UiT
THE ARCTIC
UNIVERSITY
OF NORWAY

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS

Nest predation in birds of conservation concern

Case studies of monitoring and management

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Jennifer Stien

A dissertation for the degree of Philosophiae Doctor – April 2015

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A dissertation for the degree of Philosophiae Doctor
UiT – The Arctic University of Norway
Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology
Spring 2015

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Front cover:

Common eider (J. Stien) and Slavonian grebe (K.B. Strann) attend their nests.

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List of original papers

Paper I

Stien, J., Yoccoz, N.G. and Ims, R. A. 2010. Nest predation in declining populations of common eider (*Somateria mollissima*): an experimental evaluation of the role of hooded crows (*Corvus cornix*). Journal of Wildlife Biology (16), 123 – 134. doi: http://dx.doi.org/10.2981/09-060

Paper II

Stien, J. and Ims, R.A. Negative effects of human disturbance on nest success in declining eider colonies in northern Norway. In Review: IBIS

Paper III

Stien, J. and Ims, R.A. 2015. Management decisions and knowledge gaps: learning by doing in a case of a declining population of Slavonian grebe (*Podiceps auritus*). Journal of Wildlife Biology (21), 1, 44 - 50. doi: http://dx.doi.org/10.2981/wlb.00026

Paper IV

Stien, J., Strann, K.B., Jepsen, J., Frivoll, V. and Ims, R. A. Breeding persistence of Slavonian grebe (*Podiceps auritus*) at long-term monitoring sites: Predictors of a steep decline at the northern European range limit. In Review: Journal of Ornithology

Paper V

Stien, J. and Hausner, V.H. (manuscript). Volunteer hunter motivation and engagement to control the invasive alien American mink (*Neovison vison*) in Norway.

Abstract

In this thesis, I explored management options aimed at increasing breeding success of vulnerable species of ground nesting birds in Norway. Appropriate conservation management varies between species and between systems due to their differing and often complex abiotic and biotic interactions. To gain experience in working in this context dependent and multifaceted field, I used case studies of nest management of 2 species, common eider (*Somateria mollissima*) and Slavonian grebe (*Podiceps auritus*) in 2 different, but connected ecosystems; coastal and lacustrine.

In papers I to III, I explored the management actions of increasing nesting success in coastal nesting common eider and lacustrine nesting Slavonian grebe, and discussed whether these management actions could achieve the goal of halting the declines in these populations. In papers I and II, I investigated the reasons for nest failure of common eider. In paper I, I used the *a priori* hypothesis based on casual observation, that the hooded crow (*Corvus cornix*) was responsible for nesting failure, and carried out a crow removal experiment to test this. Using the results from paper I to define the scope of an observational study for paper II, I investigated the processes of nesting failure in common eider in order to find potential management actions that could increase nesting success in the study area. The combined results from papers I and II indicated that crows were the main proximate cause of nesting failure while human disturbance was the ultimate cause of nesting failure. Furthermore, the results indicated that decreasing nesting failure was potentially manageable by decreasing disturbance during nesting time and/ or guarding of nests while incubating females were absent from nests. These management actions should be tested in order to see if they can halt the declines in the local eider colonies.

In paper III, I used the *a priori* hypothesis that the invasive alien species American mink (*Neovison neovison*) was an important cause of nest failure of Slavonian grebe and carried out a series of experiments using an adaptive management approach. The hypothesis was based on a non-empirically assessed risk of factors pertinent to the decline of the Norwegian population and the observation that mink were present in the study system. The results from the study indicated that mink was unlikely to be a significant cause of nesting failure in the study system. The study further indicated a relevant framework for finding management solutions in the maze of management possibilities, where key system information and time to implement management is lacking. Based on the results from paper III, the knowledge that very few breeding grebe remained in northern Norway and availability of annual breeding data from a monitoring program in this region, I carried out a longitudinal study for paper IV in order to investigate pertinent factors in the apparent regional decline of the species. The results indicated that the grebe breeding population had declined steeply over the two last decades. Breeding

site persistence was positively related to the number of breeding pairs in the initial year of monitoring and in the final year of the data was negatively related to altitude. Testing of appropriate management is some way off, since there is a lack of understanding of the pertinent factors involved in population dynamics of the species in Norway or any other areas of its distribution. Furthermore, in Norway there is no monitoring of grebe population trends at the national level.

In paper V, I investigated the potential to engage hunters in large-scale and collaborative efforts to control mink populations in Norway. I used a questionnaire to examine the conservation support for-, and the level of efforts to remove mink expressed by mink hunters. I supplemented this with information gathered about current mink control projects and municipal paid bounty. The results suggested that state-led efforts are best concentrated around "conservation hotspots", involving contract operators, bounty payments and awareness and recruitment programs. Few hunters were interested in mink control but those participating believe that mink is a conservation concern and particularly to ground nesting birds, suggesting that these popular species could be used to attract more hunters. As mink catch varies from low to high, control will probably require organization of hunter networks acting at an appropriate scale. Control projects could benefit from carefully targeted bounty payments as there was both a positive relationship between payment of bounty with the number of mink caught and was the main recommendation of hunters to make mink hunting more appealing to hunters.

1. Introduction

1.1 What are birds of conservation concern?

According to the IUCN Red List of Threatened Species, birds of conservation concern include species with a relative high risk of extinction. Criteria to assess this risk include small and / or declining populations with the decline assessed in terms of threshold proportional losses of their national or global population (Kålås et al. 2010). Depending on the scale of assessment, global or national, and the distribution of the species, holarctic or regional, the same species may have dual status as of conservation concern or not of conservation concern. In addition to the threat of imminent extinction, changes in ecosystem functioning and ecosystem processes due to large-scale declines of common species not yet applicable for Red List inclusion indicate that common species can also be of conservation concern (Inger et al. 2015). Thus, birds of conservation concern can be considered as potentially any bird population with a declining trend, with the decline being determined by the scale of the species population trend assessment.

