Nest predation in declining populations of common eiders Somateria mollissima: an experimental evaluation of the role of hooded crows Corvus cornix

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Nest predation in declining populations of common eiders *Somateria mollissima*: an experimental evaluation of the role of hooded crows *Corvus cornix*

Jennifer Stien, Nigel G. Yoccoz & Rolf A. Ims

We evaluated the effect of the removal of hooded crows *Corvus cornix* on common eider *Somateria mollissima* nesting success using a partial Before and After Comparison of Impact (BACI) design over three years in two eider breeding colonies (Håkøya and Grindøya) in northern Norway. These breeding colonies had over the last decades been subject to severe declines in number of breeding birds and it was suspected that increasing nest predation by crows was contributing to the declines. Eider nesting success was monitored in both colonies during 2006-2008. Crows were removed by live-trapping from Håkøya in 2007 and from Grindøya in 2008. We monitored the number of nesting pairs of crows and general crow activity. Crow removal was generally successful in reducing the number of established territorial and visiting crows. Modelling of daily nesting success probabilities according to a logistic exposure model revealed that eider nests found at the start of the season had a much lower probability of success than nests found later on in the season. This is likely to be due in part to the increase in number of active nests during the first half of the season. The effect of crow removal appeared to differ between the two colonies. Eider nesting success on Håkøya increased from 61% in the pre-removal year 2006 to 80% during crow removal in 2007 and declined to 74% in the post-removal year 2008. In contrast, nesting success on Grindøya remained constantly low (38-40%) during the same period. This difference between the two colonies could be explained by a difference in predation pressure, or by a higher general disturbance level on Grindøya making unattended nests vulnerable to predation by a range of alternative predator species acting compensatory to the removal of crows. New investigations should be undertaken to clarify the interaction between crows and other nest predators in determining eider nesting success. Where compensation appears to occur, conditions for this process should be investigated. This will help to indicate when crow removal can be effective and which other actions can be employed to increase common eider nesting success.

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Predation is the main cause of mortality in many bird populations (Newton 1998), it may limit population growth and cause population regulation (see reviews in Sinclair 1989 and Turchin 1995). Several generalist predator species may concentrate on the same target prey population (Jenkins et al. 1964, Crabtree & Wolfe 1988, Jones et al. 2002), and such behaviour may be accentuated when prey is present in vulnerable life stages, e.g. during reproduction (Ims 1990). Bird populations are particularly vulnerable during the nesting period with predation being shown to be the main cause of nest loss (Martin 1993). Generalist predators can maintain a population at a reduced stable size through prey switching (Begon et al. 2006). Furthermore, generalist predators may act to accelerate declines of populations due to anthropogenic disturbances and thus contribute to increasing the likelihood of population

extinction (Bell & Merton 2002). Certain generalist predators may themselves also benefit from anthropogenic disturbance. For instance, human settlements may provide reliable food resource subsidies for generalist predators, which thus increase in numbers and exert predation pressure on prey populations (Schneider 2001, Neatherlin & Marzluff 2004). Many experimental studies involving the removal of single generalist predator species have been carried out over the years (e.g. Chesness et al. 1968, Bolton et al. 2007, see review in Côté & Sutherland 1997). However, many factors appear to be involved in molding the effects of such removals. Examples of such modifying factors are breeding densities (Gunnarsson & Elmberg 2008), compensatory effects of other predator species (Baines et al. 2004) and interactions with other stressors acting upon breeding birds (e.g. Martin 1993, Criscuolo et al. 2000, Trust et al. 2000, Hanssen et al. 2005). Only experiments conducted in different contexts can clarify the relative role of such modifying factors.

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 (Yom-Tov 1974, Coombs 1978). It is a main predator of birds' eggs and young (Sullivan & Dinsmore 1990, Mehlum 1991, Andrén 1992, Luginbuhl et al. 2001) and is sometimes targeted as a pest species, especially in game bird industries wishing to maximise fledging success (Coombs 1978). Human settlements often provide subsidies for crow populations allowing larger than expected numbers to be present in an otherwise poor food resource location (Soh et al. 2002, Chace & Walsh 2006, Marzluff & Neatherlin 2006). Some removal experiments have shown that the nesting success of ground nesting birds increases when crows are removed (e.g. Baines et al. 2004); however, control of other predators may also be necessary to reduce compensatory predation (Côté & Sutherland 1997, Baines et al. 2004, Bolton et al. 2007).

