



Bio-3910

Master of Science Thesis in Evolution and Behaviour Biology

**“Parasitized by your own kind” - The life of the Svalbard Eider
(*Somateria mollissima*).**



Jeanette Iren Hagen

November, 2008

FACULTY OF SCIENCE, DEPARTMENT OF BIOLOGY,

UNIVERSITY OF TROMSØ

In collaboration with

NORWEGIAN INSTITUTE FOR NATURE RESEARCH (NINA)

TROMSØ

Bio-3910

Master's Thesis in Evolution and Behaviour Biology

**“Parasitized by your own kind” - The life of the Svalbard Eider
(*Somateria mollissima*).**

Jeanette Iren Hagen

November, 2008

Table of contents

Abstract	7
Introduction.....	9
Materials and Methods	13
Study area and population	13
Egg data and albumen sampling	13
Catch data.....	14
Protein fingerprinting and isoelectric focusing electrophoresis	14
Data analysis.....	15
Results	17
Discussion.....	21
Conclusion	25
Acknowledgements.....	27
References.....	29

Abstract

Conspecific brood parasitism is a subtle reproduction tactic often performed by many species. The parasitizing females lay eggs in the nest of another female of the same species, and the hosting female then incubates and raises both her own and the parasite's offspring. It is highly discussed why the hosting females allow this parasitism, whether she is able to detect it, or if she receives more benefits than costs by allowing it. One benefit could be that the female "dilutes" her own offspring's chance of being caught by predators. The objects of this study were to examine some of the theories around conspecific brood parasitism in a high arctic population of Common eider (*Somateria mollissima*), especially if there was any correlation between body condition and parasitism, and number of neighbors laying at the same time. The results show no difference in condition between parasitized and non-parasitized females, but there is a significant relation between parasitism and number of neighbors laying eggs at the same time, and also between nest attendance and egg predation. I also found that both parasitism and egg predation seem to influence number of eggs laid by the host, indicating that the hosts are capable of both up- and down regulating their own clutch size in response to natural egg predation and parasitism.

Introduction

The most common, or at least most widely known, form of brood parasitism is the interspecific brood parasitism seen in birds like cuckoos or cowbirds, in several fishes, like minnows and sunfishes (e.g. Johnston, 1994), amphibians, and also in insect species (e.g. Brockmann, 1993; Tallamy, 2005). In these cases the parasitic offspring compete over food with the hosts offspring, often leading to the hosts offspring being killed (Waldeck et al., 2004; Waldeck, 2007).

Another form of brood parasitism is conspecific, or intraspecific, brood parasitism. This is a more subtle tactic, where females lay eggs in the nest of another conspecific female. The hosting female then incubates and raises the parasitizing female's offspring together with her own (Brockmann, 1993; Yom-Tov, 2001; Tallamy, 2005). This form of parasitism is common in several different species of birds, fish and insects (e.g. Brockmann, 1993; Yom-Tov, 2001; Zink, 2003; Tallamy, 2005), and it is a highly common reproductive tactic in waterfowl Anatidae (Eadie et al., 1988; Beauchamp, 1997). Waterfowl are different from other birds in the way that it is the females and not the males that are philopatric and tend to breed near their birth site (Anderson et al., 1992), which the Common eider *Somateria mollissima* is an example of. Because of this philopatric behavior a population of female eiders often consists of individuals that are more closely related than individuals from different populations (e.g. Scribner et al., 2001; Andersson and Waldeck, 2007).

The Common eider is, like other ducks, a precocial bird whose offspring does not need feeding by their parents (e.g. Andersson, 1984). The adult eiders feed mainly on mollusks and other benthic invertebrates, while the ducklings start feeding on smaller crustaceans within 24 hours after hatching. (Goudie et al., 2000). The females start breeding when they are 2-3 years old, and can reach the age of at least 25 (Fransson and Pettersson, 2001). The eiders are seasonally monogamous, and usually mate at the wintering area, from where the males follow the females to their breeding grounds (Waldeck, 2007). The males usually leaves the female after egg laying (Goudie et al., 2000), but in some places, Svalbard for instance, they stay close to the female and the nest almost until hatching (own observations).

The Svalbard population of Common eider *Somateria mollissima* usually nests on open and flat moraine islands with barely any vegetation, consisting of mainly moss (Bustnes et al. 2002). The females nest in colonies and start making nests and laying eggs from mid-May to early June, depending on when the ice melts. They lay on average 3-6 eggs with an approximately 24 hour-interval between each egg, and usually start incubating after the second or third egg (Swennen et al., 1993; Goudie et al, 2000; Hanssen et al., 2002; Waldeck, 2007). The first eggs are often covered with

vegetation, making it more difficult for predators to discover them (Waldeck, 2007). The clutch is incubated for 22-26 days (Goudie et al., 2000; Hanssen et al. 2002, Erikstad et al., 1993), by the female who seldom leaves the nest during this time (Korschgen, 1977; Parker and Holm, 1990; Bolduc and Guillemette, 2003a). Because the eiders are extreme capital breeders that rely on stored resources for egg-production and incubation, losing up to 47% of their bodyweight through stored lipids and proteins (Parker and Holm, 1990; Erikstad et al., 1993; Erikstad and Tveraa, 1995; Hanssen et al., 2002; Bolduc and Guillemette, 2003a; Waldeck, 2007) during this period; parasitism could be the only choice for some individuals. Some females abandon the nest during incubation (Bustnes and Erikstad, 1991; Hanssen et al., 2003), and others even die on the nest during incubation (Korschgen, 1977). Therefore conspecific brood parasitism could be a salvage strategy some weak or young females use when they are not able to care for their eggs and young, but just have the resources to produce the eggs (Andersson, 1984; Eadie et al., 1988; Öst, 2000; Waldeck, 2007).

