



BIO - 3910
MASTER'S THESIS IN
NORTHERN POPULATIONS AND
ECOSYSTEMS

The role of the Hooded Crow (*Corvus corone*) in the nesting success of the Common Eider (*Somateria mollissima*) at two colonies in Troms county, Northern Norway

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1. Abstract

There is evidence of a negative population trend for the two neighbouring eider colonies of Håkøya and Grindøya in Troms county, northern Norway. Casual observations suggest that nest predation may be an important factor, and that the hooded crow in particular could be the main egg predator. On this basis, a two year pilot study was conducted to investigate the role of the hooded crow in the nest predation. Eider nesting success was monitored on both colonies in 2006 and 2007, whilst in 2007, crows were removed from Håkøya. The number of nesting pairs of crows was monitored on both islands in both years, whilst in 2007 a crow activity index was estimated to assess the effectiveness of trapping. Cause of eider nest loss was recorded on Håkøya in both years. In addition we assessed if the nest habitat variables habitat (open, wood, or thicket), distance to the open and distance to the nearest crow nest were related to eider nest success. A logistic exposure model was used to analyse nest success, whilst a log-linear regression with a Quasi Poisson distribution was used to analyse crow activity. Crow removal in 2007 on Håkøya was successful in terms of removing established territorial and visiting crows and this most likely resulted in a large reduction in crow activity on Håkøya compared to the control area Grindøya. Modelling of daily nesting success probabilities revealed that eider nesting success on Håkøya increased from 61% of nests in 2006 to 80% of nests in 2007, while in contrast, nesting success on Grindøya stayed constant over the same period (38% – 39% of nests in 2006 and 2007 respectively). In addition, there was a strong season effect on the nesting success of eiders on both islands and in both years of this study, with nests found at the start of the season having a much lower probability of success than nests found later on in the season. The habitat variables did not improve the prediction of nest success.

Since the crow removal in this study was not replicated in space or time, and moreover the cause of nest failure was often undetermined, the causal link could not be verified by this pilot study. Nevertheless, the results indicate that the hooded crow could be an important factor in the decline of the breeding colonies of common eiders in Tromsø, and that a more long-term study would be valuable.

Keywords: Hooded crow, common eider, nest predation, population trends

2. Introduction

Predation is the main cause of mortality in many animal populations (Newton 1998) and may limit population growth and cause population regulation (reviews in Sinclair 1989, Turchin 1995). Often, several predator species concentrate on the same target prey population (Jenkins et al. 1964, Jones et al. 2002, Crabtree and Wolfe 1988). Generalist predators can maintain a population at a reduced stable size through prey switching (Bergon et al. 1986) and where a population is in decline, this type of predation may be a contributory factor in reducing the resilience of the prey population, increasing its vulnerability to irreversible decline and ultimately extinction (Bell and Merton 2002). Predator numbers and thus predation pressure on prey populations may be increased by the presence of a constant reliable alternative food source such as is provided by the presence of human settlement (Neatherlin and Marzluff 2004, Schneider 2001). In addition, the habitat chosen by individuals of a prey population can also influence the probability of their mortality by predation, with edge habitat often providing good conditions for generalist predators and poor conditions for their prey (Andrén 1992, Angelstam 1986a).

The Hooded Crow (*Corvus cornix*) is an opportunistic generalist predator and scavenger using mostly visual cues to find a wide range of food including grain, small mammals, carrion and rubbish (Coombs 1978, Yom-Tov 1974). It is a major predator of birds' eggs and young (Mehlum 1991, Eugimühl et al. 2001, Sullivan and Dinsmore 1990) and as such is targeted as a pest species especially in bird game industries wishing to maximise fledging success (Coombs 1978). Other generalist predators which often occur together with crows in temperate and arctic regions are red fox (*Vulpes vulpes*), stoat (*Mustela erminea*), and nearer the coast gulls (*Larus spp.*), American mink (*Mustela vison*) and otter (*Lutra lutra*), all of which can also prey on bird nests (e.g. Perkins et al. 2005, Angelstam 1986b, Nordström et al. 2003, Jenkins et al. 1964, Gerell 1985). Crow numbers are in general known to be elevated near human settlements (Marzluff and Neatherlin 2006, Soh et al. 2002, Chace and Walsh 2006), as well as in edge habitat with open areas providing good visual sight of prey combined with nesting habitat in the form of trees (Smedshaug et al. 2012, Andrén 1992). Removal experiments have shown that the nesting success of ground nesting birds' increases when crows are removed (Erikstad et al. 1982, Summers et al. 2004, Parker 1984), but that

control of other predators may also be necessary to reduce compensatory predation (Bolton et al. 2007, Côté and Sutherland 1997).

Eider colonies in Scandinavia and the arctic can be subject to high levels of nest predation (Gierell 1985, Ahlen and Andersson 1970, Melhum 1991, Noel et al. 2005). The probability of predation is highest after the first egg has been laid and decreases with subsequent egg laying (Hanssen et al. 2002), generally remaining low throughout the incubation phase (Erikstad and Tveraa 1995). In addition, females laying large clutches on average start incubation later than those laying small clutches and thus the time that these nests are left unattended is longer than for small clutches (Hanssen et al. 2002). The first egg is left unattended hidden under vegetation, whilst after each subsequent egg is laid, the female spends increasing amounts of time at the nest. During incubation the female is in almost continual attendance of the nest. Thus the presence of the female is largely seen as an effective predator defence (Melhum 1991, Swennen 1993). On Grindøya and Hakøya islands, Troms county, northern Norway, the hooded crow is thought to be a main egg predator of the common eider (*Somateria mollissima*) population (Erikstad and Tveraa 1995; Pettersen, pers. comm.), with several active crow nests and flocks being observed on both islands during the eider breeding season. The current eider population on Grindøya is estimated to be between 400 and 500 pairs (Yoccoz et al. 2002) and the Hakøya population is thought to be between 200 and 300 pairs (pers. obs.). Both colonies were historically much larger than present (in the 1950's there were an estimated 1000-2000 pairs and more than 600 pairs on Hakøya and Grindøya respectively; Olsen, Pettersen pers. comm.) as they formed part of a widespread Norwegian coastal industry of down and egg collection. As such, eiders were encouraged to breed in high densities and were protected from predators by local landowners (Pettersen, pers. comm.). The cause of the decline is unknown but increased nest predation pressure could be one factor as the local focus on predation control has declined over the last 30 years. Crow nest predation pressure on the colonies could well be elevated by the nearby settlements on Tromsøy, Kvaløya, Håkøya and the mainland, which have a combined human population of 50,000 to 60,000 (Statistisk Sentralbyrå 2008). Other potential nest predators in the area are the greater black-backed gull (*Larus marinus*), the herring gull (*L. argentatus*), raven (*Corvus corax*), the American mink, otter and stoat. The habitat on both islands is similar and consists of a mixture of wooded areas of mountain birch (*Betula pubescens*) and willow (*Salix spp.*), open pastures, open heath (family *Ericaceae*) containing dwarf mountain birch

and willow, and mire habitat. Both wooded and open areas are chosen as nesting locations by breeding eiders.

Here, I report on the results from the first 2 years of a study to assess the effect of crow removal on eider nesting success on Hakoya. In both years we collected data on eider clutch size, date of nest initiation, and success or failure of nests on each visit in order to assess nesting success at the two colonies. In the second year of the study we tested the hypothesis that nesting success of eiders is improved in the absence of crows. We did this by trapping crows near the eider colony at Hakoya throughout the eider breeding season. We recorded the number of breeding crows, flocks of crows and activity of crows at both islands to assess the effectiveness of crow removal. We also recorded data on nest initiation and breeding success of crows as an estimate of the degree of crow predation pressure on the eider colonies. Presence of mammalian egg predators was recorded to investigate the potential for compensatory predation in the absence of crows.

We expected eider nesting habitat to be a predictor of nesting success with nests situated in woods and thickets having a higher success than those situated in the open. Also nests situated near crow nests were expected to have a lower success than those situated farther away from the crow nests. To evaluate these predictions we used a subset of nests to record the habitat characteristics of each nest, their distance to the open, and their distance to nearest crow nest.