Eider colonies in Scandinavia and the Arctic can be subject to high levels of nest predation from a range of species (Ahlén & Andersson 1970, Gerell 1985, Mehlum 1991, Noel et al. 2005). On the islands of Grindøya and Håkøya, in Troms county, northern Norway, the hooded crow is thought to be a main egg predator of the common eider *Somateria mollissima* (Erikstad & Tveraa 1995, Y. Pettersen, pers. comm.). Furthermore, Erikstad et al. (1993)

showed that complete clutch loss was the normal mode of egg predation in this colony, rather than partial egg loss. The current eider population on Grindøya is estimated to be between 400 and 500 pairs (Yoccoz et al. 2002), and the Håkøya population is between 200 and 300 pairs (J. Stien, unpubl. data). Both colonies were historically much larger than at present. In the 1950s, when both colonies formed part of a widespread Norwegian coastal industry of down and egg collection, there were 1,000-2,000 pairs and > 600 pairs on Håkøya and Grindøya, respectively (E. Olsen and Y. Pettersen, pers. comm.). At that time, the colonies were protected from predators by local landowners (Y. Pettersen, pers. comm.). Thus although the cause of the decline of the common eider is unknown, increased nest predation pressure is a probable factor, as the local focus on predation control has declined over the last 30 years. In addition, crow nest predation pressure on the colonies could well be elevated by food subsidies from the growing City of Tromsø, which presently has a human population of about 60,000 (Statistics Norway 2009) and a nearby rubbish sorting depot from which crow flocks forage daily.

In this study, we tested the hypothesis that nesting success of eiders on the two neighbouring colonies of Håkøya and Grindøya is improved when crows are removed experimentally by intensive live-trapping. In three breeding seasons (2006-2008) we monitored eider clutch size, date of nest initiation and success or failure of nests in order to assess nesting success on the two colonies. The removal of crows followed a partial BACI design (Before and After Comparison of Impact; Underwood 1994). On Håkøya, 2006 was a pre-removal season, whilst crows were removed in 2007 and post-treatment effects of removal were recorded in 2008. On Grindøya, a pre-treatment year occurred in 2006, whilst in 2007 the colony acted additionally as a control for treatment effects on Håkøya. In 2008, crows were removed from Grindøya whilst Håkøya acted as the control site. No post-treatment year was undertaken on Grindøya. In all years we recorded the number of breeding crows and their breeding success, and in the year of removal the general activity of crows at both islands was quantified to assess the effectiveness of crow removal. Presence of other avian predators, along with mammalian egg predators was recorded to investigate the potential for compensatory predation in the absence of crows.
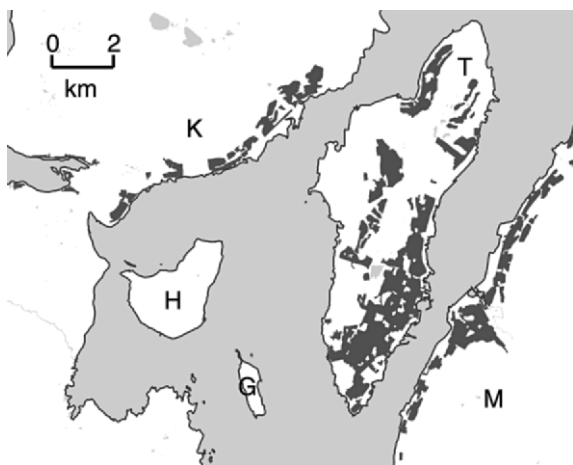
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Figure 1. The study areas of Grindøya (G) and Håkøya (H) in relation to the growing city of Tromsø situated on the island of Tromsøy (T). Shaded areas on land refer to densely populated areas on Tromsøy, Kvaløy (K) and the Norwegian mainland (M).