Another tactic the female eider may use when breeding in a place with harsh climate and short productive window, is to take over an already finished built nest and save 2-3 days for egg laying (Waldeck, 2007). These nest take-overs often happen at the one egg-stage (Robertson, 1998), when also the egg-predation risk is highest (Swennen et al., 1993; Hanssen et al., 2002). This could be seen as risk assessment of the nest, and by taking over a ready built nest with an egg that has survived predation, this nest could be safer than other nesting sites (Robertson, 1998; Waldeck and Andersson, 2006). This should not be seen upon as “truly” parasitism, since it is the overtaking female that usually incubates the clutch. “Truly” parasitism is when a parasite dumps an egg in an already established nest with egg(s), but leaves the incubation to another female.

With an increased clutch size, the host may suffer from higher fitness costs in form of reduced hatching success and decreased survival of chick or parent, or even reduced future reproduction (Andersson et al., 1980; Milonoff et al., 2004; Waldeck, 2007), especially since eiders that incubate experimentally enlarged clutches lose more body mass during incubation than eiders with normal-sized clutches. It is also in accordance to previous findings that brood rearing strategies in eiders are associated with difference in body condition (Bustnes and Erikstad, 1991; Hanssen et al., 2003). It is therefore highly discussed why the hosting females allow parasitism from other females. It could be that the host cannot discriminate between her own eggs and others (Riedman, 1982; Eadie et al., 1988). Perhaps the female receives more benefits than costs, or at least the costs by allowing parasitism are negligible (Andersson and Eriksson, 1982; Eadie et al., 1988). Parasitism could also be a helping behavior towards relatives, or a defense tactic; by “diluting” her offspring’s chance of being caught by predators (Riedman, 1982; Eadie et al., 1988; Bolduc and Guillemette, 2003b). “Diluting” the

clutch at the egg stage could also be beneficial for later forming of crèches, a form of alloparental care common in birds, where two or more females amalgamate their broods and raise them together (Munro and Bedard, 1977; Waldeck, 2007). Perhaps then the parasite will join her egg's host and help raise and protect the chicks. Whatever the reasons for conspecific parasitism are, the parasite escapes the costs of incubation and brood rearing (Waldeck, 2007).

Results from Erikstad et al. (1993) show that female eiders do not have a fixed optimal clutch size, but that it varies between seasons, according to stored body reserves. There has also been reported that nest parasitism often lead to larger clutch sizes than normal (Erikstad and Bustnes, 1994), but some studies have shown results that indicate reduced size of host clutch in parasitized nests (Lokemoen, 1991), whilst other studies have not (Robertson et al., 1992; Bjørn and Erikstad, 1994). This may indicate that a hosting female is able to adjust her clutch size also within a season, and that number of eggs a female can lay is not pre-determined. The rapid follicle growth in eiders is six days (Hickling unpublished data in Alisauskas and Ankney, 1992), so perhaps the females are able to resorb follicles that are not fully grown if they receive parasitic eggs in their nests. This could be the case if they also somehow recognize they have been parasitized, either recognizing their own eggs from foreign, or the number of eggs laid by themselves. The resorbed resources could come in handy in case of extreme conditions during incubation, rearing of chicks, or even later when the population migrates. This would make parasitism beneficial for the host, especially in a population that has such a short reproduction window, and lives under so harsh conditions as this Svalbard population do before they migrate south for the winter (Bustnes et al., 2002).

The main objectives of this study were to examine some of the theories concerning conspecific brood parasitism in a high arctic eider population. We wanted to see if we could find any connection between the hosts condition and parasitism in a dense population with such a short reproduction season, whether the more fit females were more or less parasitized than the not so fit females. If a fitter and bigger host is also tougher and more aggressive, she may not allow parasitism, or maybe she accepts parasites more often because she has the resources to afford it. We also wanted to check if having one or several neighbors, especially those in the same phase of egg-laying, would have any effect on the rate of parasitism. Perhaps nesting in established neighborhoods may reduce nest parasitism if aggressive females manage to chase parasitizing females away. On the other side, maybe nesting together with many egg-laying females would increase the chances of accidental egg dumping. It could also be easier for parasites to find potential hosts in aggregations of egg-laying females, and thereby lead to increased parasitism in dense neighborhoods. Last we wanted to see if a female is able to adjust her own clutch-size according to parasitism and egg predation. If she for

instance is able to compensate for eggs lost to predators with new eggs, or if she does not lay all her eggs when being parasitized, but instead resorbs the egg follicles and thereby gain extra resources for incubation.

Materials and Methods

Study area and population

The population of common eider in this study breed on the Prince Heinrich island about one km south-east from Ny Ålesund in Kongsfjorden, West Spitsbergen (79°N, 12°E). The island is lying about 350 m offshore, and it is about 400 m long and 150 m at the widest (Campbell, 1975). The vegetation on this moraine island is low; mainly moss, or bare gravel, and the nests are located in the open, on moss or gravel, under wooden boxes (from earlier experiments), or on the beach sheltered by overhanging cliffs. 133 nests on this island were sampled from late May to late June 2007.