1.2 Can nest predators cause declines in bird populations?

In stable populations, the number of sub-adults exceeds the breeding population, allowing a high mortality rate from multiple sources without leading to a decline in breeding populations. However, nest predation can be a significant determinant of population dynamics, especially in ground nesters (Martin 1993, Ibánez-Álamo et al. 2012), and as such has the potential to both limit and regulate populations (Sinclair 1989, Newton 1998). Long-lived birds tend to have low annual productivity with occasional bonanza years, suggesting that low nesting success is of little consequence to population stability in these species (Gaillard et al. 2000, Coulson 2010). However, prolonged low productivity in long-lived species has been shown to result in declining populations (Hario and Rintala 2006, Reiertsen et al. 2013) suggesting that mortality due to predation may be important.

Generalist predators may have the ability to maintain prey populations at low numbers via prey switching (Redpath and Thirgood 1999, Šálek et al. 2004, Valkama et al. 2005, Begon et al. 2006, Matthiopoulos et al. 2007), thus preventing prey from escaping density dependent predation. This not only has an impact on the adult population but also on the reproductive effort of predated individuals. Furthermore, predation pressure by generalist predators may be exacerbated by anthropogenic effects (Schneider 2001, Neatherlin and Marzluff 2004). An extreme case is that of introduced generalist predators, as non-dependence on one particular prey combined with prey naivety, rapid predator population growth, high dispersal ability and density-dependent survival result in negative effects for many prey populations (Park 2004, Bonesi and Palazon 2007).

1.3 How should we investigate and mitigate nest predation in declining bird populations?

1.3.1 General approaches: Adaptive management and monitoring

Conservation involves the intervention in focal species ecology in order to prevent their decline and potentially to reverse this decline; i.e. management. Before we manage, we must decide what it is we need to manage. Should we modify the habitat in which the species resides, or should we modify some aspect of its ecological interactions (competition, predation), or should we do a combination of both in order to increase in population size? More often than not, we are faced with little or no knowledge of the pertinent processes in focal species ecology and at what life state the population is most sensitive to decline and/ or increase. We can learn about these processes from observational and experimental studies based on ecological theory and *a priori* hypotheses. We can use modelling, before empirical studies to reduce uncertainty in likely relevant parameters or estimates and underway incorporate new knowledge into these models. Observational studies may be informative in suggesting pertinent factors helpful to conservation management but lack the power of experiments to test whether manipulation is effective i.e. cause and effect. Effects measured in experiments can be informative to suggest management actions, but these effects are often not transferable to larger scale where management is practiced due to context dependent and cross scale effects (e.g. Castilla 2000). Furthermore, modifying the environment modifies the interactions with potential unforeseen consequences (Ruscoe et al. 2011, Norbury et al. 2013). Walters and Holling (1990) suggested the use of an adaptive management framework to inform management. This framework treats management actions as scientific experiments at management scale, allowing robust testing of effectiveness of experimental interventions and reducing structural uncertainty. Furthermore, it incorporates knowledge gained during the trials to modify the direction of future investigation and is considered a ‘learning by doing’ process as opposed to ‘ad hoc’ trial and error. Thus, it is a learning framework that can cope with dynamic (changing) systems. Learning is a two-phase (loop) process initialized by institutional learning also involving process learning, and an iterative phase involving monitoring, assessment and decision-making (Williams 2011).

Equally important as the spatial scale of investigation is the temporal scale, as salient factors change as uncertainty in the system is reduced. The adaptive monitoring framework (Lindenmayer and Likens 2009) incorporates the approach of the adaptive management framework and also emphasizes the importance of long-term monitoring designed to answer pertinent questions relevant to management. Research questions should be explicitly linked to management needs with the ability to incorporate learning into future direction and changing management goals. The introduction of the framework was a response to the wide-scale failure of monitoring programs to remain relevant to management objectives. Potential pertinent factors are explicitly represented by a conceptual model, thus maintaining focus on the management objective. Adaptive monitoring shares the essential characteristics of adaptive management; i.e. reducing structural uncertainty by large-scale experimentation based on a priori based hypothesis and double loop learning. However, the double loop learning is in the evolution of questions designed and does not involve an institutional learning phase (Lindenmayer and Likens 2009).

Regardless of the approach used to investigate population decline, being able to monitor the response in question is vital in order to provide baseline data for measuring future change (observational study), or to measure the response to a perturbation or a human intervention (observational, experimental study, adaptive management and monitoring) (Lindenmayer and Likens 2009). In order to test management interventions, monitoring should be carried out both before and after the perturbation in an experiment design, the so called Before and After Comparison Investigation (BACI) design (Underwood 1994). In nest predator removal, a variety of monitoring methods exist for monitoring both the effect of removal on predators on predator numbers and the effect of predator removal on target populations, including observational counts, camera trap, or track traps (e.g. Graham and Lambin 2002a, Reynolds et al. 2004, Richardson et al. 2009).

1.3.2 Nest predator removals: An option for adaptive management of declining bird populations?

Predator removal has been successful in cases where nest loss due to predation is additive to other causes of mortality, and has led to increases in the number of hatching, fledging and breeding individuals (e.g. Chesness et al. 1968, Côté and Sutherland 1997, Bolton et al. 2007, Smith et al. 2010, Hanssen et al. 2013). These studies have been both small - and large-scale, however none have been published as, or mentioned as an adaptive management or monitoring approach. According to predator- prey theory (Holling 1959), the resulting increase in population size may lead to its escape from predator regulation, even when predators are no longer managed. Many predator removal studies fail to show such a population increase and attainment of new equilibrium. The lack of expected prey population response to predator removal can be due to compensatory predator mortality through inefficient management (Côté and Sutherland 1997) or changing systems leading to novel predator species, or other forms of compensatory mortality including disease and starvation (Camphuysen et al. 2002, Hario and Rintala 2006). Alternatively, lack of philopatry by breeding females could result in the lack of direct numerical increase (Pieron et al. 2013).