Material and methods

Common eider colonies

Grindøya and Håkøya are two small islands (of 65 ha and 361 ha, respectively) situated 2 km from each other along the coast of northern Norway at 69°38'N, 18°52'E and 69°39'N, 18°49'E (Fig. 1). Both islands are low-lying with mosaic of open and wooded areas. The whole of Grindøya was used in our study as it was combined with nests used for research studies on other aspects of eider breeding biology by NINA (Norwegian Institute for Nature Research). On Håkøya, we used the northern part of the island, as the area is of a similar size to Grindøya (64 ha and 65 ha, respectively), and holds the majority of the eider colony (J. Stien, pers. obs.). Håkøya has a settlement of approximately 60 dwellings and several low intensity farms, whilst Grindøya has three holiday huts along the coastline which are now seldom used. Both islands are located only 2-3 km from urban areas of the city of Tromsø. Grindøya is a nature reserve with one of the largest concentrations of breeding eiders in the vicinity of the city. The Grindøya colony has been subject to several studies of common eider breeding biology (e.g. Bustnes & Erikstad 1993, Erikstad & Tveraa 1995, Yoccoz et al. 2002, Hanssen et al. 2005), so the breeding success over a period of years before our study was known. Access to the general public is limited on Grindøya between 1 May and 30 June to limit disturbance to the eider colony. There is little movement of breeding eiders away from Grindøya

to neighbouring areas (Bustnes & Erikstad 1993), and eider hatching success seems to have been relatively stable over the last 10 years. The colony has been decreasing, which has occurred in association with decreasing female survival over recent years (Anker-Nilssen et al. 2008). Potential nest predators other than crow observed on both islands are the greater black-backed gull *Larus marinus*, herring gull *L. argentatus*, raven *Corvus corax*, white tailed eagle *Haliaeetus albicilla*, American mink *Mustela vison*, otter *Lutra lutra* and stoat *Mustela erminea*.

Common eider nest success monitoring

Searching for eider nests in the colony areas (see Fig. 1) commenced at the onset of breeding in both colonies between 15 and 22 May (the onset differed slightly between years). Nest locations were marked with plastic tape fixed around nearby vegetation. In total, 582 eider nests were located and monitored over the three years. The monitoring period ended between 28 and 30 June in the different years. All nests were revisited within two days of nest finding. Due to logistical constraints and combined effort with another study on breeding biology on Grindøya (S.A. Hanssen, unpubl. data), the monitoring schedule differed somewhat between the islands. The nests on Håkøya were monitored most frequently, i.e. every second day until nest completion, in an attempt to document cause of predation. The nests on Grindøya received up to three subsequent visits over the seven days following nest discovery in order to determine maximum clutch size. On these first three visits the birds were not handled. Nests with a known lay-date received up to six visits after maximum clutch size was recorded. On the fifth day of incubation (five days after the last egg had been laid) the birds were caught, ringed and weighed, and on day 20 they were caught again and reweighed. Visits 3-6 consisted of recording nest outcome and colour marking the successfully hatched chicks. On Håkøya, birds were disturbed from the nest during incubation in order to determine clutch size, but not subsequently. Lay-dates could not be established for 31% of all nests as these nests either failed before a subsequent increase in egg number could be recorded, or were found after laying was complete. However, they were included in the nesting analysis, as they contribute valuable information when estimating nesting success (Johnson 2007). In 2006, nests of unknown lay-date received *ad hoc* visits. In

2007 and 2008, nests of unknown clutch size received six visits during 3-30 June.

On both colonies, all nesting data based on the 3,018 nest visit intervals were used to model the average daily nesting success (i.e. active or failed) for each island in each year. We followed 543 nests to completion of the nesting attempt and used the data to calculate the colony nesting success (i.e. the proportion of nests where at least one egg hatched) for each island in each year. In addition to nesting outcome, we recorded the number of eggs in each nest at nest discovery (initial clutch size) and the maximum number of eggs laid in each nest (maximum clutch size). Maximum clutch size was calculated as the unchanged clutch size recorded on two subsequent visits (Yoccoz et al. 2002).

Where nests failed on Håkøya, the cause of failure was recorded whenever possible. Small fragments from eider egg remnants were recorded as a sign of mammalian nest predation (Summers et al. 2004). Eggs found with a single hole or split into two parts were recorded as a sign of bird nest predation (Brown et al. 1999, Summers et al. 2004), but 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 & Göransson 1978, Summers et al. 2004).

Monitoring and manipulation of crow numbers

The most intensive monitoring of crows was conducted in the two years of crow removal (2007 and 2008), whereas only the number of nesting pairs and their breeding success were registered in 2006. Crow monitoring was aimed at recording breeding pairs as well as general activity including flocks of non-breeding birds. Territorial crows and their nests were recorded whilst walking weekly transect lines spaced 80 m apart through all woodland in the two study areas. Sightings of ≥ 3 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.

