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Neighbourhood watch among common eiders (*Somateria mollissima*) – Does group nesting reduce nest predation?

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Cover page photos. Front: A predated common eider egg. Back from top to bottom: 1, A female common eider *Somateria mollissima*) incubating the nest, 2, a great black-backed gull (*Larus marinus*) taking a common eider egg from an unprotected nest. All photos are by the author.

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1. Abstract

Colony nesting is thought to be an example of the selfish herd strategy, where aggregating behaviour may be an evolutionary adaptation to reduce the risk of predation. The common eider (*Somateria mollissima*) is a ground nesting sea bird susceptible to high nest predation rates through the nesting period. They often nest in groups, yet some also choose to nest solitarily. I examined whether group nesting was associated to nest predation in a sub-arctic common eider colony on Grindøya, Northern Norway. Earlier studies relatively homogenous arctic habitats have shown reduced predation rates among high-density nesters, however the heterogenous and vegetation-rich habitat on Grindøya may reduce the advantage of group nesters over solitary nesters. Data containing GPS-location of nests, clutch size, laying-date, weight of the female and nesting success from 2011-2021 were analysed to see if the distance to nearest neighbour and number of neighbouring nests within a 20-meter radius was associated with predation rates. Both distance to nearest conspecific neighbour and number of neighbouring nests were significantly associated with predation in the models, indicating a strong group effect in reducing predation. Predation increased significantly during the study period, correlating with a significant increase in amount of group nesters. Thus, group nesting could be a behavioural adaption to increased predation pressure. However, the condition and experience of the nesting female seem to be the most important factors in reducing nest predation, as both an early egg laying-date and a larger clutch size are associated with reduced nest predation, the latter having the strongest relation to predation in the analyses. Nevertheless, group nesting seems to be an advantageous behavioural adaptation to high predation pressure, indicating an independent selfish herd effect among nesting common eiders.

Keywords: nest predation, selfish herd, group nesting, colony nesting, common eider, *Somateria mollissima*, Grindøya

2. Introduction

Predators often target isolated and marginal individuals, and selection is therefore likely to favour individuals who stay close to others (Hamilton, 1971). Thus, aggregating behaviour can be beneficial for the individual, and is therefore thought to be an evolutionary adaptation to reduce the risk of predation (Hamilton, 1971). Colony nesting is thought to be one example of a so called "selfish herd" strategy (Hamilton, 1971), a common strategy among seabirds to avoid predation - or more specifically nest predation (Andersson & Waldeck, 2006; Götmark & Ahlund, 1988; Hamilton, 1971; Patterson, 1965). Nest predation is one of the most important mortality factors among birds (Ricklefs, 1969) and nesting at high densities have many advantages in reducing predation, for example, trough communal mobbing of predators, communal vigilance and by making it more difficult for predators to detect unattended nests through a dilution mechanism (Pratte et al., 2016; Rolland et al., 1998).

Even though colonial nesting is a well-used strategy among seabirds to reduce predation, it is one of the least understood of avian breeding systems (Brown & Brown, 2001). Dense colonies seem to confer large disadvantages for individuals, for example through competition for resources and space, through higher risk of transmission of infectious organisms, through increased brood parasitism and through higher stress levels (Coulson, 2002; Møller, 1987; Waldeck et al., 2004). Although gregarious behaviour in mobile groups have been shown to be advantageous in predator avoidance, the fixed nature of bird colonies may limit these advantages (Varela et al., 2007). Colonies of nesting sea birds may even attract predators as they represent areas of abundant food availability, and colonial nesting may thus increase predation (Varela et al., 2007). Nevertheless, evolution of gregarious tendencies may persist even though it can result in lowering the overall mean fitness (Hamilton, 1971).

The common eider (*Somateria mollissima*) is one example of a colony nesting sea bird where nest predation is substantial (Andersson & Waldeck, 2006; Erikstad & Tveraa, 1995; Stien et al., 2010). That is, predation on the adult incubating females occur, yet most often predation are targeted towards eggs, i.e., nest predation (Mallory, 2015; Öst & Steele, 2010). Most eider colonies are situated on islands, and this is thought to be an adaptation to avoid mammalian

predators (Ahlén & Andersson, 1970; Goudie & Robertson, 2020; Mallory, 2015). The female common eider usually lay between 3 to 6 eggs (more eggs is most likely a result of brood parasitism (Kilpi et al., 2004)), with a following incubation period of 25–28 days (Lorentsen, 2020; McDougall & Milne, 1978). Common eiders are ground nesters, and in addition to relying on camouflage from their cryptic plumage, female eiders often establish nests in dense vegetation, shrubs or in sheltered sites, for example under rocks or in crevices (Waltho & Coulson, 2015). Their eagerness in utilizing man-made eider-houses set up in relation to the eider-down harvesting also indicates a strong selection towards nesting in sheltered sites (Fageraas, 2016). Nests are normally established along the shoreline, but can also be found in the forest, however normally within 200 meters from the sea (personal observations, (Waltho & Coulson, 2015)). In areas with no vegetation as shelter, nests may be established on bare ground, moss or shingle/gravel (Waltho & Coulson, 2015) where they can be more exposed to both predation and heat loss (D'alba et al., 2009; Öst et al., 2008). The male usually accompanies the female until she has laid all the eggs, leaving the female to take care of the incubation on her own (Waltho & Coulson, 2015). After hatching, the female heads to the ocean with the younglings within 24 hours (Kilpi & Lindström, 1997).