1.3.3 Finding solutions to implementing efficient management

Research-based management may well find salient factors underlying population decline and ways in which manipulation of these can be implemented to have desired objectives to halt the decline of target populations. However, by the very nature of the large scale of species distributions and the number of species of conservation concern, implementation can be a considerable challenge. Control of established invasive alien species is a particular example where large-scale management is required and has become a responsibility for individual states (EU 2014). Invasive species are responsible for the loss of species diversity that in turn can lead to alteration and degradation of ecosystems (Baillie et al. 2004, Poorter et al. 2007, Simberloff et al. 2013) and are estimated to cost Europe at least 12.5 billion euros per year (Kettungen et al. 2008). Invasive alien species, such as mammalian predators, can exert negative effects via novel predation strategies on native prey species that have not had time to evolve successful predator avoidance strategies, which in many cases eventually have caused local extinctions (e.g. Atkinson 2001, Didham et al. 2005). Management of established invasive alien species is based on the goal of control, due to the recognition that distribution is too large and recolonization likelihood is too high to be able to eradicate the species at a national scale (EU 2014). This does not remove the requirement of management occurring at large scale, as small-scale action is likely to result in harvesting rather than control. Thus, inclusion of non-professional volunteers in a coordinated campaign can be a key method of attaining sufficient temporal and spatial scale and could significantly improve current invasive alien species removal (Gosling and Baker 1989, Bremner and Park 2007, Bell and Vanner 2011, Bryce et al. 2011).

One approach for control is for governments to invest in harvest incentives (i.e. *government based programs*). These may include i) *bounty programs* that give participants monetary rewards based on sufficient evidence of removal; ii) *contract operators* in which public or private organization are directly paid to remove or harvest the invasive species; iii) *recreational harvest* facilitated by training, education and outreach programs or by iv) encouraging harvest of the targeted species by *regulatory modifications* such as changing hunting seasons, licensing practices or bag limits.

As control of established invasive alien species is a long-term strategy, the retention of a sufficient volunteer pool is a key element for successful *volunteer based control programs*. Volunteers have diverse motives for participating in volunteer projects that also include personal benefits such as sociality and knowledge gain, in addition to the apparently obvious aiding conservation (Asah and Blahna 2012). In addition, deeper held beliefs and values may influence whether invasive alien species management is successful (Sharp et al. 2011, Fischer et al. 2014). Fulton et al. (1996) indicate that in western countries values regarding wildlife range along a continuum from domination to mutualism and that these values are important for explaining differences in acceptability of lethal control in particular. Thus, invasive alien species management may well recruit volunteers with different motives than other conservation stewardship programs. Investigation of volunteer motivations and values may therefore lead to tailoring of programs that are likely to be successful.

2. Scope of the thesis

In this thesis, I used 2 ground nesting species, the common eider (*Somateria mollissima*), a coastal breeder and Slavonian grebe (*Podiceps auritus*), a lacustrine breeder as case studies of the role of nest predation in population decline. Both species have large Holarctic distributions. However, the grebe was red-listed in Norway between 2006 and 2010 and there is still uncertainty over its population trend. The eider has experienced national declines and specifically the study colonies have experienced dramatic recent declines. A key aim of my study was also to investigate whether local predator removals could be effective for both species. In addition, I investigated the use of volunteer hunters in reducing the mink (*Neovison neovison*) predation (nest and adult) of ground nesting sea birds on a national scale. The specific questions I addressed were:

1. Does removal of hooded crow (*Corvus cornix*) result in an increase in common eider nest success at declining eider colonies?

2. What are the processes determining nest predation at declining common eider colonies?

3. Does a reduction in American mink increase the nesting success of Slavonian grebe?

4. What factors are involved in the decline in persistence of Slavonian grebe breeding sites at the northern edge of its range?

5. Do volunteer hunters have the potential to aid state managed mink control in populations of ground nesting sea birds, and how?

3. Study design and sampling methods

3.1. Papers I and II

3.1.1. Study area for papers I and II

The study area for papers I and II consists of two small low-lying islands Grindøya and Håkøya 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 (Figure 1). The whole of the Grindøya (65 ha) was used while on Håkøya 64 ha of a total 361 ha was used. Both islands are located 2 - 3 km from urban areas of the city of Tromsø. Grindøya is a nature reserve with the largest concentration of breeding eider in the vicinity of the city. Both islands are low-lying with mosaics of open and wooded areas consisting of heath, mire and mountain birch (*Betula pubescens)*. Håkøya has in addition, areas of grazed farmland and a settlement of approximately 60 dwellings (in 2006), whilst Grindøya has 3 coastal cabins that are now seldom used. Sheep have grazed the entire island of Grindøya annually between early June and the end of October since 2007. Access to the general public is limited on Grindøya between 1 May and 30 June to limit disturbance to ground nesting birds, particularly eider.

Both eider colonies are in long-term decline. The population on Grindøya has decreased steeply from over 500 pairs in 1995 to c.150 pairs in 2009 and onwards (Erikstad et al. 2010). Adult female survival decreased from > 80 % between 1986 – 2002 to a low of 53% in 2005 with the decrease in 2002 and continued low survival being attributed to mink predation of incubating females (Erikstad et al. 2009, 2010). Nest failure is as high as 62 % (Stien et al. 2010). The Grindøya colony has been the site of annual long-term monitoring since 1985 by NINA (Norwegian Institute for Nature Research) and is a key monitoring site in the Norwegian seabird monitoring program (SEAPOP). Data regarding Norwegian mainland vital rates for eider come from this colony, and the population is the source for a host of ecological, evolutionary and behavioural studies (Erikstad et al. 1998, Hanssen et al. 2002, Hanssen et al. 2003d, Hanssen et al. 2006). It is also a key site in terms of education, providing data for several PhD and Masters studies. The Håkøya colony has been the focus of low intensity annual nest monitoring since 2006. The colony is a remnant of an active eider down colony with an estimated population of over 600 nesting individuals (Olsen pers. comm.) in the middle of last century. The study area contained at least 49 nesting individuals in 2006, which decreased to 26 in 2011. Individual nest fates are followed but not individual females. Disturbance from other human activity was limited during the study period 2006 – 2011 as the colony area was little used during the study period. Nest failure is up to 39 % (Stien et al. 2010).