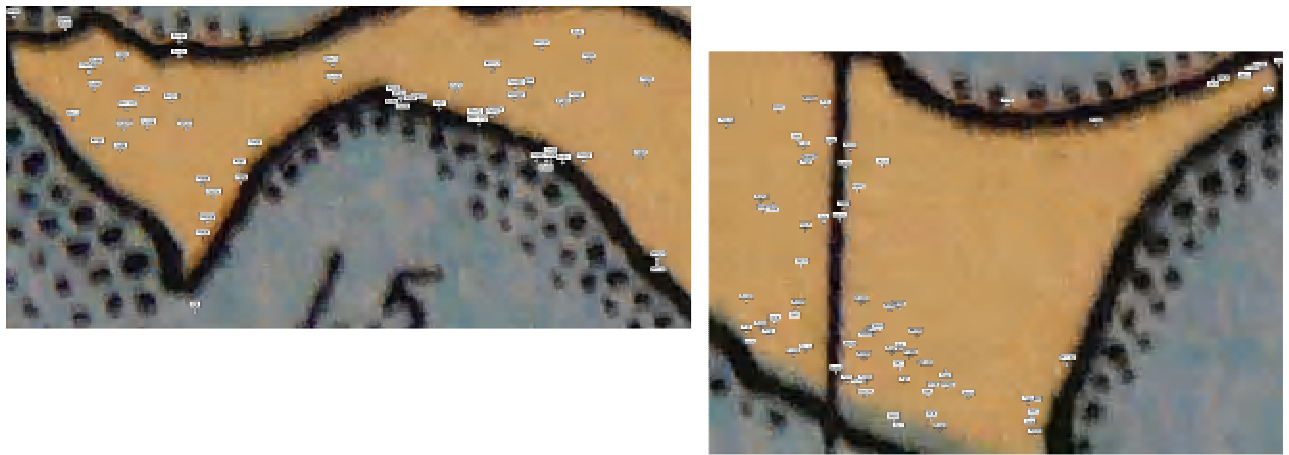


Fig. 1: Map over Prince Heinrich Island with GPS-plots of the nests, showing nest density.

Egg data and albumen sampling

A one mm hole was drilled approximately 5-10 mm from the pointy end of the egg, and about 0.3 ml albumen was extracted with a syringe (see Andersson and Åhlund, 2001 for details). The hole was then sealed with cyanoacrylat glue (Loctite Superattack) and a drop of activator (Loctite TAK PAK 7452) was added to accelerate hardening of the glue. The samples were stored in -20°C until electrophoresis. The sampled eggs were marked with a felt pen on the day of discovery, and the length and width was measured by calipers to the nearest ± 0.1 mm. After the sampling the eggs and nest was covered with down if present, or otherwise moss. The positions of the nests were recorded with a GPS device (Garmin GPS Map 76). The first nests were visited twice a day in the beginning of the period, and once every day after a week and a half to minimize the disturbance. When the nest was complete (no new eggs over a three-day period) we left it until we caught the female. Predation, take over by geese and abandoning of nests was noted.

Catch data

The females were captured when lying on the nest. Criscuolo (2001) found that female eiders were more likely to abandon their nests if handled at the beginning of incubation. Therefore, we waited until the females had incubated for at least a week before we tried to catch them. By using a fishing pole with a nylon loop we could sneak the loop over the female's head and thereby catch it. The bird was laid upside down in the assistant's lap with the head against the crotch to keep it calm and dark. The field worker then took a blood sample of about 0.1 ml with a syringe from the eider's leg, measured both wings with a ruler, measured the head and both tarsus with a caliper and weighed it. The ring number of the previous marked birds was registered and the unmarked birds got a numbered metal ring around the right leg before release. The sampling was always done by the same person. After being caught the bird often flew off to the water when released, so we covered the nest with down before leaving.

Protein fingerprinting and isoelectric focusing electrophoresis

Further analyses of the albumen samples were made by Peter Waldeck at the University of Gothenburg. The albumen samples were analyzed by using isoelectric focusing electrophoresis in precast gels with a fixed pH gradient. This is a high-resolution technique that separates proteins according to their isoelectric points (see Åhlund and Andersson, 2001; Waldeck et al., 2004 for details). The egg albumen patterns only represent the female and are usually different between individuals.

For resolving an adequate number of protein variants, the albumen samples were run on four types of gel (Amersham Pharmacia Biotech (Uppsala, Sweden), Immobiline DryPlates pH 4.7 code no. 80-1128-28, pH 4.2-4.9 code no. 80-1128-29 and pH 4.5-5.4 code no. 80-1128-30 (run with two recipes)). The gels were rehydrated for 2-4 hours by using recipes modified from Andersson and Åhlund (2001) (see Table 1).

Electrophoresis was performed with Amersham Pharmacia Biotech Multiphor II System and power supply EPS 3501 (see Waldeck et al. 2004 for details).

Table 1: Rehydration solutions for the different gel types (Waldeck et al, 2004)

Rehydration, chemicals/gel	Gel type A (pH 4.2-4.9)	Gel type B (pH 4.5-5.4)	Gel type C (pH 4-7)	Gel type D (pH 4.5-5.4)
TRIS 2 mM (ml)	150	200	150	150
Urea (g)	6	8	8	8
DTT (g)	0.2	0.2	0.2	-
Glycerol (ml)	5	-	5	5
Ampholyt (pH 3-10) (μ l)	-	-	150	-
Ampholyt (pH 4.2-4.9) (μ l)	150		-	-
Ampholyt (pH 4.5-5.4) (μ l)	-	150	-	150
Sample volume (μ l)	5	5	5	5

Data analysis

From the 133 sampled nests, 57 were excluded due to predation and abandoning after the first egg or before catching of the female, missing data on either the female or egg samples, taken over by barnacle geese *Branta leucopsis*, or because they were destroyed by water or landslide. This left us with 76 nests with data on wing size, weight, catch date, weight stage (number of days between last date of egg-laying and date of catching), parasitized nests, number of eggs both from host and parasite, nests with parasitic egg as 1. egg, nests with parasitic eggs between host eggs, number of eggs predated in each nest, nest-takeover with egg(s), nest-takeover without eggs and frequency of nest attendance, and these data were used for further analysis. The data was plotted in Microsoft Office Excel 2007 and the data analysis was done in SAS statistical software 9.2 (SAS Institute Inc. 1999).