In 2006, transects were carried out between 6 May and 24 June on Håkøya. In 2007, when removal of crows was undertaken, transects were walked five times before eider nesting began (during 24 April - 16 May 2007) in order to record territories where trapping would take place. Based on the experience

from this first trapping year, the number of these early (eider pre-breeding) transect walks required to locate territories on Håkøya was reduced to three in 2008 (during 27 April - 14 May). Crow territory location transects were subsequently walked over the course of the eider breeding season at weekly frequencies during 2007 and every five days in 2008. Due to logistical constraints of accessing Grindøya during late winter, crow transects began later than on Håkøya, with location of territories being achieved over two transect repetitions during 12-16 May, commencing on 13 and 12 May in 2007 and 2008, respectively, and continued to the end of the eider breeding season with the same frequency as Håkøya in respective years.

Crow removal was carried out under approval by the Directorate for Nature Management (reference 2007/1327 ART-VI-JAA 2008/4341 ART-VI-ID). We set out 10 Larsen Traps (Game Conservancy Trust 2007) on 14 May on Håkøya in 2007 and Grindøya in 2008 in order to remove territorial pairs and roaming birds utilising each area. Each trap is compartmentalised, allowing the housing of a caught crow in order to initiate a territorial response of a territory holder, increasing the likelihood that it would enter a neighbouring compartment and also be caught. Placement of traps reflected crow territories held within the study area and/or copses situated within the main eider monitoring area. 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.

The effectiveness of crow removal on crow activity was assessed by undertaking 12 paired watches on both islands between 19 May and 29 June in 2007 and between 20 May and 27 June in 2008. Watches of one hour duration were undertaken for each island 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 undertaken from a boat anchored approximately 300 m from the high-tide line of each area in light to medium breeze and dry conditions or light showers.

Other predator activity

Tree nesting predatory birds were recorded during crow nest transects in all years, whilst the maximum count of large gull nests obtained from two counts,

the first during the end of May and the second during mid June, were used to give a rough estimate of gull colony size and distribution. After sightings of stoat on both islands in 2006, stoat activity was monitored in both areas during 2007 and 2008 using tracking tunnels adapted from Graham & Lambin (2002). We set out 17 tracking tunnels in the study area on Håkøya and 16 on Grindøya during 12-16 May. Positioning of tracking tunnels reflected areas of dense eider nesting. Tunnels were checked weekly throughout the eider breeding season for tracks, and papers and ink were renewed when necessary. Scat piles of otter located in the study areas were checked weekly and used as evidence of otter presence.

Statistical analysis

Statistical analysis was performed using software R 2.4.1 ® Development Core Team 2008). All estimates are given with standard errors unless otherwise stated.

Eider clutch size
Eider nests are vulnerable to predation throughout the nesting attempt (Erikstad et al. 1993). Where the main predators are crows or gulls, predation mostly occurs when nests are unattended (Mehlum 1991, Swennen et al. 1993). Eiders leave their nest for up to three days at the start of egg laying with full attendance starting from the second or third egg (Hanssen et al. 2002). During incubation, females leave their nests for short periods every 1-3 days in order to drink (Mehlum 1991, Swennen et al. 1993). In addition, Erikstad et al. (1993) showed that females with larger clutches tended to have higher survival than those with smaller clutches. Thus, if the nests were discovered at different stages of laying between colonies and years and with different clutch sizes, our estimate of nesting success could be biased. To investigate if such biases were present in our data, we applied log-linear models with a Poisson distribution, first to the number of eggs found in the nest upon nest discovery and second to the clutch size at completion of egg laying. Predictor variables were day (after 15 May), area (i.e. colony) and year. We compared models containing the interactions between day and area and day and year (i.e. indicative of area or year biases) to models containing the variables day, area and year. We used Akaike's Information Criteria (AIC; Burnham & Anderson 2002) to select the best model.