Eggs are mainly preyed upon when they are unattended, as most predators are not able to drive the large females off the nest (Götmark & Ahlund, 1988). However, larger predators, such as great skuas (*Stercorarius skua*), white-tailed sea eagles (*Haliaeetus albicilla*), large gull species (*Larus* spp.), and larger mammals may scare the female eiders off the nest, or even predate on both the adult female and on the eggs (Ekroos et al., 2012; Mehlum, 1991; Waltho & Coulson, 2015). During the egg laying-period, the female eider lay one egg per day and leaves the nest unattended (although concealed with nest material) until the next day (Watson et al., 1993). This is also when most nest are predated (Andersson & Waldeck, 2006; Hanssen et al., 2002; Hanssen & Erikstad, 2012; Mehlum, 1991). Earlier studies suggest that the female eider increases nest attendance after the second egg is laid. Consequently, while the predation rate on the first egg is 48.7% the predation rate of nests with two eggs is 3.43% (Hanssen et al., 2002). The time spent on the nest by the female eiders increases for each egg until the second last egg is laid, and the incubation starts (Cooch, 1965; Hanssen et al., 2002). During incubation, the female eider only leaves the nest to drink every 2nd or 3rd day during

"natural recesses" for no more than approximately 4 minutes at the time (Erikstad & Tveraa, 1995; Mehlum, 1991; Watson et al., 1993). The almost constant nest attendance during the incubation period of 25 to 28 days comes at a huge cost for the female eider, where she may lose more than 30% of her body weight due to anorexia (Korschgen, 1977; Parker & Holm, 1990). The high nest attendance is, however, a rather successful strategy to prevent nest predation (Korschgen, 1977; Mehlum, 1991; Milne, 1976). Studies have shown that nest predation is less than 1% per day from when the female starts incubating the full clutch (Andersson & Waldeck, 2006). Female eiders also seem to take more risks as incubation progresses, giving greater protection to the clutch from predators later in the incubation period (Bolduc & Guillemette, 2003; Dawkins & Carlisle, 1976).

To reduce risk of nest loss during the "natural recesses" the female eiders conceal the nest with down and nest material (McDougall & Milne, 1978; Stien & Ims, 2016). However, when female eiders flee from the nest due to disturbance (for example from human activities), there is no time to cover the nest, resulting in a large increase in nest predation (Bolduc & Guillemette, 2003; Götmark & Åhlund, 1984; Stien & Ims, 2016). This suggests that disturbance can have large effects on the reproductive success of eiders (Bolduc & Guillemette, 2003; Stien & Ims, 2016). Even though the fleeing eiders have no time to conceal the nest, they often defecate over their eggs as they leave (Beetz et al., 1916; McDougall & Milne, 1978). This is thought to be an antipredator response as the faeces from incubating birds are acidic and smelly and different from those of non-incubating birds. The defecation has been shown to deter both mammals and crows from taking fouled eggs (Beetz et al., 1916; McDougall & Milne, 1978). This adaptive behavioural response suggests that predation has been important in selection among common eiders. Despite the defecation strategy, fled nests still have a higher risk of nest predation, perhaps also because the noise and movements of the fleeing female eider can act as cues for predators (Stien & Ims, 2016).

Common eiders may have evolved camouflage, high nest attendance and nest defecation in response to predation. They are also known to nest in relation to or even within colonies of vigilant species such as arctic terns or gulls, so called protector species, as a means to reduce nest predation on own eggs (Gerell, 1985; Pratte et al., 2016). Earlier studies have also shown

that a larger clutch size seems to be associated with lower nest predation (Erikstad & Tveraa, 1995; Gerell, 1985; Hanssen et al., 2003; Yoccoz et al., 2002), and, as predation rates and habitat features (e.g. vegetation cover) can vary over the nesting season, the timing of egg laying may also influence predation rates on nests (Andersson & Waldeck, 2006). One additional behavioural response that eiders also seem to utilize is group nesting (Ahlén & Andersson, 1970; Hamilton, 1971; Mehlum, 1991; Pratte et al., 2016). A large amount of nests on Grindøya, a common eider-colony in the Troms og Finnmark county, Northern-Norway (SEAPOP, 2022) are aggregated. However, there are some females nesting solitarily, often several hundred meters from the nearest neighbour. Is there an adaptive cause for the aggregation of nests? A nest site selection purely based on trial and error would involve a high risk of predation, suggesting that eiders may use some decision rules when deciding whether to nest in groups or solitarily (Swennen, 1989). Common eiders are known to utilize a wide variety of nest habitats with different extent of vegetation cover (Gerell, 1985; Laurila, 1989). Eider colonies in arctic habitats with relatively homogenous nesting habitats have been shown to have less clutch predation among high nest-density groups than among low density-nests, indicating a group effect in reducing predation in vegetation-poor habitats (Ahlén & Andersson, 1970; Mehlum, 1991; Pratte et al., 2016). Is this "selfish herd"-effect also present in a heterogeneous and vegetation rich nesting habitat, such as that on Grindøya? As the female eiders rely on their cryptic plumage and often nest under the cover of dense foliage or tree trunks, one may presume that the solitary nesting individuals could have an advantage over more-easily detectable groups of nesting individuals in such habitats. Crows, being the main nest predator on Grindøya (Erikstad & Tveraa, 1995; Stien et al., 2010), are also known to continue to search around an area once they have discovered one nest, and may therefore fly from nesting group to nesting group (Franck et al., 1967), giving an advantage to solitary nesters. This study examines whether nest predation is lower and nesting success higher among group nesting common eiders than solitary nesting common eiders in a heterogeneous habitat, and whether the distance to the nearest neighbouring conspecific nest has an effect on nest predation.