By plotting the nest GPS-coordinates in Microsoft Office Excel 2007, we were able to make “neighborhoods” around every nest manually with dividers ($r \approx 12.5$ m) and count how many neighbors each nest had. By plotting numbers of neighbors finished with egg-laying, and number of neighbors still laying eggs in the existing Excel file and using logistic regression in SAS we were able to see if having neighbors had an effect on parasitism.

Results

Among the 76 nests analyzed, 23 nests were found to be parasitized (30.3%), i.e. they had eggs from two or more females. Of the 23 parasitized nests 13 (56.5%) also suffered from partial egg predation in comparison to 14 of 53 non-parasitized nests (26.4%). Of a total of 320 laid eggs 41 (12.8%) were from parasites, and of these parasite eggs, 33 (80.5%) were taken by predators. Of the 279 host eggs, 33 eggs (11.8%) were taken by predators (Arctic Skua *Stercorarius parasiticus* and Glaucous gull *Larus hyperboreus*).

By using binomial logistic regression we tested whether the partial egg predation was influenced by body condition, nest attendance and parasitism. We used a backwards selection procedure, sequentially removing the weakest variables. The resulting model showed that parasitism is associated with a higher probability of egg predation (Figure 2), and there was a tendency for less egg predation in nests with high attendance by the female, (parasitism $\chi^2_{1,75}=5.48$, $p=0.019$, nest attendance; estimate $\chi^2_{1,75}=3.52$, $p=0.06$). Rejected terms; date of last egg laid $\chi^2_{1,75}=2.97$, $p=0.09$, body mass (corrected for incubation stage at capture and body size) $\chi^2_{1,75}=0.02$, $p=0.88$).

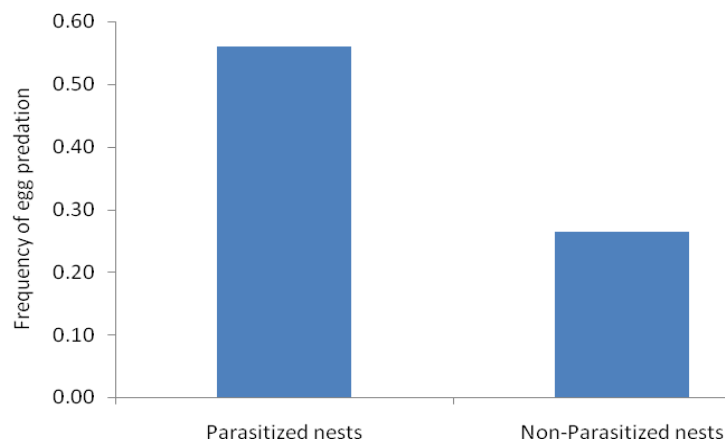


Fig. 2: Frequency of partial egg predation in parasitized nests compared to non-parasitized nests.

When analyzing the frequency of parasitism, we started with a full model including nest attendance, last egg laying date, body condition, number of already incubating neighbors, and the number of egg laying neighbors. The resulting model showed that only the number of egg laying neighbors influenced the probability of being parasitized (Figure 3, egg laying neighbors; estimate 0.60 ± 0.23 , $\chi^2_{1,75}=7.39$, $p=0.007$). Rejected terms; frequency of nest attendance $\chi^2_{1,75}=0.30$, $p=0.58$, date of last

egg laid $\chi^2_{1,75}=0.84$, $p=0.36$, body mass (corrected for incubation stage at capture and body size) $\chi^2_{1,75}=0.51$, $p=0.48$, incubating neighbors $\chi^2_{1,75}=1.33$, $p=0.25$).

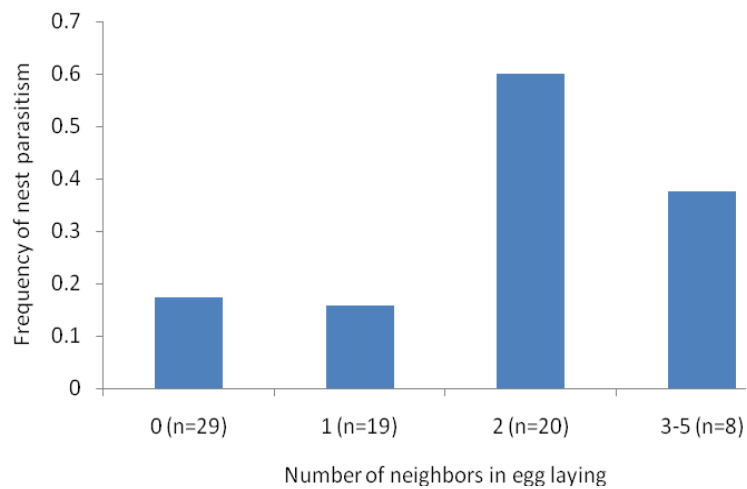


Fig. 3: Frequency of nest parasitism according to number of neighbors still laying eggs.