Eider nesting success
We analysed eider nesting success on Håkøya and Grindøya by applying a logistic exposure model (Shaffer 2004) to the nest visitation data. The most complicated model contained the interactions between area and year, day and area, day and year, day^2 and area, day^2 and year, whilst the minimum model contained area, year, their interaction and the predictor variable day. The focal term, which is indicative of an effect of crow removal, is the interaction between area and year. We based our model selection on AIC (Burnham & 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 $(x_{ij, j=1,\ldots k})$ using the logit link function g(i):

$$g(s_i) = \log_e\left(\frac{s_i}{1 - s_i}\right)$$
$$= \beta_0 + \beta_1 x_{t1} + \beta_2 x_{t2} + \cdots + \beta_k x_{tk} \qquad (1).$$

This formulation ensures that estimated values for s_i are in the range of 0-1. The daily survival probabilities can be back-calculated from the estimated regression coefficients using:

$$s_i(x) = \frac{e^{\beta_0+\beta_1 x_{t1}+\beta_2 x_{t2}+\cdots+\beta_k x_k}}{1 + e^{\beta_0+\beta_1 x_{t1}+\beta_2 x_{t2}+\cdots+\beta_1 x_{t1}}} \qquad (2),$$

where x_{ij} refers to the predictor variables day, day^2, area and year. The data available contain observations of nest survival over the time period from one nest visit to the next. Assuming constant daily survival over 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:

$$\theta = s^t \qquad (3a),$$

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

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

$$h(\theta) = \log_e\left(\frac{\theta^{1/t}}{1 - \theta^{1/t}}\right) \qquad (4).$$

When using this link function the estimated parameters in the fitted regression equations relate directly to the daily survival probability s following

equation 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_i, where nest survival (y_i) was coded as 0 for failed nests and 1 for surviving nests (y_i = binomial ($p = \theta_i$, $n = 1$)).

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. χ^2 test with df $=8$ was used to assess the fit of observed to expected values.

Crow activity

The number of crows observed in each of the 12 paired watches per year and area was analysed in a log-linear regression model to evaluate the effect of the removal on the general activity of crows. Because the dispersion was larger than expected compared to a Poisson distribution, the observed crow numbers were analysed using quasi-likelihood and the variance function $Var_i = qE_i$, where E_i and Var_i are respectively the mean and variance of the activity index for area i and q is a proportionality parameter (Burnham & Anderson 2002).

Results

Eider clutch size

Mean clutch size on nest discovery and on completion of egg laying (n = 581) was 3.16 $\pm$ 2.09 (range: 1-9) and 4.25 $\pm$ 1.09 (range: 1-9), respec-

tively. Although the most appropriate model for number of eggs at first visit included both interaction terms (i.e. day*area and day*year), the interaction effects were too small to have a sizeable biasing effect on our estimates of nesting success (day*area coefficient estimate for Grindøya was 0.045 $\pm$ 0.001 and for Håkøya 0.040 $\pm$ 0.002; day*year coefficient estimate was 0.036 $\pm$ 0.001 for 2007 and 0.038 $\pm$ 0.001 for 2008). The most appropriate model for complete clutches included only the intercept (adding the variable day to the constant model did not lower the AIC value, $\Delta = 1$). Thus there was no supportive evidence that for a given day there was an area or year effect on the maximum clutch size.

Eider nesting success

Hatching success over the three years on Grindøya was approximately constant and substantially lower than on Håkøya, which had a temporally variable hatching success over the years (Table 1). 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 (Table 2). The model fitted the data well (Hosmer Lemeshow χ^2-test: $\chi^2 = 7.71$, P = 0.46, df = 8). The interaction was due to nests on Håkøya having a higher probability of daily nesting success in 2007 than in 2006 (Fig. 2A). The nature of the season effect is shown in Figure 2B. The daily probability of success increases sharply before reaching an asymptote which for Grindøya in all years is about 9 June (day 40), whereas for Håkøya the asymptote is reached earlier, by about 30 May (day 30).

Cause of eider nest failure

Cause of failure of nests on Håkøya was difficult to ascertain in 2006 and 2007 (eight out of 20 nests with

Table 1. Summary of the monitoring and removal of hooded crows and common eiders from Grindøya and Håkøya during 2006-2008. Number of crow nests shows the number of breeding attempts of which those that were successful are shown in parentheses.

| Area | Year | Crows | | | Number of eider nests | | Breeding success (%) ($\pm$ se) |
| | | Number | | | | | |
		of nests	removed	seen per hour ($\pm$ se)	Hatched	Total	
Grindøya	2006	4 (3)	-		52	135	38 $\pm$ 4
	2007	4 (3)		26.5 $\pm$ 6.1	62	159	39 $\pm$ 4
	2008	6 (2)	15	13.2 $\pm$ 4.2	47	117	40 $\pm$ 5
Håkøya	2006	5 (1)	-	-	30	49	61 $\pm$ 7
	2007	3 (0)	10	5.8 $\pm$ 1.8	36	45	80 $\pm$ 6
	2008	1 (1)		10.6 $\pm$ 3.2	28	38	74 $\pm$ 4

Table 2. Model selection for analysis of common eider nest survival data. Scaled values of Akaike's Information Criteria (AIC) and Akaike's weights (w_i) are presented for three logistic exposure models. The ΔAIC values are expressed in relation to the best fitting model.