Predator communities on Grindøya and Håkøya are fairly similar, consisting of mostly large gulls (herring gull *Larus argentatus* and to a lesser extent greater black-backed gull *L. marinus*), hooded

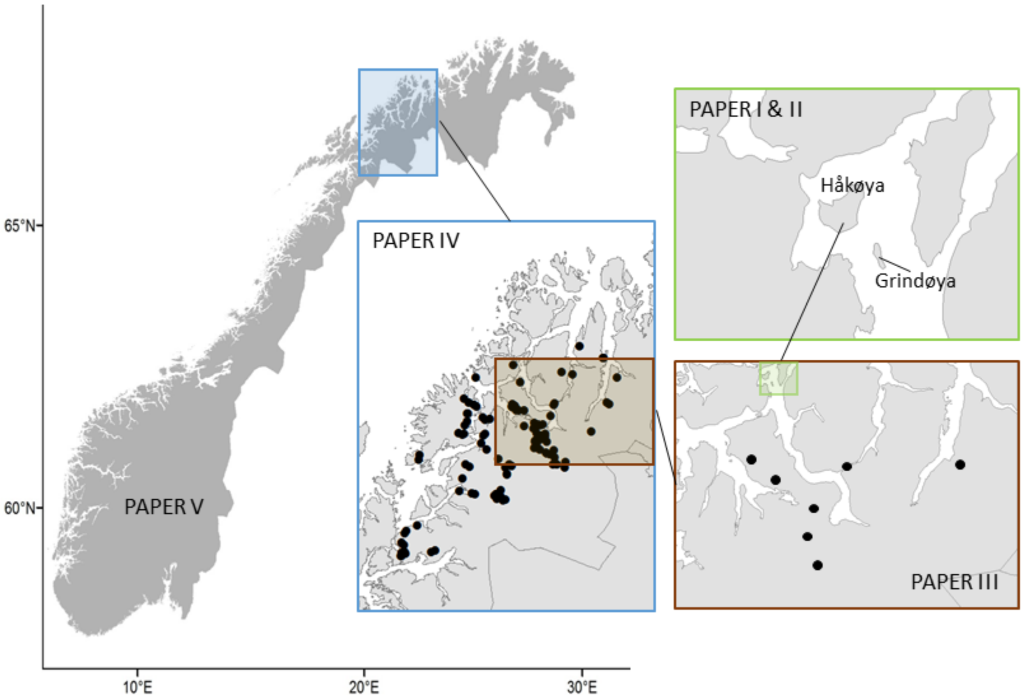

Figure 1. Study areas for the five papers in the dissertation. PAPER I & II show the location of eider colonies for the investigation of nest predation; PAPER III shows the location of Slavonian grebe breeding lakes for the investigation of mink predation; PAPER IV shows the locations for investigation of the decline in persistence of Slavonian grebe breeding lakes; and PAPER V shows the extent of mainland Norway, the scale used for the investigation of volunteer collaboration predator control management.

crow, raven (*Corvus corone*), white-tailed eagle (*Haliaeetus albicilla*), otter (*Lutra lutra*), mink (*Neovison vison*) and in addition on Håkøya, stoat (*Mustela erminea*). The occurrence of mink is sporadic, having been recorded in the Håkøya colony in 2006 and in the Grindøya colony from 2002 until 2009. The avian predators are nest predators apart from white-tailed eagle that takes adult birds on the open sea. Of the mammalian predators, stoat is a nest predator, mink predates both incubating females on the nest as well as eggs and young, while otter has not been observed predating adults or nests at either colony. At the time of the study initiation in 2006, hooded crow and herring gull were assessed as the most important nest predators (Erikstad and Tveraa 1995)

3.1.2. Study design for papers I and II

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 the Norwegian Institute for Nature Research (NINA). On Håkøya, we used the northern part of the island as it holds the majority of the eider colony (J. Stien, pers. obs.) and used a similar area to Grindøya (64 ha and 65 ha, respectively). Protocols on Grindøya followed the basic monitoring protocols used for long term monitoring by NINA researchers and nest search effort was coordinated in order to reduce disturbance to nesting birds. Research activity was intensive involving a high degree of disturbance especially during egg laying and hatching. Protocols carried out on Håkøya involved minimal disturbance as the goal was to observe nesting success only. Nests were searched for between 15 – 22 May (the onset of the breeding season varied slightly between years) and 5 June. Monitoring of nesting outcomes carried on until 28 - 30 June. The initial clutch size was used as a proxy of investment and or/ likelihood of survival at time of nest discovery. Maximum clutch size was recorded on Grindøya by revisiting the nest every 2 - 3 days until no new eggs were laid (Erikstad et al. 1993) and on Håkøya by revisiting the nest after calculating the revisit date as that allowing for a maximum of 6 eggs to be laid (Watson et al. 1993).

Study design specific to paper I

We used a BACI (Before and After Comparison Impact; Underwood 1994) design to investigate the effect of crow removal on nesting success. The nesting success of eider nests was monitored at both colonies in each of the study period years 2006 to 2008. In 2007, crows were removed from Håkøya and in 2008 were removed from Grindøya. The effect of crow removal on crow activity in each year was measured by carrying out paired colony watches of crow activity.

After eider egg laying was complete, the nests on Håkøya were monitored every second day in order to try to identify predator species. Nests on Grindøya were monitored up to 6 times after maximum clutch size was observed. These visits included catching and ringing on days 5 and 20 of incubation and checking for hatching success after day 20 of incubation. Nests of unknown lay date on Grindøya received *ad hoc* visits in 2006 and 6 visits between June 3 and 30 in 2007 and 2008. We followed 543 eider nests to completion (i.e. where at least one egg hatched) and used the data to estimate nesting success. We used a logistic exposure model to estimate daily nesting success, with the interaction between colony and year as the predictor and colony, year, Julian day, initial clutch size (t_0) and maximum clutch size as covariates.