To analyze factors that may affect the number of eggs produced by the hosting female, we started with an ANCOVA model including egg laying date, body condition, egg predation, number of egg laying neighbors and parasitism. The results showed that parasitized females laid fewer eggs themselves (Figure 4, parasitized: 3.35 ± 0.21 eggs, not parasitized: 3.81 ± 0.12 eggs), and that females that suffered partial egg predation during the egg laying phase, laid more eggs (egg predation: 3.96 ± 0.20 eggs, no egg predation 3.51 ± 0.12 eggs. Parasitism $F_{1,75}=8.37$, $p=0.005$, egg predation $F_{1,75}=8.53$, $p=0.0046$. Rejected terms; date of last egg laid $F_{1,75}=0.55$, $p=0.46$, body mass (corrected for incubation stage at capture and body size) $F_{1,75}=0.11$, $p=0.74$, egg-laying neighbor $F_{1,75}=0.08$, $p=0.77$, parasitized \times egg predation $F_{1,75}=1.63$, $p=0.21$).

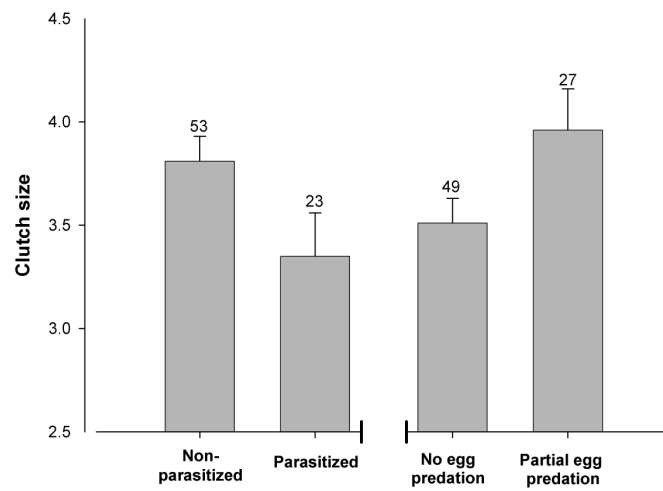


Fig. 4: Difference in mean clutch size in common eider females which suffered intraspecific brood parasitism compared to non-parasitized females, and females which lost one or more eggs during egg-laying compared to females who did not lose eggs. Sample sizes are given above error bars.

Discussion

The frequency of conspecific brood parasitism (30.3%) in this high arctic population of Common eider is in accordance with earlier findings in other studies, for instance was the frequency 30% in a Hudson Bay population (Waldeck et al. 2004) and 20% in a Baltic Sea population (Waldeck and Andersson, 2006). This indicates that conspecific brood parasitism is a reproduction strategy common amongst eiders populations, and perhaps even more common the further north the population spends its reproductive season. This could mean that the climate makes the reproductive window smaller further north, with colder weather, later snow and ice melting to uncover nesting sites, and overall a shorter season under harsher conditions (Parker and Mehlum, 1991; Waldeck and Andersson, 2006). This parasitic reproductive strategy could then have arisen in individuals attending the nesting site later in the season, putting their eggs in already finished nests and saving the 2-3 days it takes to build their own nest. It could be related to the condition of the parasitizing individuals, perhaps being in a so poorly condition that they cannot afford spending their accumulated resources on both eggs and incubation, and therefore leaving the incubating to females in better condition. Earlier studies have shown that host and parasites are more closely related than the host and other random individuals in the same population (Öst, 1999; Goudie et al., 2000; Waldeck, 2007). It has also been shown in earlier studies (Waldeck, 2007), that even if the whole population is closely related due to the natal philopatry (Andersson et al., 1984; Bustnes and Erikstad, 1993), parasites and their hosts are even closer related. This close kinship between the host and the parasite could benefit both females (Andersson and Eriksson, 1982; Andersson, 1984; 2001; Lyon and Eadie, 2000; López-Sepulcre and Kokko, 2002), perhaps in the sense that a poor or young and inexperienced relative could put an egg or two in a fitter relative's nest and thereby reproduce without the costs of incubation. Previous studies have shown no indication that parasites have nests of their own (Robertson et al., 1992; Bjørn and Erikstad, 1994). The benefits earned by the host must however be higher than the costs in rearing other's young at the expense of her own current and future reproductive fitness (Milonoff et al., 2004), for this to be an evolutionary stable strategy (ESS) (Robertson, 1998; Waldeck, 2007).

56.5% of the parasitized nests also suffered from predation in comparison to 26.4% of the non-parasitized nests. An explanation for this could be that encounters between parasites and hosts could be aggressive and loud, fighting with each other making the nest more easily discovered by predators. By own observations we know that there can be some aggressiveness between females laying on nests and others trying to intrude. It could also be that the nest site is particularly vulnerable to predation and that it for this reason would pay to allow parasites to lay eggs in it and

thereby dilute the clutch and reducing the chance of one of the host's eggs being predated. However, Bjørn and Erikstad (1994) found that there were very small differences in safety from predators among nests on the neighboring island Mietheholmen. Hosts of parasitized nests could also be more absent from their nest and then it would be easier for parasites to lay their eggs in non-attended nests, not having to encounter aggressive females. Perhaps females with fewer eggs of their own already laid chose not to fight predators, but rather start a new nest instead of risking injury. According to Hanssen et al. (2003) predation is related to clutch size, but after the fifth day of incubation they rarely start a new nest if predated.