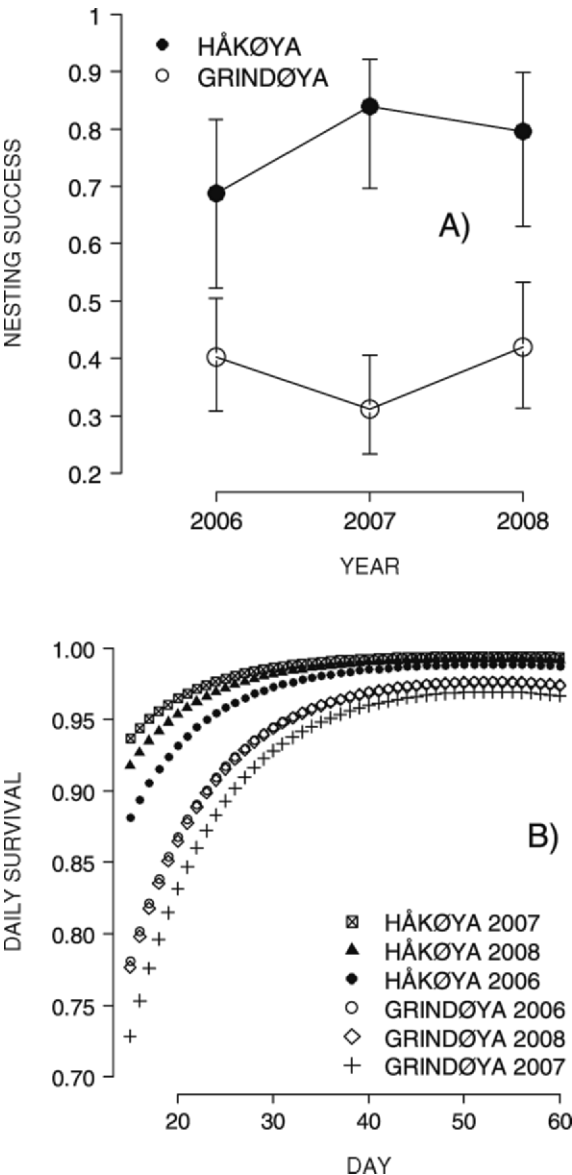|	Model	AIC	Δ AIC	w_i
1	Area, year, day, day^2, area*year, day*area, day^2*year, day*year, day^2*area	1755.15	3.31	0.16
2	Area, year, day, day^2, area*year	1751.84	0.00	0.83
3	Area, year, area*year	1808.54	56.70	< 0.0001

Figure 2. Predicted nesting success at Grindøya and Håkøya from the best logistic exposure model. A) shows the back-transformed coefficient estimates and 95% C.I. for the area*year effect with nesting success expressed as an average for the eider nesting period of 28 days (assumes average clutch size of four and average incubation period of 24 days; adapted from Erikstad et al. 1993). B) shows the estimated daily survival from all nests on the two islands during 2006-2008 with day 1 = 1 May.

cause known and three out of nine nests, respectively). In 2008 cause of failure could be determined in seven out of 11 nests. Most failed nests were found empty with no sign of predator presence at the next visit. Although the number of nests with known cause of failure is small, there were relatively fewer nests predated by birds in 2007 and 2008 than in 2006 (Table 3).

Crow numbers and removal

Table 1 summarises the results of the monitoring and the removals of crows. The number of territorial crow pairs and nesting attempts at the onset of the breeding season ranged between four and six on Grindøya and one and five on Håkøya over the three study years (see Table 1). Most of the nesting attempts failed in the years of crow removal because most of the territorial birds were removed. Two of the nesting pairs on Grindøya in 2008 showed no interest for the traps and bred successfully. Nesting attempts could, however, fail (e.g. on Håkøya in 2006) even in years of no crow removal (see Table 1).