3. Material and Methods

3.1 Study area

Grindøya and Hakøya are two small islands (65 ha and 361 ha respectively) situated 2 km from each other along the coast of northern Norway at approximately 69° 38' N, 18° 52' E and 69° 39' 18" 49". Both islands are low lying with open and wooded areas. Hakøya has a settlement of approximately 60 dwellings and several low intensity farms, whilst Grindøya has 3 holiday huts around the coastline which are now seldom used. Grindøya is a nature reserve with one of the largest concentrations of breeding eiders in the vicinity of Tromsø (Hanssen, pers. comm.). Access by the general public is limited between 1st May and 30th June to limit disturbance to the eider colony. There is little movement of breeders away from Grindøya to neighbouring areas (Bustnes and Erikstad 1993) and eider hatching success seems to have been relatively stable over the last 10 years (Hanssen unpub.). Grindøya's neighbouring island Hakøya has historically had a much larger population than present, having benefited from the protection provided by local landowners involved in the traditional practice of eider down and egg collection. Currently, eiders on Hakøya appear to nest in small loose aggregations within 30m of the coast, apart from two more concentrated groups of approximately 50 to 70 nests, one at the north end of the island and one on the east side of the island (pers. obs.).

3.2 Study species

The Hooded Crow

The hooded crow is primarily an arboreal nester with a distribution across northern, eastern and southeastern Europe, and the Middle East (Coombs 1978). It has delayed maturity not breeding before 2 years old (Coombs 1978) with annual survival rate estimates of adult birds ranging between 48% and 70% (Loman 1980, Holyoak 1971, Hankioja 1969). Breeding pairs are territorial (Yorn-Tox 1974), but generally fail to chase off non-breeding flocks. Densities of nesting birds vary, being highest where food sources are concentrated and range between 1.6-1.8 pairs km² for island habitats (Loman 1980, Parker 1985, Erikstad et al. 1982), and 0.3-0.9 pairs km² in rural areas (Loman 1980). Breeding occurs from early spring but depends on altitude (and thereby presumably snow melt), and lasts approximately 75 days from nest building to fledging of young (Coombs 1978). Birds which nest in high densities appear to be most synchronised in the timing of breeding (Loman 1980).

The hooded crow is considered to have a low level of threat of extinction (Baulhe and Groombridge 1996). The Norwegian population is estimated to be between 200,000 and 600,000 pairs and outside of the breeding season can be legally killed as it is considered a pest species (Sandvik 1998).

Common Eider

The common eider is a large ground nesting sea duck (50-71cm long, weight 1500-2300g, Cramp and Simmons 1977) with a circumpolar distribution and breeds in coastal areas in arctic, boreal and some temperate regions (Bustnes and Tertitski 2000, Cramp and Simmons 1977). Female eiders are capital breeders relying upon accumulated body reserves to cover energetic requirements during laying and incubation. They produce a clutch of 4 to 5 eggs (range 3 to 6 eggs) in a nest (Andersson and Waldeck 2006, Erikstad et al. 1993) and one brood per breeding season (Erikstad and Tveraa 1995, Hanssen et al. 2002). Eggs are laid at intervals of roughly 27 hours (Watson et al. 1993). Females adopt the extreme behaviour of continual incubation, fasting for the entire incubation period (Erikstad and Tveraa 1995, Milne 1974, Parker and Hohn 1996) and only occasionally leave the nest in order to drink (Mehlum 1991, Cristuolo et al. 2000, Swennen et al. 1993). However, females do not begin proper incubation until after the penultimate egg has been laid (Hanssen et al. 2002) and as males take no part in the care of eggs the nests are mostly unprotected for 3 or 4 days during egg laying.

The common eider is thought to have a worldwide population of between 3 - 4 million individuals and a western European population of between 2 - 3 million individuals (Bustnes and Tertitski 2000). The European population is given conservation focus under the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA 1999), whilst the Pacific American population's conservation is continued under the US Fisheries and Wildlife updated Focal Species Strategy for Migratory Birds (USFWS 2005). The Conservation of Arctic Flora and Fauna (CAFF) considers the common eider as a species of conservation concern in its circumpolar range and includes it in their conservation strategy (Matson et al. 2004). Although considered to have a low threat of extinction (Baulhe and Groombridge 1996), concern has been expressed about the common eider in recent years due to an apparent rapid decline in the numbers of some populations in both America and Europe (Soydam et al. 2000, Desholm et al. 2002, Christensen and Falk 2001, USFWS 2005). In

Norway. Bustnes and Tertiltski (2000) assessed the Norwegian Coast population as fluctuating by at least 20% over a 12 year period (1986-1998) with no clear positive or negative trend.

3.3 Common eider nest success monitoring

In this study a Before and After Comparison of Impact (BACI) type design was used (Underwood 1994) with eider nesting success being monitored before and during crow removal at one treatment site, Hakoya and on one control site, Grindøya. Four hundred and eighteen eider nests were located and monitored on Hakoya and Grindøya over the two years, 2006 and 2007. In 2006, monitoring began on Hakoya and Grindøya on 15th and 18th May respectively, whilst in 2007 birds began nesting later and first nests were found on 19th and 22nd May respectively. Monitoring ended on Hakoya on 28th June in both years whilst on Grindøya it ended on 28th June in 2006 and 29th June in 2007. All nesting data based on 2103 nest visit intervals were used to model the average daily nesting success (i.e. active or failed) for each island in each year. Three hundred and eighty eight nests were followed to completion of the nesting attempt and were used to calculate colony nesting success (proportion of nests where at least one egg hatched) for each island in each year. Twenty-four of the 30 nests not followed to completion of the nesting attempt were from Grindøya in 2006 where only nesting success of birds with known laying date was of interest (see below). In 2007, two nests on Grindøya could not be relocated due to rapid growth of dense vegetation between visits and on Hakoya, 4 nests were not followed to completion as they were still active at the end of the study period. As vegetation grows rapidly during the course of the breeding season and new nests can be established very close to existing nests between visits, nest locations were marked with plastic tape fixed around nearby vegetation in order to help relocation. In addition to nesting outcome, the number of eggs in each nest at nest discovery (initial clutch size) and the maximum number of eggs layed in each nest (maximum clutch size) were recorded. Maximum clutch size was calculated as the unchanged clutch size recorded on two subsequent visits (Yoccoz et al. 2002).

3.4 Monitoring design on Grindøya

Due to time constraints and the high level of nest predation on Grindøya, nest search effort at this site contributed to a larger project led by Dr. Svein Are Hanssen investigating the interaction between breeding success and female quality. All nests were visited within 2 days of nest finding and were checked at 2 day intervals until maximum clutch size had been recorded. Nests of eggs with known lay date were monitored by Dr. Hanssen and his field

assistant, whilst monitoring of nests of unknown lay date was carried out by Dr. Hanssen's fieldworker in 2006 and by myself in 2007. Lay date was determined either by back calculation from the number of eggs on the subsequent visit where the initial clutch size was more than one, or by the date on finding the nest when the clutch size was one at time of detection. Eiders were assumed to lay one egg per day (adapted from Watson 1993). In 2006, nests of unknown lay date received ad hoc visits after maximum clutch size had been established, whilst in 2007, visits were made on the 3rd, 12th, 17th, 23rd, 25th and 29th June (with the first visit occurring after the recording of a maximum clutch size) in order to record nesting outcome. Females of known lay date received 3 visits after egg laying, where birds were handled. On day 7 of incubation (7 days after the last egg had been laid) they were caught, ringed and weighed, on day 12 they were caught and reweighed and on day 20 they were caught, reweighed and marked for future re-sighting studies. Between one and 4 subsequent visits were carried out after day 20 to determine hatch date and colour mark chicks. Nest outcome was recorded at each visit. In 2006, incubating birds with known lay date had their wing flash colour manipulated on day 20 of incubation, whilst in 2007 blood samples were taken on each visit. In 2007, due to high predation rate of known lay date nests, 6 females incubating nests containing eggs of unknown laying date were added to Dr. Hanssen's study protocol in order to increase sample size in his detailed studies.

3.5 Monitoring design on Håkøya

Eider nests on Håkøya were searched for in a core area at the north end of the study area (Appendix Fig. 1a). Nests were followed more frequently than on Grindøya, in an attempt to document cause of predation and received visits every second day between nest finding and nest completion with the exception of the final 5 nests in 2007 where the nesting attempt was not complete by 28th June. Nests were marked and clutch size and laying dates were calculated as for nests on Grindøya. Where nests failed, cause of failure was recorded where possible. Small fragments from eider egg remnants were recorded as a sign of mammalian nest predation, whilst eggs which had a single hole or were split in two were recorded as a sign of bird nest predation (after Brown et al. 1999, Summers et al. 2004). It was not possible to distinguish between crow and gull predation in the field. The presence of an empty nest was not helpful in determining predator type as both crows and mammals can carry eggs considerable distances from the nest (Loman and Göransson 1978, Summers et al. 2004). On Håkøya, birds were disturbed from the nest during incubation in order to determine clutch size but not subsequently.