Of a total of 320 eggs laid, 41 (12.8%) showed to be from parasites, and a total of 48 eggs (14.8%) were taken by predators, but these statistics do not include the nests predated and left at the one-egg stage. Egg predation is highest at the one-egg stage (Swennen et al., 1993; Hanssen et al., 2002), and some of the nests with one egg were poorly covered leaving the egg exposed to predators. By testing if the frequency of nest attendance by a female affected the rate of predation, we found the result to be negatively significant, and that the more a female attended the nest, the less predation the nest suffered. It could be that the female is protective of her nests and is able to chase predators away, and in several studies of eider populations it has been observed that a female eider can deter attacks from predators such as gulls (*e.g.* Ahlén and Andersson, 1970; Hanssen et al., 2002). There could also be a reason that predators are less interested in nests with incubating females, perhaps risking injury themselves if being attacked by the eider female. However, Mehlum (1991) observed that gulls encountered and actively pulled the female eiders from their nests and took the eggs. Several studies suggest though that the most plausible reason for decline in predation rate after the second egg laid is increased nest attendance by the female (Swennen et al., 1993; Hanssen et al., 2002; Waldeck, 2007).

The results also showed a significant correlation between predation and number of host eggs, i.e. females that suffer partly egg predation during egg laying seem to be able to replace the lost eggs. Perhaps the numbers of eggs a female lays in one season are not determined previous to laying (Erikstad and Bustnes, 1994), but can be adjusted according to available resources, and it could be that a female has stored some "extra" resources she can spend on egg laying if necessary. It could be that these resources are marginal, so that if a female spends them on an extra egg, she may not have enough to last and keep her alive during the whole incubation and perhaps females that take this chance have a higher probability of dying on the nest.

Between the 53 non-parasitized females the average number of host eggs was 3.81, while amongst the 23 parasitized females the average number of host eggs was 3.35, almost half an egg less than the non-parasitized females. This is in accordance with Andersson and Eriksson's (1982) results on Golden eye *Bucephala clangula* which indicates that females with parasitic eggs in their nest lay fewer eggs of their own, and also with Erikstad et al.'s (1993) experiment on increased clutch size in the Common eider. Waldeck et al. (2004, 2006) also got results with the same indications. It could be that the hosts know they have been parasitized and recognize their own eggs from others, and therefore put their own "extra" eggs in other nests, being parasites themselves. It could also be that they do not recognize their own eggs from others, but resorb the follicles and thereby egg resources when the nest seems "full" in accordance to the host's available incubating resources. This could, for the same reasons as mentioned before, in addition to non-used egg-resources be more beneficial for the host accepting parasitic eggs to "dilute" her clutch (Brown and Brown, 1988). Since there is no indication that the females with nests of their own also lay eggs in other nests (Waldeck, 2007; Bjørn and Erikstad, 1994) it is more likely that they resorb the egg follicles and the resources instead of laying the "extra" eggs. However, the clutch size in the Common eider is not obligate, but changes from year to year, so perhaps letting other parasitize you and save some of your own egg laying resources could be a behavioral strategy for bonding with other females that could help you "babysit" the chicks after hatching. Some females form crèches (Munro and Bedard, 1977; Öst et al., 2002) with other "mothers", whilst other females have "aunts", females without own clutches, to help them look after the chicks. Perhaps these "aunts" are really parasites, and by having their chicks in your clutch you have a greater insurance that they will help you. At the same time you save resources for incubation and even perhaps for future reproduction. Öst et al (2005), on the other side, found the relationship between females in brood rearing coalitions not to be closer than by chance, and since parasitic eggs and host eggs show to be closer related than random, there is no indication of the parasites doing any "aunt" behavior together with the relatives that they parasitized.

In this study we also tested to see if having neighbors affected the rate of parasitism, and the results indicate that having neighbors in approximately a radii of 12.5 m away from your nest that are in the same phase of egg laying as you, will significantly affect the rate of parasitism. However, having neighbors that are finished laying eggs and has started incubation, does not affect the rate of parasitism in your nest. Several others also have results that show that nest density may cause a higher rate of parasitism (Andersson, 1984; Beauchamp, 1997; Yom-Tov, 2001). It could be that in dense communities the chance of making a mistake of laying an egg in the wrong nest is higher than

in more scattered communities, and then by accident some individuals parasitize other nests. On the other hand it would also be easier to find potential nests and deliberately parasitize them in denser communities. This would also agree with Waldeck et al.'s (2008) findings according to decreasing relatedness with increasing nest distance, and the higher degree of relatedness between parasites and hosts (Andersson and Waldeck, 2007). This tactic should therefore be more beneficial to parasites than if they would have to travel greater distances to find suitable hosts, either them being closer related than the neighbors, or if the parasites would have to go further away from their natal neighborhood to avoid parasitizing close relatives.

Conclusion

This study shows results that are in accordance with earlier studies, although it may indicate a higher rate of parasitism the further north the population of Common eider spends its reproductive season. The findings of females that seem to be able to replace predated eggs should be further investigated to determine whether they really can redirect resources to new eggs if predated, and if they can resorb extra resources already put in egg follicles when receiving parasitic eggs. Since we do not have data on the parasitizing individuals it is difficult to say something specific about the relationship between host and parasite, or which tactic the parasite uses to get her progeny raised. There are still many questions to be answered, especially about this population and how it differs from southern populations of Common eider. Further studies are needed to determinate the causes behind conspecific parasitism in the Common eider, especially studies from the angle of the parasite. It could be difficult to gather data on the parasites, and may require a huge amount of resources, both in form of video recording, catching and other ways of collecting data.