3. Material and methods
## 3.1. Common eiders (*Somateria mollissima*)

Common eiders are the only *Anatidae* occupying marine environments all year round and the largest duck in the Northern hemisphere (Waltho & Coulson, 2015). They are large (1,5–2,5 kg), long lived marine ducks, and reach maturity when 2-3 years old (Lorentsen, 2020). Common eiders are sexually dimorphic, males being easily recognisable on the white and black breeding plumage and yellow beaks, in addition to green markings on the neck (Svensson et al., 2017). Females and juveniles are more cryptic with a brown/grey plumage and grey beaks, the females can be separated from juveniles by white bands on the inner part of their wings (Lorentsen, 2020). The common eider is normally a resident species, although migration occur in a few populations (Hanssen et al., 2013; Svensson et al., 2017). They are benthic feeders, with blue mussels (*Mytilus edulis*) being their preferred prey (Waltho & Coulson, 2015). The common eider is a quite numerous species with a circumpolar distribution, and was in 2013 estimated to have a population size of 87 000 breeding pairs along the Norwegian coast alone (Fauchald et al., 2015). However, the population is in decline, and was listed as "vulnerable" on the Norwegian red list in 2021 (Stokke et al., 2021). There are several subspecies of *Somateria mollissima*, but this study will focus on the *Somateria mollissima mollissima* found along the Norwegian coast.

3.2. Study site

Grindøya is a small island situated at 69°38′N, 18°52′E, approximately 2 km south-west of the city of Tromsø along the coast of Northern Norway. The island covers 0.65 km^2, is quite flat (highest point is 12 meters above sea-level) with both wide-open meadows, tall-herb woodlands, crowberry dominated hills and thick scrub marches. Grindøya is part of a nature reserve with a public access restriction from the 1st of May until 30th of June, implemented in order to limit disturbance on nesting birds. It hosts a breeding colony of common eiders, which is the only large breeding colony of eiders in the area (SEAPOP, 2022). The colony has been a subject for yearly research since 1984 and has since 2009 been a SEAPOP key site for monitoring seabird populations along the Norwegian coast. In 1995 it was estimated to be more than 500 common eider-nests on Grindøya (Erikstad et al., 2010). However, there was a

substantial decrease in the breeding population in the early 2000s (figure 1). The breeding population on Grindøya has been fairly stable in the last decade, and in 2021, 143 nests was registered on the island (figure 1).
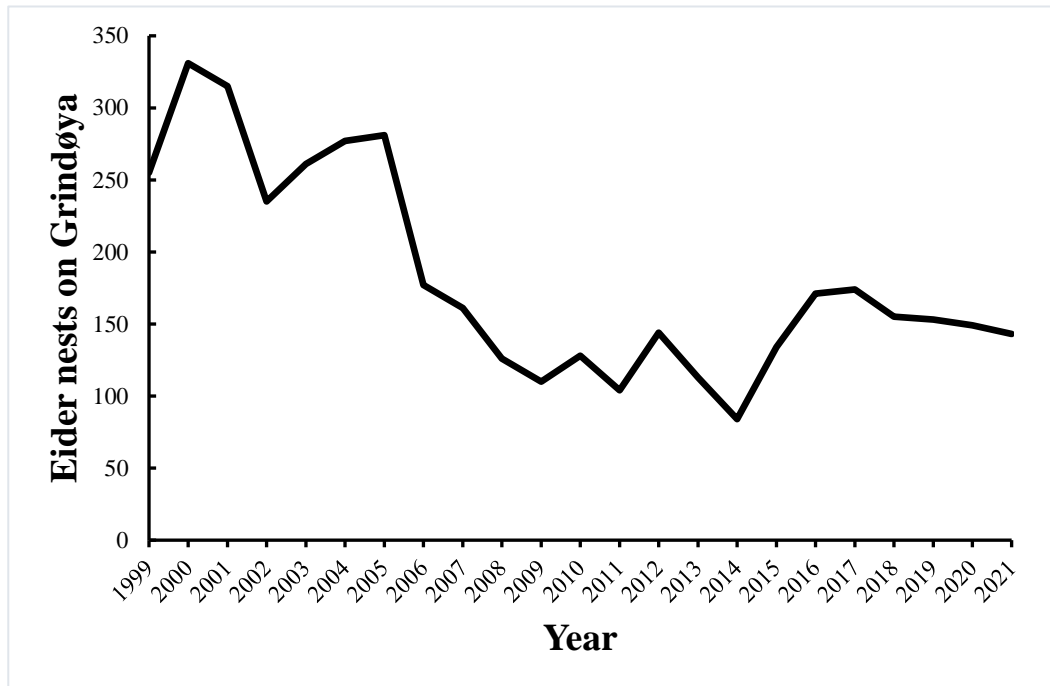
Figure 1: Number of registered common eider-nests on Grindøya from 1999 to 2021.

Dense vegetation has been shown to reduce nest predation rates (Ekroos et al., 2012; Lusignan et al., 2010; Martin, 1993), and dense foliage and lots of small microhabitats makes Grindøya a heterogenous nesting area with many sheltered nest sites. Despite this, nest predation rates on Grindøya are high (Stien & Ims, 2016), and predation may pose the largest threat to the breeding population on the island, especially when combined with other anthropogenic stressors (e.g. disturbance, pollution and climate change) (Bårdsen et al., 2018). The public access restrictions may reduce disturbance compared to other nesting sites, but active monitoring and research on the nesting eiders have been shown to elevate predation rates compared to control sites and may be a contributing factor to the high predation levels at Grindøya (Stien & Ims, 2016). Additionally, sheep (*Ovis aries*) grazing on the island may also contribute to disturbance-mediated predation.

The main nest predators on Grindøya are hooded crows (*Corvus cornix*), herring gulls (*Larus argentatus*) and great black-backed gulls (*Larus marinus*), all effective in raiding unprotected nests (personal observations, (Erikstad & Tveraa, 1995; Stien & Ims, 2016; Stien et al., 2010)). Other possible nest predators on Grindøya includes ravens (*Corvus corax*), white-tailed eagles (*Haliaeetus albicilla*), stoat (*Mustela erminea*), american mink (*Mustela vison*) and otter (*Lutra lutra*) (Stien et al., 2010). White-tailed eagles have not been observed stealing eggs from nest but have been preying on incubating female eiders in addition to younglings after hatching (pers. observation). American mink, having the potential to have large impacts on both adults and eggs (Erikstad et al., 2010), has not been observed to prey on incubating eiders on the island since 2010, after actively being hunted by government officials. As Grindøya is situated close to the fairly large and expanding urban area of Tromsø, high levels of crow nest predation is probably elevated by anthropogenic food subsidies both for resident crows on the island as well as for ranging crows from the city (Stien et al., 2010).