3.6 Common eider nest habitat characteristics

Habitat characteristics were obtained on the initial nest visit from all recorded nests on Håkøya. On Grindøya, habitat characteristics were recorded for a sample of 76 nests in 2006 and 118 nests in 2007. In total, 1804 nest visit intervals were recorded from nests which were also sampled for habitat characteristics on both islands. These nest visit intervals were used to calculate average daily nesting success in the analysis of nest habitat characteristics as predictors of nesting success. Due to partitioning of nest monitoring on Grindøya it was not possible to relocate all failed nests in order to record nest habitat characteristics.

Nest positions were logged with handheld GPS and macro habitat and nest distance to the open were recorded. Macro habitat was classified as the general habitat type in which nests were located and consisted of 3 classes: open area, wood and thicket. The distance of each nest to open areas was estimated to the nearest metre by eye. Open landscape in the study area on Håkøya consisted of dry ling heath (*Empetrum hermaphroditum*, *Vaccinium spp.*) with a few small mountain birch (*Betula pubescens*) bushes (canopy cover with a maximum of 2m in diameter). On Grindøya, in addition to the habitat described for Håkøya, open mire with a few mountain birch or willow bushes (*Salix spp.*) existed. The habitat type woodland consisted predominantly of mountain birch on both islands with willow stands in wet areas. Thicket habitat was classified as woodland that was difficult to move through, having trunk distances of less than 40cm. Distance from crow nests were later calculated from the GPS positions of eider and crow nests.

3.7 Monitoring and manipulation of crow numbers

Crow monitoring was aimed at recording breeding pairs as well as general activity including flocks of non-breeding birds. The study area for crows on Håkøya (Appendix Fig. 1) was limited to a 1 km radius from the northern tip of the eider nesting area in order to be of a similar area to that on Grindøya (64 ha and 65 ha respectively). Crow nests were logged with handheld GPS whilst walking weekly transect lines spaced 80m apart through all woodland in the two study areas. Sightings of 3 or more crows in a group which did not subsequently disperse and return to individual territories within the study areas were recorded as a flock count. This count was used as an index of activity of non-breeding birds.

Five surveys were carried out on Håkøya between 24th April and 16th May 2007 before eiders started egg laying in order to log crow nest positions and to determine the number and

location of territorial crows to be removed. Crow removal was carried out under approval from Direktoratet for Naturforvaltning, reference 2007/1327 ARL-VI-JAA. Ten Larsen Traps (Game Conservancy Trust, 2007) were placed over the study area on 14th May in order to remove territorial pairs and roaming birds utilising this area. Placement reflected crow territories held within the study area and/or coops situated within the main eider monitoring area (Appendix Fig. 1). Traps were baited with hens' eggs and checked daily. Caught birds were kept in traps for up to 48 hours to improve the efficiency of the traps. These birds were provided with food and water and checked every 24 hours and thereafter humanely killed. Due to logistical constraints of accessing Grindøya during late winter, crow transects in 2007 began later than on Håkøya, commencing on 13th May before eiders started nesting and continued to the end of the eider breeding season.

The effectiveness of crow removal on crow activity on Håkøya was assessed between 19th May and 29th June 2007. Twelve paired watches were carried out at Håkøya and Grindøya on subsequent days at the same hour, with the number of crows seen within each hour being used as an index of crow activity. Watches were initially carried out over 2 hours but then reduced to 1 hour when it became apparent that this was sufficient to measure a difference in activity between the two areas. Watches were undertaken from a boat anchored c.300m from the high tide line of each area in light to medium breeze and dry conditions or light showers.

3.8 Other predator activity

Stoat

After sightings of stoat on both islands in 2006, stoat activity was monitored in both areas during 2007 using tracking tunnels adapted from Graham et al (2002). Seventeen tracking tunnels were laid out in the study area on Håkøya and 16 were laid out on Grindøya between 12th and 16th May. Positioning (Appendix Fig. 1), reflected dense areas of eider nesting within the 3 broad habitat categories used to classify eider nest habitat characteristics. Tunnels were checked weekly throughout the eider breeding season for tracks, and papers and ink were renewed when necessary.

Otter

Scat piles located in the study areas were checked weekly and used as evidence of otter presence.

3.9 Statistical analysis

All statistical analysis was performed using software R 2.4.1 (R development core team, 2007)

Clutch size

Area based differences in nesting success could have been due to a bias in the proportion of nests found with differing clutch size, or the proportion of nests discovered at different stages of laying, i.e. clutch size during laying. A log-linear model using a Poisson distribution was used to investigate influence of laying stage and maximum clutch size on nesting success. Models containing the interactions between day and area and day and year were compared to models containing the variables day, area and year to predict nesting success. The predictor variables used were firstly number of eggs found in the nest upon nest discovery, and secondly clutch size. Akaike's Information Criteria (AIC; Burnham and Anderson 2002) were used to select the best model. Between area bias due to differences in either variable would be indicated by a positively signed interaction between day and area.

Eider nesting success

The eider nesting success on Håkøya and Grindøya was analysed to see if crow removal was associated with an increase in eider nesting success on Håkøya in 2007. A significant improvement in eider nesting success on Håkøya between 2006 and 2007 with no similar change between years at Grindøya would suggest that crow removal could be the cause of improvement of nesting success on Håkøya. The effect of a reduction in crow numbers and activity would appear as a positive signed interaction between area and year. Seasonal effects were modelled as day after 15th May (day) using a second order polynomial. The most complicated model contained the interactions between area and year, day and area, day and year, day² and area, day² and year, whilst the minimum model contained area, year and their interaction and the predictor variable day. The data was modelled using the logistic exposure model (Shaffer 2004), where optimum model choice was based on AIC (Burnham and Anderson 2002).

The logistic exposure model is a variation of ordinary logistic regression, where the predicted daily survival probability of nest i (s_i) is modelled as a linear function of k predictor variables (x_1, \dots, x_k) using the logit link function:

$$g(s_i) = \log \left(\frac{s_i}{1 - s_i} \right) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k \quad (\text{Eq. 1})$$

This formulation ensures that estimated values for s_i are in the range zero to one and that the daily survival rate can be back-calculated from the estimated regression coefficients using:

$$s_i(s) = \frac{e^{\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k}}{1 + e^{\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k}} \quad (\text{Eq. 2})$$

In the main nest survival analysis x_j refers to the variables day, day², area and year; whilst in the habitat characteristic analysis, the additional variables habitat, distance to the open, and distance to the nearest crow nest were also included. The data available contain observations of nest survival over the time period from one nest visit to the next. Assuming constant daily survival over this time interval (t) between visits, Shaffer (2004) made use of the following relationship between the survival probability over the interval t , $\theta(t)$, and the daily survival probability s :

$$\theta = s^t \quad (\text{Eq. 3a})$$

$$s = \theta^{1/t} \quad (\text{Eq. 3b})$$

The expression for s in Eq. 3b was entered into Eq. 1 to obtain the logistic exposure link function:

$$h(\theta) = \log \left(\frac{\theta^{1/t}}{1 - \theta^{1/t}} \right) \quad (\text{Eq. 4})$$

When using this link function the estimated parameters in the fitted regression equations relate directly to the daily survival probability s following Eq. 2. For the logistic regression, the models were fitted as generalised linear models assuming a binomial distribution for the observed nest survival (y_i) over the time interval t , where nest survival (y_i) was coded as zero for failed nests and one for surviving nests ($y_i \sim \text{binomial}(p = \theta, n = 1)$).

Assumptions underlying the logistic-exposure model are that all nests survive or fail independently of one another and that daily survival probabilities are homogeneous among nest-days having the same values of explanatory variables (Shaffer 2004). The goodness of

fit of the model was tested using the Hosmer • Lemeshow goodness of fit test (Harrell 2001), whereby observations were split into 10 groups each covering one 0.1 quantile of the predicted daily nesting survival probabilities calculated from the model. Chi-squared test with 8 d.f. was used to assess the fit of observed to expected values.

The predictor variables area, year and day after 15th May were used to predict average daily nesting success for the subsetted nest data collected for analysing nest habitat characteristics. The candidate models were the same as for the complete nesting data in order to see if the subset of data biased the overall nesting success results. AIC criteria were used to choose the best model and the AIC ranking of models was compared to that from the full data set. The best fit model from the analysis of nesting success using the complete data set was used as a base model into which each of the nesting habitat characteristic variables (nucleo habitat, distance to the open, distance to the nearest crow nest) was entered in turn. Distance to the open was modelled as a 3rd order polynomial. Models were ranked using AIC weights (Burnham and Anderson 2004).