Acknowledgements

I thank my supervisor at NINA, Sveinn Are Hanssen for all the help he has given me with statistics and writing, and Peter Waldeck for allowing me to be his assistant on Prince Heinrich and for letting me use his lab. results in my master thesis and all the help he has provided. I also thank Kings Bay in Ny-Ålesund and all the people I met up there for my pleasant stay on Svalbard during the fieldwork period. Last but not least I want to thank all my friends in and outside Tromsø for all the love and support they have given me during frustrated times.

References

- Alisauskas, R.T. and Ankney, C.D.** (1992). The cost of egg-laying and its relationship to nutrient reserves in waterfowl. In: Ecology and management in breeding waterfowl (B.D.J. Batt, B.D. Aftoen, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec and G.L. Krapu, eds). University of Minnesota Press, Minneapolis and London: 30-61.
- Andersson, M. and Waldeck, P.** (2007). Host–parasite kinship in a female-philopatric bird population: Evidence from relatedness trend analysis. *Molecular Ecology*, 16(13): 2797-2806.
- Andersson, M. and Åhlund, M.** (2001). Protein fingerprinting: A new technique reveals extensive conspecific brood parasitism. *Ecology*, 82(5): 1433-1442.
- Anderson, M.G., Rhymer, J.M. and Rohwer, F.C.** (1992). Philopatry, dispersal, and the genetic structure of waterfowl populations. -In: Ecology and management in breeding waterfowl (B.D.J. Batt, B.D. Aftoen, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec and G.L. Krapu, eds). University of Minnesota Press, Minneapolis: 365-395.
- Andersson, M.** (1984). Brood parasitism within species. In: Producers and scroungers (C.J. Barnard, ed.), Croom Helm, London: 195-228.
- Andersson, M. and Eriksson, M.O.G.** (1982). Nest parasitism in Golden eyes *Bucephala clangula*: Some evolutionary aspects. *American Naturalist*, vol. 120: 1-16.
- Andersson, M., Wiklund, C.G. and Rundgren, H.** (1980). Parental defense of offspring: a model and an example. *Animal Behaviour* 28: 536-542.
- Ahlén, I. and Andersson, Å.** (1970). Breeding ecology of an eider population on Spitsbergen. *Ornis Scandinavica*, nr. 1: 83-106.
- Åhlund, M. and Andersson, M.** (2001). Female ducks can double their reproduction. *Nature*, 414: 600-601.
- Beauchamp, G.** (1997). Determinants of intraspecific brood amalgamation in waterfowl. *Auk*, vol. 114: 11-21.
- Bjørn, T.H. and Erikstad, K.E.** (1994). Patterns of intraspecific nest parasitism in the High Arctic common eider (*Somateria mollissima borealis*). *Canadian Journal of Zoology*, vol. 72: 1027-34.

- Bolduc, F. and Guillemette, M.** (2003a). Incubation constancy and mass loss in incubating Common Eiders (*Somateria mollissima*). *Ibis*, vol. 145: 329-332.
- Bolduc, F. and Guillemette, M.** (2003b). Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. *Biological Conservation*, vol. 110: 77-83.
- Brockmann, H.J.** (1993). Parasitizing conspecifics: comparisons between hymenoptera and birds. *Trends in Ecology and Evolution*, vol. 8:2-4.
- Brown, C.R. and Brown, M.B.** (1988). A new form of reproductive parasitism in cliff swallows. *Nature* (London.), vol. 331: 66-68.
- Bustnes, J.O., Erikstad, K.E. and Bjørn, T.H.** (2002). Body condition and Brood abandonment in Common Eiders breeding in the high Arctic. *Waterbirds* vol. 25(1): 63-66.
- Bustnes, J.O. and Erikstad, K.E.** (1993). Site fidelity in breeding common eider *Somateria mollissima* females. *Ornis Fennica*, vol. 70: 11-16.
- Bustnes, J.O. and Erikstad, K.E.** (1991). Parental care in the Common eider (*Somateria mollissima*) – Factors affecting abandonment and adoption of young. *Canadian Journal of Zoology*, vol. 69(6): 1538-1545.
- Campbell, L.H.** (1975). Predation on Eiders *Somateria mollissima* by the Glaucous Gull *Larus hyperboreus* in Spitsbergen. *Ornis Scandinavica*, vol. 6 (1):27-32.
- Criscuolo, F.** (2001). Does blood sampling during incubation induce nest desertion in the female Common Eider *Somateria mollissima*? *Marine Ornithology*, vol. 29: 47-50.
- Eadie, J.M., Kehoe, F.P. and Nudds, T.D.** (1988). Pre-hatch and post-hatch amalgamation in North American Anatidae: a review of hypotheses. *Canadian Journal of Zoology*, vol. 66: 1709-1721.
- Erikstad, K.E. and Tveraa, T.** (1995). Does the cost of incubation set limits to clutch size in common eiders *Somateria mollissima*? *Oecologia*, 103:270-274.
- Erikstad, K.E. and Bustnes, J.O.** (1994). Clutch size determination in Common Eiders: an egg removal and egg addition experiment. *Journal of Avian Biology*, 25: 215-218.
- Erikstad, K.E., Bustnes, J.O. and Mow, T.** (1993). Clutch-size determination in precocial birds: A study of the Common eider. *Auk*, 110(3): 623-628.

Fransson, T. and Pettersson, J. (2001). Svensk ringmärningsatlas, vol. Naturhistoriska riksmuseum & Sveriges ornitologiska Forening, Stockholm.