3.3. Fieldwork

Fieldwork for this study was conducted from the end of May until early July in 2021. The study location was visited approximately three times a week through this period. In the beginning the fieldwork consisted of searching the whole island systematically for nests. When an established nest was found the location was registered with a GPS, eggs counted and measured (i.e., length and width). The nest location was sometimes marked with an orange rubber band if it was hard to detect. Every egg was marked to make it possible to distinguish new eggs on future visits and to determine egg laying-dates (the female common eider lay one egg per day (Watson et al., 1993)). Every nest was carefully covered with down and nest material after inspection to reduce chance of predation due to our visit (Götmark & Åhlund, 1984). If there were no change in clutch size from the first visit, the nest was already fully laid and the female had started incubating at the time of our first visit. Thus, for those nests we could not determine egg laying-date with certainty. Only nests with a known laying-date or birds previously ringed were followed up through the nesting season. These nesting females were also captured, weighed, and measured (length of head/beak, wing and tarsus) on day 5 and on day 20 of the incubation period. Empty nests at revisits were registered as predated

unless it was at the end of the season and the eggshells were stacked nicely together. Then they were registered as hatched. We could not distinguish between nests that had been predated or nests that had first been abandoned by the female and then predated, thus they were all categorized as predated. The field season ended when all nests that were followed up had either hatched or been predated. The fieldwork for this thesis was part of a long-time monitoring study on the eider colony on Grindøya as a part of the SEAPOP monitoring-programme (https://seapop.no/en/activities/monitoring), conducted by NINA – Norwegian Institute for Nature Research.

3.4. Data analysis

The data gathered during this field season was compiled with the data from the last ten years using the same data-gathering procedures, resulting in a dataset covering the years from 2011 to 2021 (except for 2012). In preparing for the analysis, the data was sorted by only including nests with known egg laying-dates and nesting individuals with ring-markings. Nests that were in the egg laying-phase (1 or 2 eggs) but were predated between the first and second visit were included in the study despite not having a certain laying-date. Most nest predation occur during egg laying (Andersson & Waldeck, 2006; Hanssen et al., 2002; Hanssen & Erikstad, 2012; Mehlum, 1991), and not including those nests would give an unrealistic representation of the amount of predation. However, the models were run both with and without nests with clutch sizes of one or two eggs to see if there were any bias in including those nests.

GPS-locations of every registered common eider-nest from each year where uploaded to Garmin Basecamp (https://www.garmin.com/en-AU/software/basecamp/), and each of the nests were then registered with its distance to the nearest neighbour, and the number of nests within a radius of 5, 10 and 20 meters. Nests with one or more neighbouring nests within the 20-meter radius were defined as group nesters, while solitary nesters were defined as nests with no neighbouring nests within a 20-meter radius.

Bird colony structures are fluid, and through the nesting period female eiders establishing solitary nests might unintentionally end up in the middle of a group of nests due to other

eiders establishing nests around. On the other hand, a nest in the middle of a group may suddenly be in the outskirts of a group, or even solitary, due to neighbouring nests being predated or hatched (Kharitonov & Siegel-Causey, 1988). This makes it hard to measure the effect of group nesting, because only one value can be used for the distance between, and the number of neighbouring nests. However, for the predated nests, the measurements are from the date of predation, which is the date when the group effect matters. For successful nests, there may be a group effect through the whole nesting period, thus every nest that was in a neighbouring distance during the nesting period was included in the measurements. The number of measured solitary nests may also be exaggerated, as some group nesters end up as solitary nesters due to predation or hatching of neighbouring nests.

Analyses were done with predated/not predated as dependent variables in logistic models. All nests where at least one egg hatched were defined as "not predated". Distance to nearest neighbouring nest and number of neighbouring nests within radiuses of 5, 10 and 20 meters were tested as independent variables to check for any associations of group nesting on predation. Clutch size (original clutch size before any partial predation), weight of nesting female on day 5 of incubation and laying date were also checked as independent variables as these factors are indicators of the female condition, which have been shown to have an association with predation in earlier studies (Erikstad & Tveraa, 1995; Gerell, 1985; Hanssen et al., 2003; Yoccoz et al., 2002). When significant differences were found in the analyses, independent variables were added to full models and removed when not significantly contributing to the model (P>0.5) unless otherwise stated. Evaluations of model fit (AICC) were also performed. All values are presented as means ± standard error (SE). All statistical analyses were conducted using SAS statistical software (SAS Inc. 1999).

4. Results

Table 1: A summary of the statistics from hatched and predated common eider-nest at Grindøya from 2011 to 2021, including number of nests (n), distance to nearest nest, number of nests within a 20-meter radius, egg laying-date, clutch size and weight on day 5 of incubation. All values (except number of nests) are presented as mean ± standard error.