The number of territorial crows was recorded at both colonies in all years of the study, using transects spaced at 80 m intervals to locate territories and thereafter the territories were searched to locate the nests. Transects were walked between 24 April and 16 May (the onset varied slightly between years). On Grindøya, transects started on 12 May due to logistical constraints of reaching the island earlier. Larsen Traps were used to trap territorial pairs of crows. We assessed the effectiveness of crow removal by monitoring crow activity at both colonies using paired counts (carried out in successive days at each colony and at the same hour) over a range of times during the breeding season. We used log-linear regression with Poisson distribution and interaction colony*year to predict the number of crows at each colony.

The activity of other predator species was monitored in all years by recording aboreal nesting predators during eider nest searches, and gull numbers by two counts one at the end of May and one during mid – June. Stoat activity was recorded in 2007 and 2008 by weekly checking of tracking tunnels laid out on a grid system across the study areas between 12 – 16 May (Graham and Lambin 2002). Sixteen tunnels were used on Grindøya and 17 on Håkøya with positioning reflecting high-density areas of eiders.

Study design specific to paper II

We monitored the nesting success of a total of 1003 eider nests at both colonies between 2006 and 2011. At 205 of these nests, we deployed RECONYX^{TM} cameras to allow detailed knowledge of predation events to be investigated at the nest level. At camera monitored nests, variables pertinent to eider nesting success were collected (Götmark 1989, Mehlum 1991, Hanssen et al. 2003a, Noel et al. 2005, Andersson and Waldeck 2006). These variables were initial clutch size, Julian day, nesting habitat, nesting cover, nearest neighbour distance and distance to the sea. Exploration of the camera data allowed complete nest leaving histories with nest leaving classified as either disturbance or 'natural' to be identified. Combining these nests with environmental variables gave a sample of 103 camera monitored nests to explore the effect of the contrast in disturbance rates between the 2 colonies. We used disturbance as a predictor of nesting success and natural nest leaving (recess) and the environmental variables as covariates. We controlled for the possible effects of camera deployment on nesting outcome (Richardson et al. 2009) by comparing nesting success of 41 paired camera and non-camera monitored nests at both colonies in 2009. We estimated the number of breeding crows and large gulls in all years using transects spaced at 80 m intervals over the entire area of each colony to estimate crow territories and counts during searches for eider nests to estimate gull numbers (pairs).

3.1.3. Study species for papers I and II

Common eider

The common eider is a well-studied sea duck that has been the focus of many evolutionary, physiological and ecological studies throughout its circumpolar range (e.g. Mehlum 1991, Erikstad et al. 1998, Desholm et al. 2002, Hanssen et al. 2003d, Hanssen et al. 2006, Hario and Rintala 2006, Öst et al. 2007, Coulson 2010, Wilson et al. 2012). Most studies focus on the females as males are not actively involved in nesting or raising of young (Steele et al. 2007). The eider has a circumpolar distribution with an estimated population of over 3 million individuals (Bird Life International 2015).

As such, it is listed as ‘least concern’ on the IUCN species Red List. However, the population has been in wide scale decline in recent years (Desholm et al. 2002, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Adult survival is typically high, breeding is delayed with first breeding from 2 years of age, and periodic non-breeding years occur due to high energetic costs of breeding (Yoccoz et al. 2002, Hanssen et al. 2003, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Females have high natal-, and general philopatry (Swennen 1991, Bustnes and Erikstad 1993, Hanssen and Erikstad 2012) and are short – distance migrants (Bustnes and Erikstad 1993, Camphuysen et al. 2002, Lehikoinen et al. 2006).

As a capital breeder, female condition is expected to play an important role in reproductive output and indeed recruitment. Female condition has been linked to large-scale climatic processes on the wintering areas (Lehikoinen et al. 2006, Descamps et al. 2010) and reproductive output is positively related to female condition with clutch size, hatching success and fledging success being positively related to female body mass (Erikstad et al. 1993, Erikstad and Tveraa 1995, Hanssen et al. 2003a). Further, recruitment has been linked positively to fledging success 3 years earlier (Hario and Rintala 2006). Impacts related to nest predation may also influence fledging success and recruitment, reducing the likelihood of breeding in up to 2 successive years after nest loss (Hanssen and Erikstad 2012). Nesting and fledging success may be highly variable between years (Noel et al. 2005, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012).

Eiders have a low clutch size (mean 4 eggs, range 1 - 6). They display both partial delayed onset of incubation and complete fasting during incubation, leaving the nest for short periods during incubation only in order to drink (Erikstad and Tveraa 1995). This behaviour is seen as a trade-off between food resource maintenance and predator defense (Andersson and Waldeck 2006). The predation rate of nests decreases from a high rate of 48 % for clutches of one egg to an average of 3 % from the second egg (Hanssen et al. 2002). Incubation lasts roughly 20 days (Erikstad et al. 1993). As a consequence of complete fasting, females may loose up to 40 % of their pre-nesting body mass (Parker and Holm 1990). Young are nidifugous and leave the nest after a few days, often to be cared for in crêches by several females (Öst et al. 2007).