Goudie, K.I., Robertson, G.J. and Reed, A. (2000). Common eider (*Somateria mollissima*). In: Poole, A., Gill, F., eds. The birds of North America, no. 546. Philadelphia, PA: The birds of North America, Inc, 31 p.

Hanssen, S.A., Erikstad, K.E., Johnsen, V. and Bustnes, J.O. (2003). Differential investment and costs during avian incubation determined by individual quality: an experimental study of the Common eider (*Somateria mollissima*). Proceedings of the Royal Society of London B., 270: 531-537.

Hanssen, S.A., Engebregtsen, H. and Erikstad, K.E. (2002). Incubation start and egg size in relation to body reserves in the common eider. Behavioral Ecology and Sociobiology, vol. 52: 282-288.

Johnston, C.E. (1994). The benefit to some minnows of spawning in the nests of other species. Environmental Biology of Fishes, vol. 40: 213-218.

Korschgen, C.E. (1977). Breeding stress of female eiders in Maine. Journal of Wildlife Management, vol. 41: 360-373.

Lokemoen, J.T. (1991). Brood parasitism among waterfowl nesting on islands and peninsulas in North Dakota. Condor, vol. 93: 340-345.

López-Sepulcre, A. and Kokko, H. (2002). The role of kin recognition in the evolution of conspecific brood parasitism. Animal Behavior, vol. 64: 215-222.

Lyon, B.E. and Eadie, J.M. (2000). Family matters: Kin selection and the evolution of conspecific brood parasitism. Proceedings of the National Academy of Science, vol. 97: 12942-12944.

Mehlum, F. (1991). Egg predation in a breeding colony of the Common Eider *Somateria mollissima* in Kongsfjorden, Svalbard. Norsk Polarinstitutt Skrifter, 195: 37-45.

Milonoff, M., Pöysä, H., Runko, P. and Ruusila, V. (2004). Brood rearing costs affect future reproduction in the precocial common golden eye *Bucephala clangula*. Journal of Avian Biology, 35: 344-351.

Munro, J. and Bedard, J. (1977). Crèche formation in the Common Eider. The Auk, vol.94 (4): 759-771.

Öst, M., Vitikainen, E., Waldeck, P., Sundström, L., Lindström, K., Hollmén, T. Franson, C. and Kilpi, M. (2005). Eider females form non-kind brood-rearing coalitions. *Molecular Ecology*, vol. 14: 3903-3908.

Öst, M., Mantila, L. and Kilpi, M. (2002). Shared care provides time-budgeting advantages for female eiders. *Animal Behaviour*, 64: 223-231.

Öst, M. (2000). Feeding constraints and parental care in female eiders. PhD-thesis, University of Helsinki, Helsinki.

Öst, M. (1999). Within-season and between-year variation in the structure of common eider broods. *Condor*, 101: 598-606.

Parker, H. and Mehlum, F. (1991). Influence of sea-ice on nesting density in the Common Eider *Somateria mollissima* in Svalbard. *Norsk Polarinstitutt Skrifter*, 195: 31-36.

Parker, H. and Holm, H. (1990). Patterns of nutrient and energy-expenditure in female common Eiders nesting in the High Arctic. *Auk*, vol. 107: 660-668.

Riedman, M.L. (1982). The evolution of alloparental care and adoption in mammals and birds. *Quarterly Review of Biology*, vol. 57: 405-435.

Robertson, G.J. (1998). Egg adoption can explain joint egg-laying in common eiders. *Behavioral Ecology and Sociobiology*, vol. 43: 289-296

Robertson, G.J., Watson, M.D. and Cooke, F. (1992). Frequency, timing and costs of intraspecific nest parasitism in the common eider. *The Condor*, vol. 94(4): 871-879.

Scribner, K.T., Petersen, M.R., Fields, R.L., Talbot, S.L., Pearce, J.M. and Chesser, R.K. (2001). Sex-biased gene flow in spectacled eiders (anatidae): Inferences from molecular markers with contrasting modes of inheritance. *Evolution*, vol. 55: 2105-2115.

Swennen, C., Ursem, J.C.H. and Duiven, P. (1993). Determinate laying and egg attendance in common eiders. *Ornis Scandinavica* vol. 24: 48-52.

Tallamy, D.W. (2005). Egg dumping in insects. *Annual Review of Entomology*, vol. 50: 347-370

Waldeck, P., Andersson, M., Kilpi, M. and Öst, M. (2008). Spatial relatedness and brood parasitism in a female-philopatric bird population. *Behavioral Ecology*. 19(1):67-73.

Waldeck, P. (2007). Brood parasitism, sociality and kinship in the Common Eider. Department of Zoology, Göteborg University, Box 453, 405 30 Göteborg, Sweden.

Waldeck, P. and Andersson, M. (2006). Brood parasitism and nest takeover in Common eiders. *Ethology*, vol. 112: 616-624.

Waldeck, P. , Kilpi, M., Öst, M. and Andersson, M. (2004). Brood parasitism in a population of common eider (*Somateria mollissima*). *Behaviour*, vol. 141: 725-739.

Yom-Tov, Y. (2001). An updated list and some comments of the occurrence of intraspecific nest parasitism in birds. *Ibis*, vol. 143: 133-143.

Zink, A.G. (2003). Intraspecific brood parasitism as a conditional reproductive tactic in the treehopper *Publilia concave*. *Behavioral Ecology and Sociobiology*, vol. 54: 406-415.