Crow activity

An index of crow activity on Hakoya and Grindoya in 2007 was analysed in order to see if crow removal on Hakoya resulted in lower crow activity than the control area Grindoya. The activity index was expressed as the number of crows seen within an hour. No flocks were observed on Hakoya, whilst on Grindoya territorial birds occasionally formed flocks of up to 4 in order to defend their territories against raven and white-tailed eagle. As birds were seen individually before forming flocks and quickly broke up after the threat had gone, the data was entered as a maximum number of birds seen, rather than being distinguished in a separate category as a non-breeding flock. Thus, no data on flock activity was used in this analysis. The variables area and year were entered as factors into a log linear regression model to predict an index of crow activity at each study area. Because of overdispersion in relation to a Poisson distribution, the activity index was analysed assuming the variance function $\text{Var}_i = qE_i^2$, where E_i is the level of the activity index for area i and the variance (Var) is equal to the proportionality parameter q multiplied by the mean (E).

4. Results

4.1. Eider clutch size

Mean clutch size on nest discovery and on completion of egg laying was 3.23 ± 2.04 (range 1–9) and 4.21 ± 1.94 (range 1–9) respectively. The most appropriate model for investigating the effect of clutch size on nesting success contained the interaction between day and area and day and year ($\Delta AIC = 2.06$ for model containing day and year additive effects). For a given sampling day there was no strong area or year effect on number of eggs found in nests on first visit ($n = 417$; coefficient estimate: -0.015 ± 0.010 day:area; coefficient estimate: 0.017 ± 0.009 day:year). There was no supportive evidence that for a given day there was an area or year effect for the maximum clutch size. The most appropriate model for investigating the effect of number of eggs found in a nest when egg laying was complete included only the intercept (although the AIC value for the variable day; $AIC = 1085.27$ was very similar to that of the intercept; $AIC = 1085.15$).

4.2. Eider nesting success

Hatching success was constant over the two years 2006 and 2007 on Grindoya and was much lower than on Håkøya (Table 1). On Håkøya hatching success increased from 0.61 ± 0.07 in 2006 to 0.80 ± 0.06 in 2007. The most appropriate model of daily nesting success based on all nests included the interaction between area and year and a second order polynomial of season (Tables 2 and 3). The model fitted the data well (Hosmer Lemeshow Chi square test, $\chi^2 = 8.17$, $P = 0.42$, d.f. = 8). The same best model applied to the subset of data for which the effect of habitat characteristics also could be assessed (Table 2). Thus the measured habitat variables explained little of the variation in nesting success area, year and day effects were taken into account. The interaction was because nests on Håkøya had a higher probability of daily nesting success in 2007 than in 2006, whilst nests on Grindoya had similar nesting success in the two years (Fig. 1a). The nature of the season effect is shown in figure 1b. The daily probability of success increases sharply before reaching an asymptote which for Grindoya in both years is about 9th June (day 40), whereas for Håkøya the asymptote is reached earlier by about day 30th May (day 30).

Table 1. Summary of the monitoring of hooded crows and common eiders from Grindoya and Ellikoya over the two years 2006 and 2007. The table shows number of crow nests, number of crows seen per hour (only data from 2007), number of eider nests that succeeded in hatching, together with the total number of nests monitored to end of nesting attempt, and finally the breeding success (number of monitored nests which succeeded to hatching). Values for the subset of data on Grindoya used to analyse the effect of habitat characteristics are shown in parenthesis. Standard errors based on Poisson distribution for number of crows seen per hour and the binomial distribution for breeding success.

Area	Year	Number of active crow nests	Number of crows seen per hour	No. of eider nests		Breeding success (%)
				Hatched	Total	
Grindoya (Grindoya)	2006	4	-	52 (35)	135 (76)	38 : 4.19 (46 : 5.75)
Grindoya (Grindoya)	2007	4	26.70 : 1.56	62 (56)	159 (118)	39 : 3.88 (47 : 4.61)
Ellikoya	2006	5	-	30	49	61 : 7.04
	2007	1	6.20 : 0.75	36	45	80 : 6.03

Table 2. Model selection for analysis of common eider nest survival and habitat characteristics data. Scaled values of Akaike's Information Criteria (AIC) and Akaike's weights (w_i) are presented for 6 logistic exposure models. The AIC values are expressed in relation to the best fitting model, model 2 and are shown for the full data set used for estimating nesting success in relation to crow activity and the subset of data which was used to estimate the covariates habitat, distance of nest to open (open) and distance of nest to crow nest (nearest.crow.nest). Sample size (number of nest intervals) for complete data set is 2103 and for subset of data is 1804.

Model	Full data set			Subset of data		
	AIC	Δ AIC	w_i	AIC	Δ AIC	w_i
1 Area, year, day, day ² , area:year, day:area, day ² :year, day:year, day ² :area	1273.12	4.07	0.12	911.53	0.78	0.23
2 Area, year, day, day ² , area:year	1269.05	0.00	0.88	910.75	0.00	0.49
3 Area, year, area:year	1303.04	33.99	0.01	919.06	8.31	0.01
4 area, year, day, day ² , area:year, habitat	-	-	-	910.89	0.14	0.43
5 area, year, day, day ² , area:year, nearest.crow.nest	-	-	-	912.71	1.99	0.07
6 area, year, day, day ² , area:year, open, open ² , open ³	-	-	-	914.85	4.10	0.01

Table 3. Parameter estimates with standard errors for area and year effects for the best model of daily nesting survival of eiders (Table 2) from full nesting data and from subset of data used to analyse the effect of habitat characteristics on Grindaya. Intercept, day and day² estimates for full nesting data are 3.29 (0.12), -16.54 (3.34) day⁻¹, 9.94 (3.08) day⁻²; and for subset of nesting data are 3.54 (0.17), -11.23 (3.95) day⁻¹, 6.40 (3.52) day⁻².

Variable	Parameter coefficient	
	Full	Partial
Year (2007)	-0.24 ± 0.16	-0.24 ± 0.22
Area(Häkova)	-0.76 ± 0.26	-0.41 ± 0.29
Häkova:2007	-0.94 ± 0.44	-1.02 ± 0.46

4.3 Cause of eider nest failure

Cause of failure of nests on Hakoya was difficult to ascertain (8 out of 20 nests with cause known in 2006 and 3 out of 9 nests in 2007). Most failed nests were found empty with no sign of predator presence on the nest visit. Although the number of nests with cause of failure is known is small, there were fewer nests predated by birds in 2007 than in 2006 (Table 4).

Table 4 Cause of known nest failure for nests on Hakoya in 2006 and 2007. ¹ nest predated by both bird and mustelid, ² the adult female was found killed near the nest; ³ 2 nests were empty with nest linings ripped out

Year	Cause of failure				Total
	Bird	Mustelid	Deserted	Unknown	
2006	5	2	1	12	20
2007	1 ²	1 ³	1	6 ³	9

4.4 Crow numbers, removal and activity

In 2006 there were 5 nesting attempts made by crows in the Hakoya study area (Appendix Fig. 1, Table 11). One pair remained active throughout the eider nesting period, whilst the other 4 failed part way through. In 2007, three nesting attempts were made and trapping reduced the number of active nests to one. Birds were removed from 2 territories using Larsen Traps on 19th and 21st May respectively, which resulted in the subsequent failure of these nesting attempts. As birds were not individually marked it was not possible to see if the second member of a territorial pair was caught or not. Trapping was not carried out at the third territory due to landowner's reluctance. However, the third nesting attempt later failed probably due to the nest being robbed by ravens (pers obs.)

Ten crows were caught between 16th and 27th May. Crows showed no interest in the traps or hens eggs placed on top of the traps after this date. Most birds (6 out of 10) were caught using bait alone and no lure bird. Two territorial birds captured from the study area were caught in the presence of a lure bird.

On Grindoya, 4 nesting attempts were made in both years. In 2006, three pairs were active throughout the study period, whilst one pair at the north end had failed by 26th May. In 2007,

one pair failed towards the end of the study period, whilst the other 3 pairs had a total of 9 large young

In 2007, Grindoya had on average more than 3 times the activity of crows per hour than Håkoya (Table 1, Fig. 2). Crow transects, activity watches and casual sightings revealed very little sign of flock activity in the two study areas. No flocks were observed on Håkoya in either year. On Grindoya, no flocks were observed in 2006, whilst in 2007 one flock of 7 crows was seen on the shore on Grindoya during eider nest checks.