Population declines in eiders have been attributed to reduction in adult survival (both on wintering and breeding grounds) due to unknown cause (Coulson 2010), large scale mortality due to starvation on wintering grounds (Camphuysen et al. 2002) and prolonged successive high annual mortality of ducklings due to outbreaks of viral infections (Hario and Rintala 2006, Hario and Rintala 2009). Predation of adults may also be important in causing declines (Erikstad et al. 2009). Population declines are associated with a sex-biased higher mortality rate of females, occurring both at the pre-breeding and adult stages (Lehikoinen et al. 2008, Erikstad et al. 2010). Evidence for compensating mechanisms in eider populations are equivocal. Density dependence (acting on the fledging rate) has been demonstrated in long term studies in southern Finland, though was insufficient to halt a long term decline in the population (Hario and Rintala 2006). The decline was also not compensated for by a decreased age of first breeding, with food shortage and/ or non-lethal viral infections being suggested as reasons for late maturation (Hario and Rintala 2009). In long-term studies in north east England, density dependence has not been demonstrated at any life stage (Coulson 2010). In the light of population decline and biased ratios towards males, there is also no evidence of (facultative) manipulation of sex ratios at laying or hatching stages to favour increased production of female offspring (sensu Fisher 1930).

Hooded crow

The hooded crow is a common generalist predator with a wide distribution across north, eastern and southeastern Europe and the Middle East (Coombs 1978). No estimate is available for its worldwide population size as it was until recently considered as a subspecies of the carrion crow (*Corvus corone*), and as such has been assessed as having lowest concern on the IUCN Red List (BirdLife International 2014). In Norway, the population of hooded crow is estimated to be between 200,000 and 600,000 pairs and outside of the breeding season can be legally killed. Hooded crow has delayed maturity, not breeding before 2 years old (Coombs 1978), with annual survival rate estimates of adults ranging between 48 % and 70 % (Haukioja 1969, Holyoak 1971, Loman 1980). Productivity defined as the mean number of fledglings per clutch varies between 0.72 and 3.20 (Zduniak and Kuczyński 2003). Densities of nesting pairs vary, being highest where food sources are concentrated and range between 1.6 – 1.8 km^2 for island habitats (Loman 1980, Erikstad et al. 1982, Parker 1985) and 0.3 – 9.0 pairs km^2 in rural areas (Loman 1980). The species has been recognised as a benefitting from anthropomorphic subsidies (Marzluff and Neatherlin 2006). Nesting habitat is primarily aboreal, with breeding occurring from early spring (depending on altitude) and lasts approximately 75 days from nest building to fledging of young (Coombs 1978, Zduniak and Kuczyński 2003). Crows are smart, demonstrating good cognitive ability in obtaining and securing food resources (Picozzi 1975, Sonerud and Fjeld 1987, Sonerud 2001, Neatherlin and Marzluff 2004, Marzluff and Neatherlin 2006, Melletti and Mirabile 2010). Removal studies, both experimental and observational indicate that crows may have a negative impact on nesting success but often do not due to compensatory predation by other predator species (e.g. see review in Madden et al. 2015). Thus, though appealing, this management action may be costly and fail in its goal.

3.2. Papers III and IV

3.2.1. Study area for papers III and IV

The study area for paper III is located between 69˚ 04’ and 69˚ 24’ N and 18˚ 39’ and 20˚ 20’ E III and is a sub area of the study area for paper IV which is located between 68˚30’ and 69˚43’ N and 16˚39’ and 22˚09’ E (Figure 1). Located in northern Norway in Troms and Nordland counties, the study areas consisted of 7 and 104 breeding lakes for Slavonian grebe in papers III and IV respectively. All sites were part of a long term monitoring of annual breeding success project, carried out annually since 1991 by researchers at NINA and were therefore active at the start of monitoring.

The area forms the northern range of the European population of Slavonian grebe (Fjeldså 1973a) (as well as quite possibly the northern range for the global population (Fournier and Hines 1999)) and was the former core of the breeding population in Norway. Water bodies between 0 m and 269 m above sea level are used as breeding sites. All sites were ice covered during the winter with ice melt varying between late May and mid-June. All sites were inland and fed by streams or rivers and/ or had rivers as outflows. Average (mean) water body area was 93 ha (median 19.18, range 0.34 – 1521 ha) and mean altitude was 90.98 m (median 91.00, range 0-269 m). Immediate (within 200 m of lake edges), surrounding vegetation was dominated by mosaics of mountain birch, Scots pine (*Pinus sylvestris*), mire, heath and grassland. Agricultural grassland also existed around some lowland lakes. Lake bedrock was mostly calcareous rock, with smaller frequencies of marble and occasional granite. Lakes were mostly oligotrophic with several mesotrophic and eutrophic lakes. Dominant shallow water vegetation included bottle sedge (*Carex rostrata*) and to a lesser extent bogbean (*Menyanthes trifoliata*), and provided nesting habitat for the grebe. Lake vegetation was sparse in oligotrophic lakes forming small pockets of nesting habitat, and more or less continuous in eutrophic lakes, providing continuous nesting habitat around the lake edge perimeter.

At the beginning of the monitoring period in 1991, 104 sites were occupied giving a total of 405 pairs (mean number of pairs per lake at the start of monitoring was 3.91 ± 0.24). By 2012, the site occupancy for the whole area had decreased to just 25 % of that in 1991 and the number of breeding pairs had decreased to 49 (mean 0.50 ± 0.10 per site, n = 104). A national action plan for conservation of the species assessed that decline was most likely due to a range of negative effects during the breeding period and singled out predation by mink during the nesting period as a probable factor in the decline of the Norwegian population (DN 2009). In addition to mink, other common species of the nest predator community were hooded crow, heron (*Ardea cinerea*), common gull (*Larus canus*) and otter.

3.2.2. Study design for papers III and IV

Study design for paper III

The study took place between 2010 and 2011 with 7 lakes being chosen in the same region and near each other so as to represent a single management area. Lakes were expected to be independent with respect to individual mink during their breeding season, with Euclidean distance (range 5 – 43 km) between study lakes being greater than reported mean home range for territorial males during the breeding season in freshwater habitats (Gerell 1970, Dunstone and Davies 1993). Three sequential experiments were undertaken.