Fate	Number of nests (n)	Mean distance to nearest nest	Mean number of nests within a 20-meter radius	Mean egg laying-date	Mean clutch size	Mean weight on day 5 of incubation
Hatched	185	20.2 m (± 1.8)	2.47 (± 0.22)	27.05 (± 0.5 day)	4.55 eggs (± 0.09)	1995.2 g (± 13.6)
Predated	325	46.0 m (± 4.0)	1.33 (± 0.09)	30.05 (± 0.5 day)	2.68 eggs (± 0.09)	1988.3 g (± 17.8)

A total of 510 nests were analysed in this study. 63.7% of these nests were predated. There was a significant increase in nest predation throughout the study period ($F_{1.508}=22.18$, $p<0.0001$), but predation seems to level off at 70-80% in the last four years (figure 2). Females with nests that hatched were slightly heavier early in the incubation period compared to females that later lost their nest, however this difference was not statistically significant (table 1, $F_{1.141}=9.09$, $p>0.7659$). The mean egg laying date was later for predated nests, that is, the 30th of May, while the mean egg laying-date for successful nests was the 27th of May (table 1). Earlier egg laying-date shows a significant association with less predation when tested alone ($F_{1.363}=21.30$, $p<0.0001$). Yet, when tested together with the effect of neighbouring nests and clutch size, it is no longer entirely significant ($F_{1.361}=3.82$, $p=0.0514$). The mean clutch size for predated nests was 2.68 eggs (n=325), while it was 4.55 eggs for successful nests (n=185) (table 1). If only fully laid nests are included, the mean clutch size for predated nests was 3.36 eggs (n=181), while it was 4.54 eggs for successfull nests (n=184).
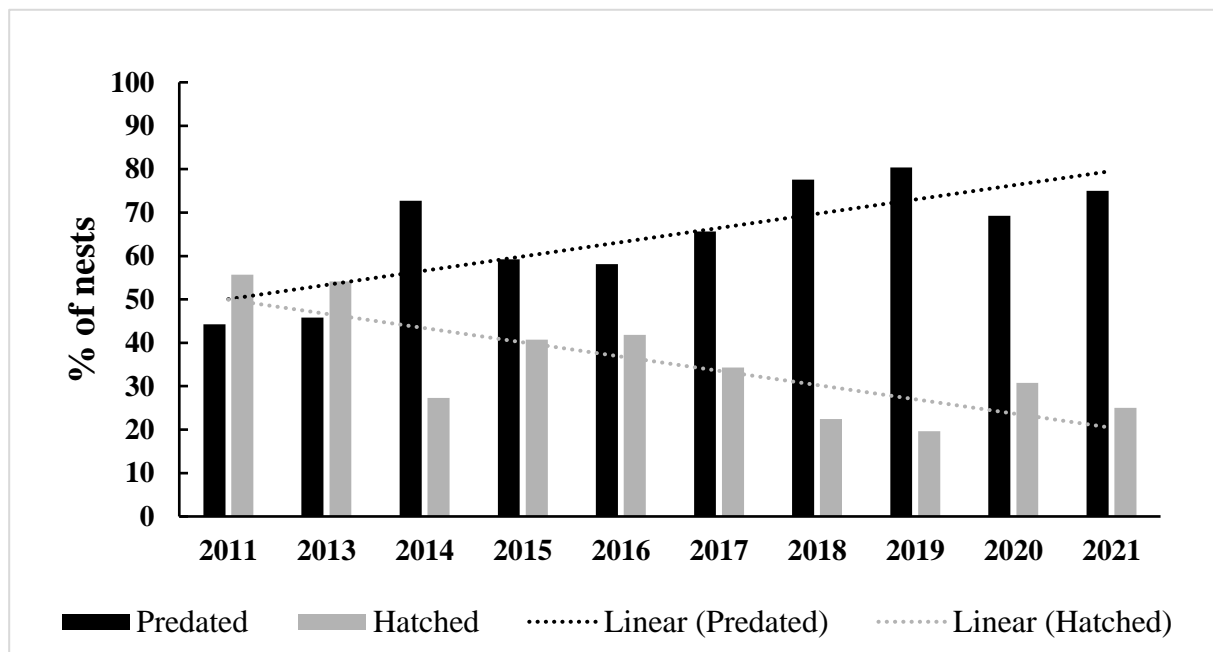
Figure 2: Amount of predated nests (black columns) vs. hatched nests (grey columns) by year. Dotted lines represent trendlines for predated nests (black) and hatched nests (grey), showing a significant increase in amount of predation over the study period ($F_{1.508}$=22.18, p<0.0001).
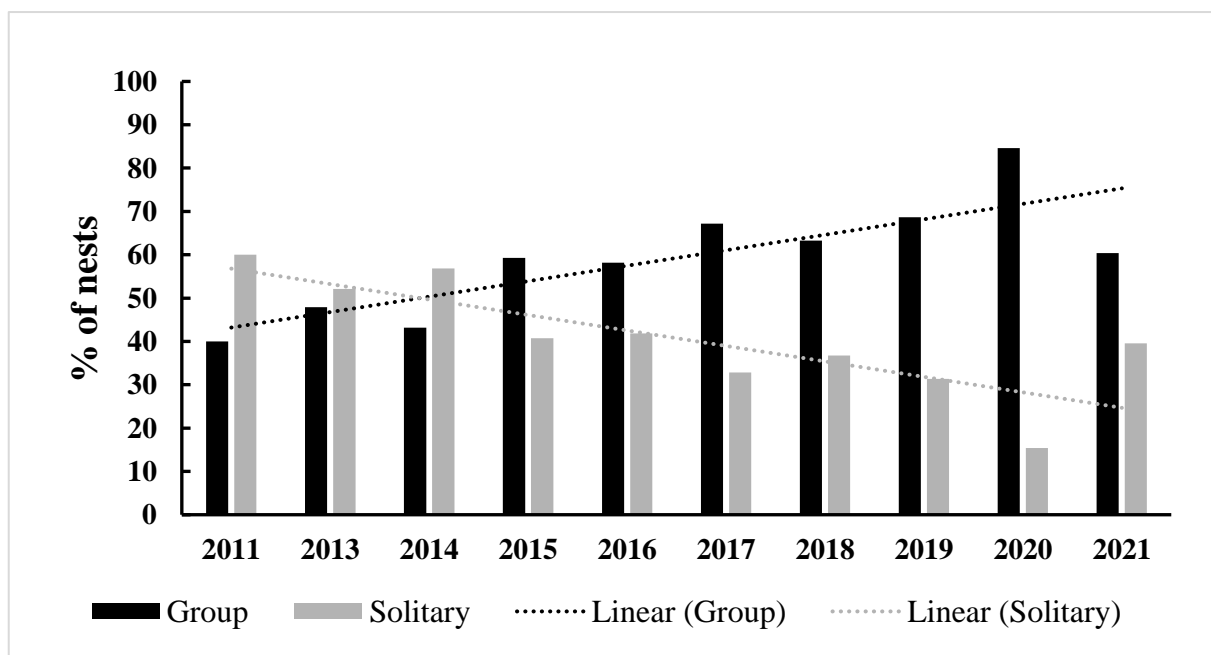