4.5 Other predator presence

No stoat activity was registered by use of stoat tunnels on Grindoya or Håkoya in 2007. New ester spraints were present throughout the whole study period in both years and caches of adult female eider carcasses characteristic of mink predation were found on Grindoya in 2007 throughout the breeding season.

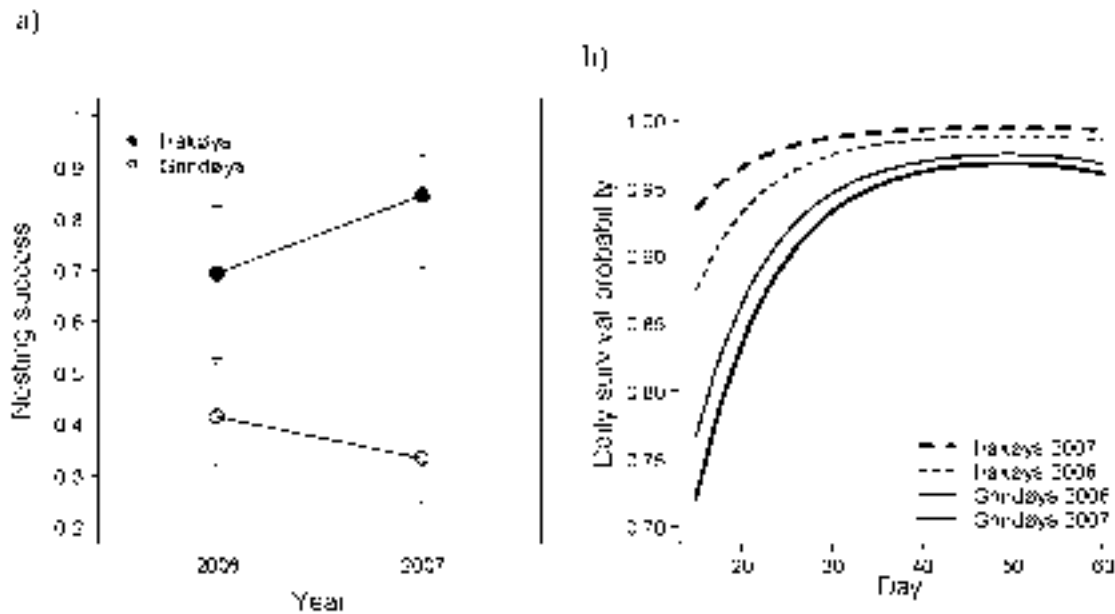


Figure 1. Predicted nesting success from the best logistic exposure model.

a) Back-transformed coefficient estimates and 95% C.I. for the area:year effect. Nesting success is expressed as an average for the entire nesting period of 28 days (assumes average clutch size of 4 and average incubation period of 24 days (adapted from Erikstad et al. 1993)). b) Estimated daily survival from all nests on Girndøya and Håkøya in 2006 and 2007 where day 1 is 1st May.

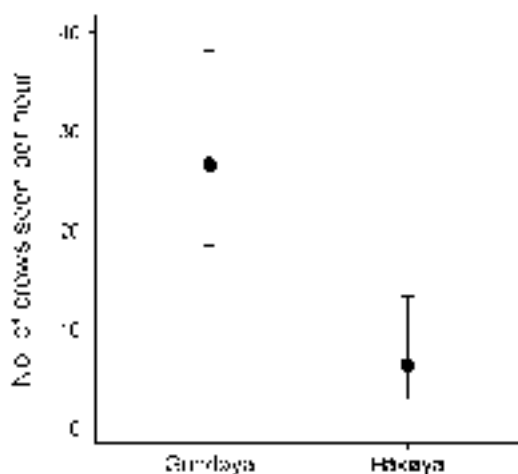


Figure 2. Mean number of crows seen per hour during 12 watches on Girndøya and Håkøya between 19th May and 29th June 2007. Estimates are back calculated from a regression model assuming an overdispersed Poisson distribution and are plotted with 95% C.I.

5. Discussion

5.1 Summary of results

Crow removal in 2007 was successful in terms of removing established territorial and visiting crows. This corresponded with the much lower crow activity on Håkøya compared to the control area Grindøya. Eider nesting success on Håkøya increased from 2006 to 2007, while in contrast, nesting success on Grindøya stayed constant over the same period.

5.2 Comparison with previous crow removal studies

Since the crow removal in this study was not replicated in space or time and moreover, since the cause of the eider nest losses was often undetermined, the causal link cannot be verified by this pilot study. Nevertheless, I will in the following discussion evaluate the significance of the findings in the light of previous studies of crow predation on ground nesting birds.

The removal of 10 crows from the study area on Håkøya was successful in clearing territorial nesting crows from the trapping area. Similar crow removal success has been recorded in longer term studies involving crow egg nest predation of willow ptarmigan (*Lagopus lagopus*), black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*) (Parker 1985, Summers et al. 2004). The removal of crows from Håkøya also probably resulted in low crow activity as measured by a crow activity index. There appears to be no other published crow removal study that compares the within year affect of crow removal on crow activity with the activity at a corresponding control site over the whole nesting period of the prey species.

In the present study there was no evidence of flocks of non-territorial birds utilising areas cleared of territorial crows (Håkøya in 2007), or areas where territorial birds were established (Grindøya in 2006 and 2007, Håkøya in 2006). In some ways this is surprising as the presence of large human settlements nearby would be expected to support a surplus of non-breeding crows (Marzluff and Neatherlin 2006) which are known to associate in flocks (Coombs 1978). Erikstad et al. (1982) reported crow flocks feeding on rubbish dumps situated at nearby settlements rather than focussing on the nests of willow ptarmigan and black grouse. A similar behaviour may occur in the present study, with the large settlements close to Grindøya and Håkøya providing the main food source, so that eider colonies are not required as feeding locations by flocks of non breeding crows.

The general pattern shown by the removal of one predator in multi-predator systems, where the prey is ground nesting bird eggs seems to be one of compensatory predation. An alternative predator increases its egg consumption so that no noticeable effect of predator removal is apparent (Parker 1981, Chasnes et al. 1968). However, in the case of Summers et al.(2004), compensatory predation was not sufficient to negate the positive effect of crow and fox removal on the reproductive success of capercaillie and black grouse. There was no good evidence of variation of predator assemblages over time and between areas in this study. Moreover, assessment of the cause of nest loss was largely unsuccessful. We can conclude, however, that the reduction in nest loss between 2006 and 2007 on Hakoya, in association with the reduced number of crows, was not compensated for by the other predators recorded on the island in the same year, which were greater black-backed gull, herring gull and otter.

5.3 Area and season dependant predation rate

The nest success rate on Grindoya was constant between years and much lower than on Hakoya (Fig 1). Casual observations suggested a higher number of egg predators on Grindoya than Hakoya. The Grindoya colony is larger and more concentrated than on Hakoya and is one of the largest eider colonies in Troms county. As a nature reserve, predators are protected from pest control and/or persecution unlike in the surrounding area. These factors together with the short timescale of egg availability, roughly 6 weeks, in an otherwise largely food deficient area, would be expected to attract a larger number of predators (Krebs et al. 2001, Vuorisalo et al. 2003) and thus a higher level of predation pressure than on Hakoya. In addition, the level of nest disturbance was higher on Grindoya than Hakoya due to scientific studies carried out on this island. Bolduc and Guillemette (2003) have indicated that eider nesting success can be negatively affected by predation mediated by human disturbance. Thus, the opportunity for predating unattended nests may have been greater for Grindoya compared to Hakoya.

Modelling of daily nesting success probabilities revealed that nests found at the start of the season had a much lower probability of success than nests found later on in the season. Similar seasonal effects have been found for crow predation on artificial eider nests placed in eider colonies in south-west Sweden (Gotmark and Årland 1989), and Glaucous gull (*Larus hyperboreus*) predation on eider nests in Svalbard colonies (Mehlum 1991). In contrast, (Milne 1974), showed that the proportion of eider nests being destroyed in a north east

Scottish colony by carrion crow and herring gull (*Larus argentatus*) increased as the season progressed. There is some suggestion that the seasonal increase in nesting success found in the present study may be mediated by timing and nesting behaviour of the female eiders. As in most populations, individuals vary in their timing of breeding (Newton 1998), whilst it is generally perceived that the presence of a female eider is a good anti predator strategy against avian predators (Mallum 1991). In accordance, the probability of nest failure decreases with subsequent day in the season up to the maximum number of individuals in the colony. The probability of failure also decreases for subsequent day within each female's laying sequence as the female increases attendance at the nest (Hanssen et al. 2002, Swennen et al. 1993). The period for eider laying is short, lasting on average 4-5 days (Watson et al. 1993), but the incubation period is relatively long, lasting on average 24 days (Erikstad et al. 1993). In the present study most birds would have been attending their nests by the second week of June, dramatically reducing the likelihood of nest predation. The observation agrees well with the pattern for daily nesting survival at Grindoya (probability of survival exceeds 0.94 at its asymptote around day 40, 9th June) which was subject to highest nest predation.