Experiment 1

The first experiment involved a paired treatment and control BACI design at five lakes, whereby the activity of mink before and after trapping events was compared to the activity of mink at monitored control lakes in order to assess the effectiveness of mink passive trapping throughout the ice-free period in 2010. At each lake, 6 mink rafts were deployed at 1 km intervals to monitor mink activity (Bryce et al. 2011) weekly between ice melt (27 May – 9 June) and re-freezing (10 October). At the treatment lakes, traps were deployed initially after mink activity was recorded and from mid-July, permanently to increase chances of capturing mink. We expected mink to be active at all sites and that removal during the grebe breeding season would result in a decrease in mink activity.

Experiment 2

The second experiment proceeded in the same treatment and control lakes in early spring between 2 and 7 April 2011, while lakes were still frozen and before the arrival of the grebes. A transect was walked along each lake edge using dogs to track mink activity between 2 and 4 April. In treatment areas, discovered mink holes were excavated to remove mink and additional traps were laid and checked up to 5 days later to increase the chance of capture after activity had been recorded. We expected mink to be active at all sites and that the removal of mink would result in a decrease in the activity of mink.

Experiment 3

The third experiment focused on assessing the predation risk on grebe nests in the following breeding season in 2011. It involved camera monitoring of artificial nests in grebe nesting habitat at 7 lakes (the original 5 plus 2 additional lakes). Five pairs of nests were deployed at roughly 250 m intervals along a 1 km transect between 22 -23 June and 14 July. The first of each paired nest was equipped with an Acorn game monitoring camera (Little Acorn 5210A) while the second had none and was used to assess the effect of cameras on predation rates. Variation in predation rate between the 7 lakes was analysed with a simple logistic regression model in R with binomial distribution. The predictor variables area, altitude, river length and distance to nearest stream were entered singularly. We expected that mink would be the main predator at the artificial nests.

Study design for paper IV

We analysed data from 104 breeding sites monitored annually between 1991 and 2012. Monitoring was based on two visits each year in the period 1991-2012. The first visit was around 22 June, roughly 3 weeks after ice melt and the second between 10 and 20 July (exceptionally the end of July). Number of nesting pairs, territorial pairs and non-territorial individuals were counted in both visits from standardised observation points using binoculars and telescope. The counts of nesting pairs were used in the analysis and were expressed as a single unit of observed number of breeding pairs per lake.

Variables pertinent to breeding success were used as predictors in Cox proportional hazards models to investigate persistence in the use of breeding sites. Persistence was defined as the number of years from the onset of the monitoring to the year grebes disappeared from the site or until the end of the monitoring series in case grebes continued to be recorded during the entire 22 year monitoring period (i.e. until 2012). In the absence of lake specific data, all predictive variables apart from number of breeding pairs were proxies for habitat quality or factors that could affect breeding numbers negatively.

3.2.3. Study species for paper III, IV and V

Slavonian grebe

The Slavonian Grebe, hereafter referred to as grebe, has a circumpolar distribution mainly at 50 – 65 ˚N in the boreal climatic zone, breeding in North America, Europe and with isolated populations in Iceland, Færoes and Scotland (Bird Life International 2011). The general trend for the population is declining but due to the size (140,000 - 1,100,000 individuals) and geographical extent of the population, the species is categorised as 'least concern' on the IUCNs red list (Bird Life International 2011).

There are no detailed estimates of adult survival or age of recruitment for the grebe, however unpublished data indicates that individuals return to breed in their second year (T. Lindberg pers. comm., S. Benn pers. comm.). Breeding success ranges from 0.20 – 1.06 fledglings (large young) per pair with a mean value of 0.58 (Ewing et al. 2013). The grebe spends most of the year in marine habitat but migrates inland to breed between May and September. Breeding can occur in both freshwater and brackish water and in a wide range of lakes sizes, with sites (< 10 ha) common in north America and the Baltic and a larger range of site area used in northern Norway and Iceland (Fjeldså 1973c, Faaborg 1976, Ulfvens 1988, Ewing et al. 2013). Sites commonly have between 1-2 pairs and seldom more than 20 pairs per lake (Fjeldså 1973e, Faaborg 1976). In Norway, winter habitat is in coastal archipelago and outer fjord systems (Fjeldså 2004) with part of the population migrating as far south as the Scottish coast (Aarvak and Øien 2009). Onset of nest building is determined by ice melt and varies considerably with latitude, altitude and season (Cramp et al. 1977, Fjeldså 2004). Nests consist of floating rafts of dead plant material, constructed in shore vegetation. Diet during the breeding season consists mostly of fish by biomass but also of aerial and aquatic invertebrates (Fjeldså 1973c, Dillon et al. 2010). Young and adults migrate to the coast in September.

The Norwegian population forms the northern range limit for the species in Europe (Fjeldså 1973a). Historical records indicate that the core area in the 1970's was in northern Norway and was estimated to be c. 400 pairs (Fjeldså 1980). Although no systematic monitoring of grebe occurs on a national scale, regional scale monitoring of core sites in Troms and bordering Nordland reveals a decrease in the use of breeding sites compared to when monitoring began in 1991 (Strann and Frivoll 2010, Strann et al. 2014). National declines have been reported in neighbouring countries with an estimated 54% decline between 1972 and 1996 in Sweden (Douhan 1998) and strong negative population change index since 1997 in Finland (Pöysä et al. 2013). In Sweden, the population appears to have increased again and in 2011 was estimated to be close to the 1972 estimate of 2200 pairs (Norevik 2014). This increase has been an accompanied by an apparent eastward shift in its range away from inland areas to areas along the Swedish Baltic coast (Norevik 2014). Declines in grebe populations have been associated with continued low breeding success (Ewing et al. 2013), deterioration in nesting habitat and increasing availability of new habitat (Douhan 1998). The Icelandic population is increasing and reproduction is generally higher than reported for European and American studies (T. Lindberg unpub.), without the drivers of the population dynamics being known.

American mink

American mink, hereafter referred to as mink is an invasive alien species in 28 countries in Western Europe, having established wild populations from escaped individuals from fur farms or, in Russia from purposeful releases for hunting (Bonesi and Palazon 2007). Mink predation causes negative effects on many native prey species in European countries and as such it has been a target of several control campaigns (Bonesi and Palazon 2007).