The watches of crow activity following the removal of birds showed that in 2007 Grindøya had on average > 4 times higher activity of crows per hour than Håkøya (see Table 1). The best model for the effects of crow removal on crow activity included a significant interaction between area and year owing to opposite signed year contrasts (2007-2008) for the colonies (Grindøya: -0.69 ± 0.33, P = 0.04; Håkøya: 1.30 ± 0.60, P = 0.03, df = 42) indicating that crow trapping in 2008 reduced activity

Table 3. Cause of known nest failure for nests on Håkøya during 2006-2008. [a] indicates that one nest was predated by both a bird and a mustelid, [b] indicates that an adult female was found killed near the nest, and [c] that nests were empty with nest linings ripped out.

	Cause of nest failure				
Year	Bird	Mustelid	Deserted	Unknown	Total
2006	5	2	1	12	20
2007	1[a]	1[b]	1	6[c]	9
2008	2[a]	3	1	5[c]	11

considerably on Grindøya compared to 2007. Activity levels on Grindøya during the crow removal treatment were at a similar level to Håkøya activity in 2008. Crow transects, activity watches and casual sightings revealed very little sign of flock activity in the two study areas. No flocks were observed on Håkøya during the study period. On Grindøya, no flocks were observed in 2006, whilst in 2007 one flock of seven crows was seen on the shore on Grindøya during eider nest checks. In 2008 two flocks were seen, the first consisting of 12 crows on 17 May and the second consisting of 21 crows on 18 May.

Other predator presence

No stoat activity was registered by use of stoat tunnels on Grindøya in 2007 or 2008. On Håkøya no activity was registered in 2007, however, in 2008 1-4 tunnels were active during the study period. Large gull nest counts revealed a colony size of between 20 and 25 on Grindøya in 2007 and 2008, whilst on Håkøya the colony size varied between 18 and 20 during the same period, with between seven and nine nests in the vicinity of the eider study area itself. Gulls were distributed over several open areas on both islands and the overall pattern did not change between years. A pair of white-tailed eagles nested on Håkøya within the study area in all years, whilst a pair of ravens nested within the Håkøya study area in 2007 and on Grindøya in 2008. New otter spraints were present throughout the whole study period in 2006 and 2007, whilst in 2008 there were very few spraints found on both islands. On Grindøya several caches of adult female eider carcasses characteristic of mink predation were found throughout the breeding season in 2007 and 2008, whilst a few carcasses of adult male or female eiders were found in open areas of the island.

Discussion

Efficiency of crow removal

The pre-removal densities of breeding crows in our study were among the highest recorded in the literature for rural and island habitats in Fennoscandia; 6.15 nests km^{-2} for Grindøya and 7.81 nests km^{-2} for Håkøya (*cf.* Loman 1980, Erikstad et al. 1982, Munkejord et al. 1985, Parker 1985). Crow trapping reduced both the number of territorial nesting crows and the general crow activity in both of the studied eider colonies. Similar crow removal success has been recorded in long-term studies of nest predation

of willow ptarmigan *Lagopus lagopus*, black grouse *Tetrao tetrix* and capercaillie *Tetrao urogallus* (Parker 1985, Summers et al. 2004). Re-colonisation by breeding pairs on Håkøya in 2008 was not rapid, suggesting that recruitment into vacant breeding territories at this location was not high in 2008. This is in agreement with the results presented by Parker (1985) and Summers et al. (2004), who also recorded depressed number of territories following trapping in previous years.

Presence and effects of other predators

Although we have no direct evidence of predation events, we assume that the majority of the events were primarily due to egg loss during nest absence. Egg predation in the presence of the incubating female could be carried out by mammalian predators (i.e. mink and otter) as well as birds of prey (e.g. white-tailed eagles), but would then be expected to result in incidents of adult female predation. The small number of carcasses in the colonies or signs of kills at nests indicate that predation of incubating females occurred infrequently. Besides crows, large gulls were the numerically most abundant predator in both breeding colonies. Although gulls can be a major predator of eider eggs (Mehlum 1991, Noel et al. 2005) studies exist to show that eiders nesting within gull colonies have higher nesting success due to nest defence responses of gulls to general predators (Gerell 1985, Götmark & Åhlund 1986). Thus, we cannot be conclusive regarding the role of large gulls in our study.