The early season nest failure in the present study could be due to predation both by breeding and non-breeding crows. All breeding crows were established on territories before eider nesting began. In 2007, when nests were monitored more closely, 5 of the seven crow pairs had either begun laying or were incubating complete clutches when the eiders started breeding. Breeding failure in crows can be high during the egg laying and incubation phase (Coombs 1978). Thus the use of nesting habitat within an eider colony would be of benefit in terms of providing a localised consistent food source during this critical phase of crow reproduction. The trapping pattern of crows on Håkoya suggested that activity of, and hence predation by, non-territorial birds was mainly in the early part of the eider breeding season. This is supported by Coombs (1978) who reports that unsuccessful prospecting birds generally leave the area later on in the crow breeding season.

5.4 Habitat dependant predation

There was no effect of nest habitat characteristics on nesting success of eiders on Grindoya and Håkoya in either of the study years. Several studies have shown that eiders use a wide variety of nest habitats with different extents of cover (Noel et al. 2005, Gerell 1985, Milne 1974, Laurila 1989). This is often interpreted as an anti-predator tactic, however, the evidence from the above studies is inconclusive. Similarly Einarsen et al. (2008) and

Pedersen et al. (2008) found no difference in crow predation rate of artificial nests located in different ages of spruce plantations within northern birch forest habitat. The high rate of predation on *Grindøya* could be due to compensatory predation, or it could be as in Pedersen's et al. study that crows do not preferential between arbitrary chosen habitat categories. Crows were found most commonly to adopt a perch hunting technique in a study by Smedshaug et al. (2002). However, in common with other studies (e.g. Milne 1974), casual observation during activity watches in this study showed that crows also carry out systematic searches. Crows would be able to search through most of the habitat classified as wood in the present study, even though they would not necessarily be able to locate the same nests via movement of nesting female eiders if the crow was located on a perch in the open. An alternative reason for no habitat effect being found could be due to lack of suitable sampling technique for nests located in different habitats on *Grindøya* in both years and lack of use of thicket habitat by eiders on *Håkøya* in 2006.

No effect of distance from crow nests on eider nesting success was found. In contrast, Loman (1978) found that artificial nests were more likely to be predated if they were less than 225m from crow nests. Similarly, Erikstad and Myrberget (1982) found a distance effect, with increasing numbers of willow ptarmigan nests being robbed within 700m and 350m of territorial crow nests. The difference in findings could be due to spatial differences between crow nests and the density of crows in the different studies. Loman (1978) does not give information on inter-nest distances, however, in Erikstad and Myrberget's study there were between one and two crow nests each year, with an inter-nest distance of c.1.30km. Conversely, the 4 crow nests on *Grindøya* were between 150m and 723m of each other and on *Håkøya* in 2006, when breeding crows were not removed, the distance varied between 248m and 517m. Thus the closeness of crow nests to each other combined with crow territorial behaviour could result in uniformly high crow predation on surrounding eider nests. The reported densities in this study of 6.15 nests km⁻² for both years on *Grindøya* and 7.21 nests km⁻² for *Håkøya* 2006 are higher than those reported for other island studies (1.6-1.8 nests per km², Loman 1980, Parker 1985, Erikstad et al. 1982) and are above the median density of c.2 nests km⁻² for 11 rural studies (cited from Munkejord et al. 1985). The reported high densities could be mediated by the abundant food supply early in the season in the form of eider eggs, at a time where energy demands and nest defence are critical to crow nesting success (Coombs 1978). Breeding crows are known to nest more densely in the vicinity of food subsidies (Richner 1990, Neatherlin and Marzluff 2004). In addition, breeding success

of crows has also been shown to be elevated in the presence of food subsidies (Yom-Tov 1974). The higher number of 2.25 large nestlings per pair recorded for *Grindaya* in 2007 compared to 4 other crow reproductive studies (range 1.2 – 1.7 nestlings per pair, Loman 1980) suggests indirectly that food supply is abundant for nesting crows on *Grindaya*.

5.5 Predation effect on eider population

Small island populations can be subject to extreme predation pressure (Bell and Merton 2002). In the case of the common eider, site philopatry is high (Bustnes and Erikstad 1993), suggesting that this species forms closed island populations rather than island colonies forming subunits of a larger scale population. Resilience of small populations is lower than for large populations and so the potential for irreversible decline of the local eider populations could be high. Adult eiders have high annual survival with delayed sexual maturity and so population growth rate is less sensitive to reproductive parameters than to adult survival (Sæther and Bakke 2000). However, reproductive parameters might be more sensitive to predation or environmental variability than to adult survival (Gaillard and Yoccoz 2003), overriding the difference in the sensitivity between reproductive and survival parameters. Thus, reproductive parameters may be important to the population growth rate of this *K*-type species. Indeed, Hario and Rintala (2006) in an analysis of eider population trends using a time series of 57 years, concluded that this species can be subject to population declines during prolonged periods of reduced breeding success. The clutch size of eiders is small compared to other sea ducks (Andersson and Waldeck 2006) and nest loss is not compensated for by laying of a replacement clutch. Nesting success may be important to population growth rates as seen in the ground nesting duck, the mallard (Hockman et al. 2002). Also, Bell and Merton (2002), and Bollon et al. (2007), conclude that the removal of ground nest predators can be an effective short-term solution to ease the pressure on small and/or declining ground nesting bird populations. Further investigation involving continuation and expansion of the experiment, together with long-term monitoring of important population parameters for both crow and eider would be needed, to address the role of the hooded crow on the local currently declining eider populations on *Grindaya* and *Hakoya*.

6. Conclusion

This study demonstrated large differences in the nesting success of common eiders at two nearby eider colonies in Troms county. The cause of the differences remained undetermined, however, the results of the removal of crows from one colony during one breeding season suggested that egg predation by the hooded crow may be an important factor. The use of habitat variables broad scale habitat, distance to open and distance to nearest crow nest were of no use in explaining the variation in eider nesting success.

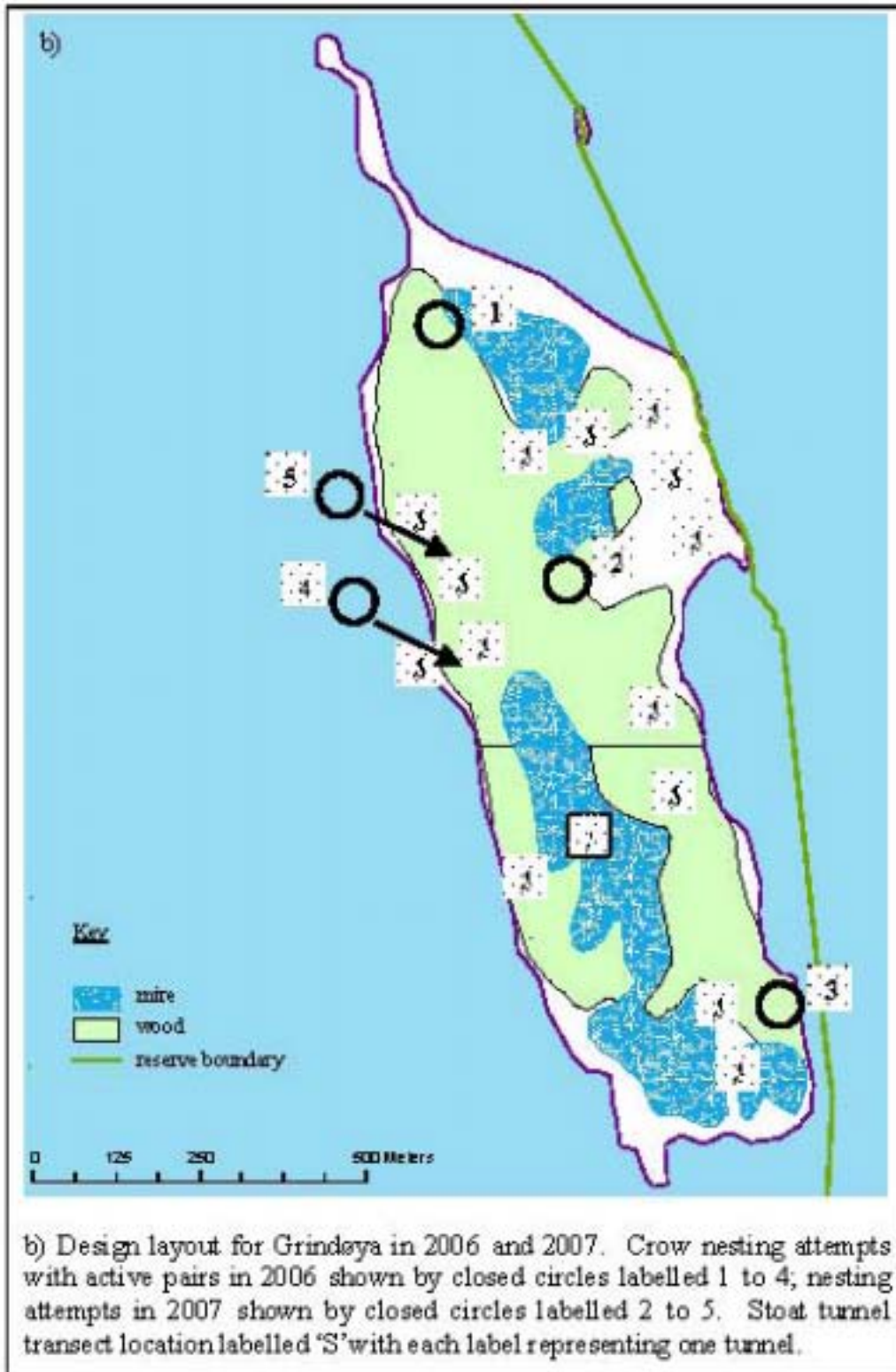
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8. Appendix