Figure 3: Group nesters (black columns) vs. solitary nesters (grey columns) by year. Group nesters are defined as having one or more neighbouring nests within a 20-meter radius. Dotted lines represent trendlines for group nesters (black) and solitary nesters (grey), showing a significant increase in group nesters over the study period ($F_{1.508}$=21.11, p<0.0001).

4.1. Group vs. solitary nesters

The majority of female eiders on Grindøya (58%) nest in groups throughout the study period (i.e., they nest with one or more neighbouring nests within a 20-meter radius). However, in 2011 (60%), 2013 (52%) and 2014 (57%), the majority of nests were solitary (figure 3) but the amount of solitary nesters has since then decreased. Overall, there is an increasing amount of group nesters over the study period ($F_{1.508}=21.11$, $p<0.0001$, figure 3). When looking at the amount of predation between solitary and group nests, there is a larger proportion of solitary nests being predated (71.4%) than group nests (58.7%), ($F_{1.509}=8.69$, $p=0.0033$, figure 4).
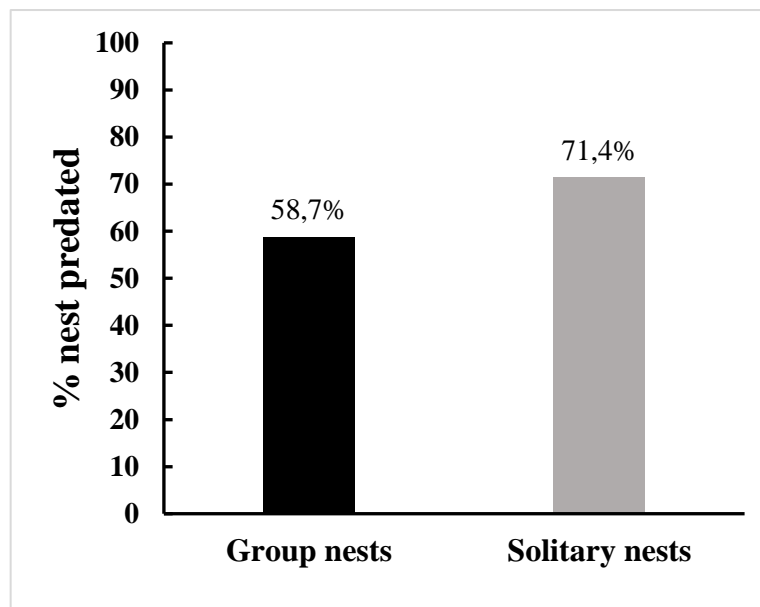
Figure 4: Amount of predated group nests (58.7%, black column) and solitary nests (71.4%, grey column) on Grindøya throughout the study period. Group nests are defined as nests with one or more neighbouring nests within a 20-meter radius.

4.2. Group nesting

4.2.1. Distance to nearest neighbouring nest

The mean distance to nearest neighbour for successful nests was 20.2 meters, while it was 46.0 meters for predated nests (table 1). The logistic regression model showed a significant association between distance to nearest neighbouring nest and predation ($F_{1.507}$=14.98, p<0.0001). Thus, having a close neighbour indicates a reduced risk of predation.

4.2.2. Number of neighbouring nests within different radiuses

The effect of number of neighbouring nests within three different distances: 5-, 10-, and 20-meter radius was tested both alone and in combination with clutch size and egg laying-date. All models gave significant results for the association between number of neighbouring nests and predation. However, the model for the effect of nests within a radius of 20 meters, clutch size and egg laying-date had the best fit (AICC=434.59). This model therefore seems to best capture the group effect, with a significant association between more neighbouring nests and reduced nest predation ($F_{1.361}$=15, p<0.0001).