Area and time dependant predation rate

It appears that different processes control nest predation in the two studied eider colonies. Nest predation was not compensated by other predators in the year of crow removal on Håkøya and thus it appears that crows had a measurable effect on this colony's nesting success. However, on Grindøya, which generally had a much higher predation rate than Håkøya, the experimentally reduced activity of crow had no effect. In lack of specific data regarding which predators were responsible for the high nest losses on Grindøya, we can only speculate about what could have caused the difference between the two eider colonies. Eider nest density was higher on Grindøya than on Håkøya, but whether this difference led to differences in predator detection probabilities or predator defence is unclear. The effect of nest density on nest survival is balanced by the opposite effects of predator attraction (causing nega-

tive density dependence) and predator dilution (causing positive density dependence; Ims 1990). Ahlén & Andersson (1970) and Mehlum (1991) have shown that eiders breeding at high densities have lower predation rates than those breeding at lower densities. However, Gunnarsson & Elmberg (2008) found the opposite effect for mallards *Anas platyrhynchos*. Which of the two opposing processes is dominating can be expected to be determined by the specific functional response and the mobility of the predators in question (Ims 1990). Thus a possible interpretation of the lack of response to crow removal on Grindøya is that some of the other predators present responded rapidly and compensated for the removal of crows. Indeed, the general impression from our observation of predators is that predator numbers and activity levels were generally higher on Grindøya than on Håkøya.

Another difference between the two colonies that may have influenced the outcome of our experiment is the level of disturbance to which nesting eiders were exposed. The probability of nesting failure is likely to be proportional to the length of time eiders leave their nest unattended. Thus a higher level of compensatory predation may have been facilitated by a higher level of nesting disturbance on Grindøya. Bolduc & Guillemette (2003) have shown that human disturbance can have a negative effect on eider nesting success. Thus, the ultimate cause of constantly low nesting success on Grindøya could be disturbance which then creates a constant window of opportunity for predators. This would result in crows being an efficient predator species even when present at low densities. When crow numbers are reduced, a relatively larger number of other predator species can compensate to maintain a constant level of nest predation.

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 southwestern Sweden (Götmark & Åhlund 1986), and glaucous gull *Larus hyperboreus* predation on eider nests in Svalbard (Mehlum 1991). In contrast, (Milne 1974) showed that the proportion of eider nests being destroyed in a northeastern Scottish colony by carrion crow *Corvus corone* and herring gull increased as the season progressed.

Predation effect on eider population

Small island populations of birds can be subject to extreme predation pressure (Bell & Merton 2002). In the case of the common eider, site philopatry is high (Bustnes & 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 & Bakke 2000). In the case of the Grindøya population adult female survival has declined from an average > 80% during 1986-2002, to < 70% between 2003 and 2006 with the lowest level of 51% for 2004-2005 (Anker-Nilssen et al. 2007, 2008). Whether this is due to increased mortality within or outside the nesting period is not clear, as we do not know whether proportion of carcasses found on the island represents adult true nesting mortality. However, in the light of the long-term decline of this population, reproductive parameters might be more sensitive to predation or environmental variability than adult survival (Gaillard & Yoccoz 2003), overriding the difference in sensitivity between reproductive and survival parameters. Thus, reproductive parameters may be important to the population growth rate in terms of impacts of predation. Indeed, in an analysis of eider population trends using a time series of 57 years, Hario & Rintala (2006), 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 that of other sea duck species (Andersson & 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 a ground nesting duck, the mallard (Hoekman et al. 2002). Bell & Merton (2002) and Bolton 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. However, as shown in our study the effect of such management actions targeting one predator species may not be efficient everywhere.

Conclusion

Our study demonstrated generally contrasting nesting success and responses to crow removal in two nearby eider colonies in northern Norway both of which have over the last decades been subject to severe declines in number of breeding birds. While eider nesting success appeared to respond positively to crow removal in a colony with a generally high nesting success (Håkøya), the nesting success was not improved by reducing the number of crows in the other colony (Grindøya) which generally had much lower breeding success. On Grindøya, other processes apparently compensated for the expected reduction in crow predation. Possible explanations could be that crows are not important predators of eider nests on Grindøya, or that disturbance is the ultimate cause of nest predation, allowing compensatory predation by other predators present in the colony. Crow trapping can therefore not be expected to be an effective management action for conservation of all declining populations of common eider. Further investigation should be undertaken to determine the role of differing predator species on eider nesting success by for example use of photographic evidence. This will help to indicate when crow removal can be effective and which techniques can otherwise be employed in order to successfully improve eider nesting success.

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