Figure 1a) Design layout for Håkøya in 2006 and 2007 with crow study area north of solid line and eider area north of dotted line. Crow nesting attempts with active pairs in 2006 shown by closed circles labelled 1 to 5; nesting attempts in 2007 shown by closed circles labelled 1,5,6. Larsen Traps for crow removal labelled 'T' plus those targeted at active nesting territories labelled with closed circles 5 and 6. Stoat tunnel transect location labelled 'S' with each label representing 3 tunnels located 30m apart.



9. References

- AEWA. 1999. <http://www.unep-aewa.org/map/parties.htm>.
- AHLEN, I. and ANDERSSON, A. 1970. Breeding ecology of an eider population on Spitsbergen. -*Ornis Scandinavica*, **1**: 83-106.
- ANDERSSON, M. and WALDECK, P. 2006. Reproductive tactics under severe egg predation: an eider's dilemma. -*Oecologia*, **148**: 350-355.
- ANDRÉN, H. 1992. Corvid density and nest predation in relation to forest fragmentation - a landscape perspective. -*Ecology*, **73**: 794-804.
- ANGELSTAM, P. 1986a. Predation of ground-nesting birds nests in relation to predator densities and habitat edge -*Oikos*, **47**: 365-373.
- ANGELSTAM, P. 1986b. Predation on ground-nesting birds' nests in relation to predator densities and habitat edge. -*Oikos*, **47**: 365-373.
- BAILLIE, J. and GROOMBRIDGE, B. 1996. *1996 IUCN Red List of Threatened Animals*, The World Conservation Union (IUCN).
- BELL, B. and MERTON, D. 2002. *Conserving bird biodiversity: general principles and their application*, Cambridge University Press.
- BERGON, M., HARPER, J. L. and TOWNSEND, C. R. 1986. *Ecology: individuals, populations and communities*. Blackwell Scientific Publications, Oxford.
- BOLDUC, F. and GUILLEMETTE, M. 2003. Human disturbance and nesting success of Common Eiders: interaction between visitors and gulls. -*Biological Conservation*, **110**: 77-83.
- BOLTON, M., TYLER, G., SMITH, K. and BAMFORD, R. 2007. The impact of predator control on lapwing *Vanellus vanellus* breeding success on wet grassland nature reserves. -*Journal of Applied Ecology*, **44**: 534-544.
- BROWN, R., FERGUSON, J., LAWRENCE, M. and LEES, D. 1999. *Tracks and signs of the birds of Britain and Europe*. Christopher Helm, A & C. -Black. London.
- BURNHAM, K. P. and ANDERSON, D. R. 2002. *Model selection and multimodel inference: A Practical Information-Theoretic Approach*, Springer.
- BURNHAM, K. P. and ANDERSON, D. R. 2004. Multimodel inference: understanding AIC and BIC in model selection. -*Sociological Methods & Research*, **33**: 261.
- BUSTNES, J. O. and ERIKSTAD, K. E. 1993. Site fidelity in breeding common eider *Somateria mollissima* females. -*Ornis Fennica*, **70**: 11-16.

- BUSTNES, J. O. and TERHISTIKI, G. 2000. *The status of marine birds breeding in the Barents Sea region*, Norsk Polarinstitutt, Rapport.
- CLACK, J. F. and WALSH, J. J. 2006. Urban effects on native avifauna: a review. - *Landscape and Urban Planning*, **74**: 46-69.
- CHIFFNES, R., NELSON, M. and LONGLEY, W. 1968. The effect of predator removal on pheasant reproduction. - *Journal of Wildlife Management*, **32**.
- CHRISTENSEN, K. D. and FALK, K. 2001. Status of the common eider breeding in the municipality of Avanersuaq (Thule), north-west Greenland. - *Polar Research*, **20**: 109-114.
- COOMBS, F. 1978. *The crows: a study of the corvids of Europe*, Batsford.
- CÔTE, J. M. and SUTHERLAND, W. J. 1997. The effectiveness of removing predators to protect bird populations. - *Conservation Biology*, **11**: 395-405.
- CRAFFTEL, R. L. and WOLFE, M. L. 1988. Effects of alternate prey on skunk predation of waterfowl nests. - *Wildlife Society Bulletin*, **16**: 163-169.
- CRAMP, S. and SIMMONS, K. F. L. 1977. *Somateria mollissima* Fider. - *The Birds of the Western Palearctic* (Ed. by S. Cramp & K. L. Simmons), 595-604.
- CRISCUOLO, E., GAUTHIER-CLERC, M., GABRIELSEN, G. W. and LEMAITRE, Y. 2000. Recess behaviour of the incubating Common Eider *Somateria mollissima*. - *Polar Biology*, **23**: 571-574.
- DESHOUAL, M., CHRISTENSEN, T. K., SCHEFFERTEL, G., HARIO, M., ANDERSSON, Å., ENN, B., CAMPBLYSEN, C. J., NILSSON, J., WALTHER, C. M. and LORENTSEN, S. H. 2002. Status of the Baltic Wadden Sea population of the Common Eider *Somateria m. mollissima*. - *Widfowl*, **53**: 167-204.
- EINARSEN, G., HAUSNER, V. H., YOCCOZ, N. G. and JMS, R. A. 2008. Predation on artificial ground nests in birch forest fragmented by spruce plantations. - *In review*. **In press**.
- ERIKSTAD, K. E., BLOM, R. and MYRBERGET, S. 1982. Territorial hooded crows as predators on willow ptarmigan nests. - *The Journal of Wildlife Management*, **46**: 109-114.
- ERIKSTAD, K. E., BUSTNES, J. O. and MOUM, T. 1993. Clutch size determination in precocial birds - a study of the common eider. - *Ibis*, **110**: 623-628.
- 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.
- GALLIARD, J. M. and YOCCOZ, N. G. 2003. Temporal variation in survival of mammals: a case of environmental canalization? - *Ecology*, **84**: 3294-3306.