4.3. Clutch size

The regression models showed a significant association between clutch size and predation, both when combined with distance to nearest neighbouring nest ($F_{1.507}=100.63$, $p<0.0001$, $n=510$) and number of nests within a 20 meters radius ($F_{1.507}=99.50$, $p<0.0001$, $n=510$). That is, a larger clutch size is associated with decrease in predation (figure 5). The association between clutch size and predation was still significant if nests with clutch sizes of 1-2 eggs were excluded from the analysis, however with a reduced sample size ($F_{1.316}=7.38$, $p=0.007$, $n=319$). The sample sizes for larger clutch sizes are small (less than five nests in each category from 7 eggs and larger), making those data less reliable. However, it seems to show the same trend as for clutch sizes of 3-6 eggs (figure 5).
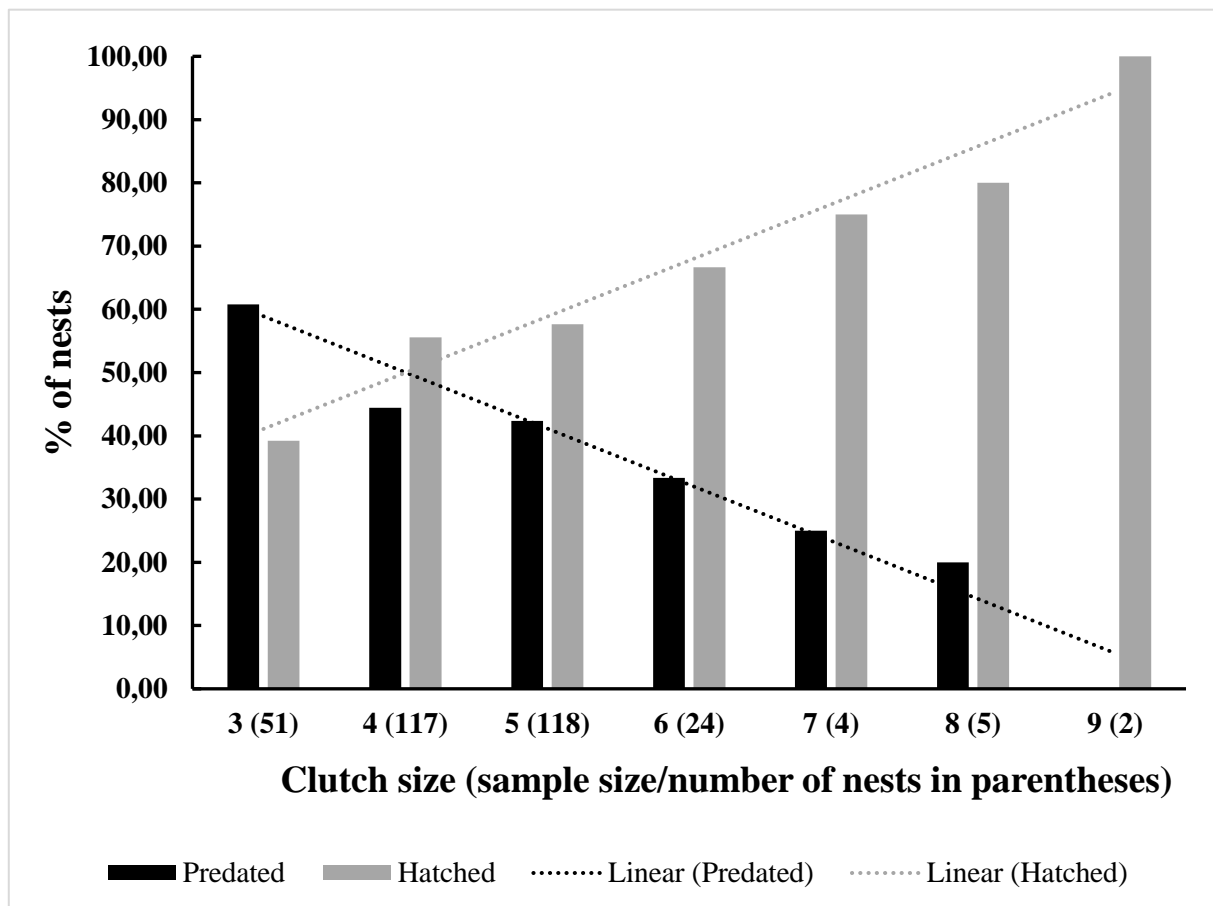
Figure 5: Percentage of fully laid predated nests (black columns) vs. hatched nests (grey columns) by clutch size with sample size/number of nests included in parentheses. Dotted lines represent trendlines for predated nests (black) and hatched nests (grey), with a significant association between a larger clutch size and decrease in predation ($p=0.007$). Nests with clutch sizes of 1 and 2 eggs are not included as they were not fully laid before being predated.

5. Discussion

Predation rates are generally high throughout the study period and have also increased during the last years (figure 2). The high predation rates are consistent with earlier studies on Grindøya (Stien & Ims, 2016). As commonly observed, most predation occurs during the egg laying (Andersson & Waldeck, 2006; Hanssen et al., 2002; Hanssen & Erikstad, 2012; Mehlum, 1991). For example, in 2021, 59% of predated nests were predated within five days of incubation. Yet, nests with more neighbouring nests and a shorter distance to nearest neighbour seem to have less nest predation than nests with fewer neighbours and longer distance in between, indicating an advantage of group nesting in reducing nest predation among common eiders on Grindøya. However, a larger clutch size seems to have an even stronger association with reduced predation. A later egg laying-date was also associated with higher predation rates, yet, egg laying-date was only significant when tested alone and not when tested together with group nesting factors and clutch size, indicating a weak effect of egg laying-date on nest predation.

5.1. Egg laying-date

The higher predation rates on nests with later egg laying-date seen in this study were expected, and lower reproductive success with later egg laying-date has also been found in other ground nesting bird species (Lepage et al., 2000; Willebrand, 1992). This can be explained by females starting egg laying later in the season often being younger, less experienced and/or in poorer condition (Blus & Keahey, 1978; Descamps et al., 2011). A female eider in poor body condition would probably need more time to build up body reserves before starting the nesting period, and therefore start egg laying later in the season. These females are often less attentive to their nests and have a higher abandonment rate, resulting in increased predation (Baillie & Milne, 1982; Hanssen et al., 2003; Öst et al., 2008). Some of the nests with late egg laying-date could also be females having a replacement clutch after being predated earlier in the nesting period (Hanssen & Erikstad, 2012). These females will have a reduced body condition due to the increased energy expenditure of producing extra eggs (Hanssen & Erikstad, 2012), and could therefore be more susceptible to either being predated or abandoning the nest. The association between predation and egg laying-date could

also be explained by late nest establishers incubating after the hatching of neighbouring nests, and therefore lack the group effect found among the most synchronized breeders (Hamilton, 1971). Yet, for this to be plausible, early nesters should also have higher predation rates, as early nesters would lack the protective group effect in the egg laying-period when they are most vulnerable to predation. At the same time, late nesters would benefit from the group effect during the most vulnerable period and should therefore be expected to experience less nest predation than early nesters. Nonetheless, this study shows that early nesters have a larger advantage in relation to nest predation than late nesters, weakening this explanation. It is therefore most likely the factors causing the late egg laying-date, e.g., body condition and experience of the female, that may increase the risk of predation, and not the egg laying-date itself.

