/2016	1400-1600
23	05/06/2016	0000-0200
24	05/06/2016	2000-2200
25	06/06/2016	1000-1200
26	06/06/2016	1600-1800
27	07/06/2016	0400-0600
28	07/06/2016	1200-1400
29	08/06/2016	1200-1400
30	08/06/2016	1600-1800
31	09/06/2016	1000-1200
32*	09/06/2016	1800-1900
33	10/06/2016	0600-0800
34	10/06/2016	1800-2000
35	11/06/2016	0600-0800
36	11/06/2016	1200-1400
37	12/06/2016	2000-2200
38	13/06/2016	0000-0200
39	13/06/2016	0200-0400
40	13/06/2016	2200-0000
41	14/06/2016	1400-1600
42	14/06/2016	1800-2000
43	15/06/2016	1400-1600
44	15/06/2016	2200-0000

Observation	Date	Time
45	16/06/2016	1600-1800
46	17/06/2016	0000-0200
47	17/06/2016	0400-0600
48	18/06/2016	0400-0600
49	18/06/2016	0800-1000
50	18/06/2016	1000-1200
51	19/06/2016	1200-1400
52	19/06/2016	1600-1800
53	20/06/2016	0200-0400
54	20/06/2016	1800-2000
55	21/06/2016	0400-0600
56	21/06/2016	0800-1000
57	22/06/2016	2200-0000
58	23/06/2016	0200-0400
59	23/06/2016	1400-1600
60	23/06/2016	2000-2200
61	24/06/2016	0600-0800
62	24/06/2016	1000-1200
63	25/06/2016	0800-1000
64	25/06/2016	1200-1400
65	26/06/2016	2000-2200
66	27/06/2016	0000-0200
67	27/06/2016	0400-0600
68	27/06/2016	1400-1600
69	28/06/2016	1000-1200
70	28/06/2016	1600-1800
71	29/06/2016	1200-1400
72	29/06/2016	1800-2000
73	30/06/2016	0200-0400
74	30/06/2016	0600-0800
75	01/07/2016	1000-1200
76	01/07/2016	1400-1600
77	01/07/2016	2200-0000
78	02/07/2016	0000-0200
79	03/07/2016	0400-0600
80	03/07/2016	0800-1000
81	04/07/2016	0800-1000
82	05/07/2016	0200-0400
83	05/07/2016	0600-0800
84	06/07/2016	1800-2000
85	07/07/2016	0000-0200