- GAMECONSERVANCYTRUST. 2007. <http://www.gct.org.uk/>.
- GERELL, R. 1985. Habitat selection and nest predation in a common eider population in southern Sweden. *-Ornis Scandinavica*, **16**: 129-139.
- GOTMARK, F. and AHLUND, M. 1989. Nest predation and nest site selection among Eiders *Somateria mollissima*: the influence of gulls. *-IBIS*, **130**: 11-123.
- HANSSON, S. A., ENGBRETTSEN, H. and ERIKSTAD, K. E. 2002. Incubation start and egg size in relation to body reserves in the common eider. *-Behavioral Ecology and Sociobiology*, **52**: 282-288.
- HARIO, M. and RINTALA, J. 2006. Fledgling production and population trends in Finnish common eiders (*Somateria mollissima mollissima*)—evidence for density dependence. *-Canadian Journal of Zoology*, **84**: 1038-1046.
- HARRELL, F. E. 2001. *Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis*, Springer.
- HAUKIOJA, E. 1969. Mortality rates of some Finnish passerines. *-Ornis Fennica*: 171-178.
- HOEKMAN, S. T., MILLS, L. S., HOWERTER, D. W., DEVRIES, J. H. and BALL, I. J. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. *-Journal of Wildlife Management*, **66**: 883-900.
- HOLYOAK, D. 1971. Movements and mortality of corvidae. *-Bird Study*, **18**: 97-106.
- JENKINS, D., WATSON, A. and MILLER, G. 1964. Predation and red grouse populations. *-The Journal of Applied Ecology*, **1**: 183-195.
- JONES, D. D., CONNER, L. M., WARREN, R. J. and WARE, G. O. 2002. The effect of supplemental prey and prescribed fire on success of artificial nests. *-Journal of Wildlife Management*, **66**: 1112-1117.
- KREBS, C. J., BOONSTRA, R., BOUTIN, S. and SINCLAIR, A. R. E. 2001. What drives the 10-year cycle of snowshoe hares? *-BioScience*, **51**: 25-35.
- LAURILA, T. 1989. Nest site selection in the common eider *Somateria mollissima* - differences between the archipelago zones. *-Ornis Fennica*, **66**: 100-111.
- LOMAN, J. 1980. Reproduction in a population of the hooded crow *Corvus cornix*. *-Holarctic Ecology*, **3**: 26-35.
- LOMAN, J. and GORANSSON, G. 1978. Egg shell dumps and crow *Corvus cornix* predation on simulated birds nests. *-Oikos*, **30**: 461-466.
- LUGINBUHL, J. M., MARZLUFF, J. M., BRADLEY, J. E., RAPHAEL, M. G. and VARLAND, D. E. 2001. Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *-Journal of Field Ornithology*, **72**: 556-572.

- MARZLUFF, J. M. and NEATHERLIN, E. 2006. Corvid response to human settlements and campgrounds: Causes, consequences, and challenges for conservation. *-Biological Conservation*, **130**: 301-314.
- MATSON, C. W., FRANSON, J. C., HOLLAND, T., KILPE, M., HARTO, M., FLJNT, P. J., and BICKHAU, J. W. 2004. Evidence of chromosomal damage in common eiders (*Somateria mollissima*) from the Baltic Sea. *-Marine Pollution Bulletin*, **49**: 1066-1071.
- MELHJ, M. F. 1991. Egg predation in a breeding colony of the Common Eider *Somateria mollissima* in Kongsfjorden, Svalbard. *-Skogtyer Norsk Polarforsknings*: 37-45
- MILNE, H. 1974. Breeding numbers and reproductive rate of eiders at Sands of Berwick National Nature Reserve, Scotland. *-Ibis*, **116**: 135-154.
- MUNKELJORD, A., HAUGJE, E., FORKEDAL, S. and KVITNES, AND, A. 1985. Nest density, breeding habitat and reproductive output in a population of the hooded crow *Corvus corone cornix* on Karmøy, SW-Norway. *-J. V. AGRICULTURE, SER. C*, **8**: 1-8.
- NEATHERLIN, E. A. and MARZLUFF, J. M. 2004. Responses of American crow populations to campgrounds in remote native forest landscapes. *-Journal of Wildlife Management*, **68**: 708-718.
- NEWTON, I. 1998. *Population limitation in birds*. Academic Press
- NOEL, J. L., JOHNSON, S. R., O'DOHERTY, G. M. and BUTCHER, M. K. 2005. Common eider (*Somateria mollissima* ssp. *nigrum*) nest cover and depredation on central Alaskan Beaufort Sea Barrier Islands. *-Arctic*, **58**: 129-136.
- NORDSTRÖM, M., HÖGMÄNDER, J., VAINI, J., NUMMELIN, J., VANETTI, N. and KORPUNLÄKI, E. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. *-Biological Conservation*, **109**: 359-368.
- PARKER, H. 1984. Effect of corvid removal on reproduction of willow ptarmigan and black grouse. *-The Journal of Wildlife Management*, **48**: 1197-1205
- PARKER, H. 1985. Effect of culling on population size in hooded crows *Corvus corone cornix*. *-Ornis Scandinavica*, **16**: 299-304.
- PARKER, H. and HOLM, H. 1990. Patterns of nutrient and energy expenditure in female common eiders nesting in the high Arctic. *-The Auk*, **107**: 660-668
- PEDERSEN, A. O., YOCOZ, N. G. and IMS, R. A. 2008. Spatial and temporal patterns of artificial nest predation in mountain birch forests. **in press**.
- PERKINS, A. L., HANCOCK, M. H., BUTCHER, N. and SUMMERS, R. W. 2005. Use of time-lapse video cameras to determine causes of nest failure of Slavonian Grebes *Podiceps auritus*. *-Bird Study*, **52**: 159-165

- RDEVELOPMENTCORETEAM. 2007. <http://www.r-project.org/>.
- RICHNER, H. 1990. Helpers-at-the-nest in carrion crows *Corvus corone corone*. -*Ibis*, **132**: 105-108.
- SÆTHER, B. E. and BAKKE, Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. -*Ecology*, **81**: 642-653.
- SANDVIK, J. 1998. *Kråkefuglene - en del av naturens mangfold*, Norsk Ornitologisk Forening.
- SCHNEIDER, M. F. 2001. Habitat loss, fragmentation and predator impact: Spatial implications for prey conservation. -*Journal of Applied Ecology*, **38**: 720-735.
- SHAFFER, T. L. 2004. A unified approach to analyzing nest success. -*The Auk*, **121**: 526-540.
- SINCLAIR, A. 1989. *Population limitation in animals*, Blackwell Scientific Publications, Oxford.
- SMEDSHAUG, C. A., LUND, S. E., BREKKE, A., SONERUD, G. A. and RAFOSS, T. 2002. The importance of the farmland-forest edge for area use of breeding Hooded Crows as revealed by radio telemetry. -*Ornis Fennica*, **79**: 1-13.
- SOH, M. C. K., SODHI, N. S., SEOH, R. K. H. and BROOK, B. W. 2002. Nest site selection of the house crow (*Corvus splendens*), an urban invasive bird species in Singapore and implications for its management. -*Landscape and Urban Planning*, **59**: 217-226.
- STATISTISKESENTRALBYRÅ. 2008. http://www.ssb.no/english/subjects/02/02/folkendrhist_en/tables/tab/1902.html.
- SULLIVAN, B. D. and DINSMORE, J. J. 1990. Factors affecting egg predation by American crows. -*Journal of Wildlife Management*, **54**: 433-437.
- SUMMERS, R. W., PROCTOR, R., THORTON, M. and AVEY, G. 2004. Habitat selection and diet of the capercaillie *Tetrao urogallus* in Abernethy Forest, Strathspey, Scotland. -*Bird Study*, **51**: 58-68.
- SUYDAM, R. S., DICKSON, D. L., FADELY, J. B. and QUAKENBUSH, L. T. 2000. Population declines of king and common eiders of the Beaufort Sea. -*The Condor*, **102**: 219-222.
- SWENNEN, C., URSEM, J. C. H. and DUIVEN, P. 1993. Determinate laying and egg attendance in common eiders. -*Ornis Scandinavica*, **24**: 48-52.
- TURCHIN, P. 1995. *Population regulation: old arguments and a new synthesis*, Academic Press, Sandiego.
- UNDERWOOD, A. J. 1994. On beyond BACI: Sampling designs that might reliably detect environmental disturbances. -*Ecological Applications*, **4**: 3-15.

- USFWS. 2005. The U.S. Fish and Wildlife Service's focal species strategy for migratory birds measuring success in bird conservation
- VUORISALO, T., ANDERSSON, H., HUGG, T., LAMMINEN, R., LAAKSONEN, H. and UJIKKAINEN, J. 2003. Urban development from an avian perspective: causes of hooded crow (*Corvus corone cornix*) urbanisation in two Finnish cities. *Landscape and Urban Planning*, **62**: 69-87
- WATSON, M. D., ROBERTSON, G. J. and COOKE, F. 1993. Egg-laying time and laying interval in the common eider. *The Ibis*, **95**: 869-878.
- YOCOZ, N. G., ERIKSTAD, K. E., BUSTNES, J. O., HANSEN, S. A. and TVERAA, T. 2002. Costs of reproduction in common eiders (*Somateria mollissima*): an assessment of relationships between reproductive effort and future survival and reproduction based on observational and experimental studies. *Journal of Applied Statistics*, **29**: 57-64.
- YOVI-TOIV, V. 1974. Effect of food and predation on breeding density and success, clutch size and laying date of crow (*Corvus corone*). *Journal of Animal Ecology*, **43**: 479-497.