5.2. Clutch size

Of the variables included in this study, a larger clutch size seems to have the strongest association to reduced predation. Yet, a larger clutch size *per se* does probably not reduce nest predation. Rather, the factors causing a large clutch size may be of importance. Larger clutch sizes are often laid by more experienced females and/or females with a better body condition (Hanssen et al., 2003). These individuals tend to have higher nest attentiveness, lower abandonment rates of nests, higher brood tendance, higher survival rates and better hatching success (Erikstad & Tveraa, 1995; Gerell, 1985; Hanssen et al., 2003; Yoccoz et al., 2002). Clutch size therefore seems to reflect the phenotypic qualities of individuals with higher nesting success (Hanssen et al., 2003). Earlier studies have also shown an increase in nest defence related to a larger clutch size (Erikstad & Tveraa, 1995; Lima, 2009). Larger clutch sizes also have a larger reproductive value and the female eider should therefore be more willing to take risks in defending the nest than a female eider with a smaller clutch size (Coleman & Gross, 1991).

5.3. Group nesting

Predation is higher among solitary nests than nests in groups (figure 3 and 4), which is also proven by the statistical analysis where both distance to nearest neighbouring nest and

number of neighbouring nests have a significant association with predation. This indicates that group nesting can in fact reduce nest predation, and that nest predation can be a driver behind the group nesting commonly observed within common eiders. This is also consistent with earlier studies (Ahlén & Andersson, 1970; Mehlum, 1991; Oro, 1996; Pratte et al., 2016). There is an interesting tendency towards group nesting over of the study period (figure 4), which also seems to correlate with the increased predation (figure 3). Could this significant increase in group nesting be a behavioural response to an increasing predation pressure? Earlier studies have shown that even though female eiders have strong nesting area fidelity (Baillie & Milne, 1982; Cooch, 1965; Swennen, 1990), predated females choose a nest site farther away from earlier nest sites than non-predated females (Bustnes & Erikstad, 1993; Hanssen & Erikstad, 2012). Yet, they still nest within the colony (Bustnes & Erikstad, 1993). As predators may also be able to remember earlier nest sites, nest relocation after nest predation could be advantageous (Lima, 2009). This may lead solitary nesters to nest closer to conspecific nests following nest predation, and since nest predation is higher among solitary nesters, this could eventually lead to increased aggregation.

Earlier studies on more arctic colonies of eiders, breeding without vegetation cover, indicates an effect of nest aggregation in reducing predation (Mehlum, 1991; Pratte et al., 2016). However, species in environments with lots of natural cover often show less aggregating behaviour (Hamilton, 1971). Also among common eiders at Grindøya, the heterogenous habitat with dense vegetation and foliage may provide sufficient cover to make group nesting redundant, yet this study indicates an advantage of group nesting also in such habitats. Similar results from areas with (this study) and without vegetation cover for breeding eiders suggest an independent effect of group nesting behaviour against predation. This also corresponds with earlier studies on Grindøya, showing no difference in predation rates between habitats (Stien, 2008).

But how can the positive effect of group nesting be explained? Group defence of nests is thought to be rare among eiders (Waltho & Coulson, 2015). After all, their strategy relies heavily on not being detected, and during our fieldwork most females laid on the nest as long as possible before fleeing the nest when approached (personal observations). However,

Mehlum (1991) observed that gulls trying to rob eggs from unattended nests were attacked by neighbouring female eiders, reducing the predation rates in groups. Thus, as some group defence seems to occur it may even just be enough to have a neighbouring eider present to prevent a crow from attempting a nest robbery.

Group nesting is associated with lower nest predation rates, so why does a large part of the colony still nest solitarily (42 %, figure 4)? One explanation could be that solitary nesters mainly consists of young and unexperienced females, not yet having experienced nest predation. Another cause for solitary nesting could be to avoid intraspecific brood parasitism (Waldeck et al., 2011). This is a widespread phenomenon among common eiders, and comes at an increased cost for the female eider hosting the parasitic eggs (Waldeck et al., 2011). Since brood parasitism increases with nest density (Waldeck et al., 2004), females may choose solitary nesting to avoid being parasitized, despite the increased risk of nest predation. Additionally, the most successful nesting strategy may vary over time, and the 10-year timespan of this study can just give a glimpse of what the most successful strategy is at this moment of time, not on an evolutionary timescale. According to Waltho and Coulson (2015), the introduction of foxes and mink in eider nesting areas led to decreasing nest density. This indicates that the effect of group nesting on predation depends on the type of predator, as nesting at high density may have a larger effect in reducing avian predation than mammalian predation (Pratte et al., 2016). This also corresponds with the results observed on Grindøya where avian predators are dominating (Erikstad & Tveraa, 1995; Stien & Ims, 2016; Stien et al., 2010).

6. Conclusion

Nest predation rates at Grindøya are high and even increasing. The condition and experience of the nesting female seem to be the most important factors in reducing nest predation, here shown through both the association reduced predation with an early egg laying-date, but most of all through the association between a larger clutch size and lower predation rates. However, the behavioural adaptation of group nesting also seems to reduce nest predation, which may also be why there is an increasing tendency towards group nesting during the study period. The increased group nesting may be an indication of the common eider being able to adapt to changing predation rates, which could reduce further decline in the population size of the threatened species. Even though predation has earlier been neglected as an evolutionary process in avian systems (Coulson, 2002; Martin, 1993), these results show that predation may play a significant role in promoting group nesting among common eiders. Group nesting seems to be an advantageous adaptation against nest predation also on Grindøya, indicating that the selfish herd model may also apply within heterogeneous nesting habitats.

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