The species inhabits semi-aquatic coastal and inland wetland systems (Halliwell and Macdonald 1996, Ahola et al. 2006), living at higher densities in coastal habitats than inland habitats (Gerell 1970, Dunstone and Birks 1983, Helyar 2005), presumably due to the greater availability of prey in coastal habitats (Dunstone and Birks 1987, Bonesi et al. 2000). Mink are generalist predators eating a wide range of aquatic and terrestrial prey (Dunstone and Davies 1993a).

Males are polygonous, with territories overlapping those of several females (Yamaguchi et al. 2004). While males range widely during the breeding season, female territories are established by late winter (February – March). Females reproduce once a year, in spring (April - June), are central foraging feeders for 5 weeks while kits are young (Gerell 1971, Dunstone and Davies 1993a, Yamaguchi and Macdonald 2003). During autumn, territories break up and family parties and adult males roam over large areas (Dunstone and Davies 1993a, Yamaguchi and Macdonald 2003). Dispersal occurs mostly along wetland corridors (Gerell 1970, Birks and Linn 1982, Bryce et al. 2011) but can also occur over land. In coastal habitats in Fennoscandinavia, dispersal is aided by winter ice (Kauhala 1996). Mountain chains and stretches of open water over 2 km appear to be effective barriers or filters to encroachment on new areas (Kauhala 1996, Craik 1997, Zalewski et al. 2009). Effective dispersal results in rapid establishment of new populations (Bevanger and Henriksen 1995, Bonesi and Palazon 2007).

Mink populations in several countries appear to have peaked and are now on a decline (Bonesi and Palazon 2007), suggesting that the invasive population has reached carrying capacity. Rapid colonisation of recently cleared areas indicate that there is still a surplus of individuals produced in neighbouring areas and that density dependent processes may operate. The occurrence of 7 year population peaks in Iceland suggest delayed density dependence may also be a feature of mink population dynamics (Einarsson et al. 2006). The occurrence of density dependence makes control programs more difficult as removal results in increased growth rate of the remaining population (Pasko et al. 2014). Source areas are probably coastal habitat, with dispersal to inland areas, at least at a small scale (Bodey et al. 2010). There is little information on either survival or age of first breeding for mink.

As an invasive species, mink has few natural predators and competitors. Red fox (*Vulpes vulpes*), white-tailed eagle and eagle owl (*Bubo bubo*) predate mink in unknown numbers. White-tailed eagle may also cause mink to alter feeding patterns and area use, and otter can outcompete mink (Bonesi and Macdonald 2004, Salo et al. 2008). However, otter and mink can co-exist, especially in coastal areas (Christensen 1995, Harrington et al. 2009).

No systematic monitoring of mink or the effects of mink removal on mink numbers and focal prey species have been undertaken in Norway. However, casual observations clearly indicate that mink can have a devastating effect on ground nesting seabirds (Stien et al. 2011). There is also a considerable population in Norway as between 5100 and 6700 mink were reported caught between 2002 and 2013 (SSB 2013b). Several grass roots initiatives in coastal areas suggest that successful removal of mink leads to an increase in focal prey species (Stien unpub.). Key factors in the successful removal of mink appear to be removal after territory establishment (Craik 1995), removal on a scale that is larger than the dispersal distance of a mink (Helyars 2005, Bryce et al. 2011) and removal over repeated years to remove reinvasions from neighbouring populations.

3.3. Paper V

3.3.1. Study design for paper V

We made a questionnaire (Questback) available via the internet to all members of the Norwegian Association of Hunting and Angling (NAHA) regarding the 2012 hunting season to investigate the prospects of engaging hunters in large scale and collaborative efforts to control mink populations in Norway. Specifically, we investigated the potential for establishing harvest incentive based mink control.

Hunting effort

The variables belief, motivation, and whether hunters received bounty payments were used to predict hunting effort which was measured by the 2 dependent variables number of mink caught-, and number of days hunting during 2012. We used hierarchical agglomerative clustering to create classes of belief, motivation and leadership and log-linear regression with Poisson error to estimate hunting effort. We predicted that consumptive motivated hunters would catch larger numbers of mink than those with more appreciative motives. We also expected that hunters receiving bounty payments would catch more mink than those not receiving bounty payments due to the incentive of economic reward. We included beliefs as a covariate in order to control for heterogeneity in respondent beliefs.

Conservation attitudes

We expected mink hunters with more utilitarian wildlife values and who hunted primarily for consumptive reasons to be more oriented towards the protection of fish and game species (sensu Kaltenborn et al. 2012). Mink hunters expressing stronger caring beliefs for animals were expected to shoot or trap mink primarily because of biodiversity protection (i.e. Red List species). We examined the relationship between beliefs, motivations and conservation attitudes using cross tables.

Leadership

We used hierarchical agglomerative clustering to form the classes of desired leadership. We used cumulative logistic models to predict the effects of belief and motivation on predict leadership classes. We expected hunters with social and/ or recreational motives to favour government leadership and included beliefs as a covariate in order to control for heterogeneity in respondent beliefs.

Recommendations

We included an open question enabling hunters to recommend ways to make hunting easier or more appealing. We used these answers to support the results from the above analysis.

4. Results and discussion

4.1. Results and discussion for paper I and II

The nesting success of common eider increased significantly during the crow removal on Håkøya in 2007, but remained constant and low during the crow removal year on Grindøya in 2008. Thus, the hypothesis that the removal of a single nest predator species would result in an increase in nesting success was only partly supported. Equivocal effects of nest predator removal as a management option to increase nest success have been shown in other nest predator removal studies (e.g. Côté and Sutherland 1997, Bolton et al. 2007). Lack of a constant positive effect has been shown to be due to incomplete removal of targeted predator species or compensatory mortality from increased predation of non-targeted nest predator species in multi predator systems (Crabtree and Wolfe 1988, Sargeant et al. 1995, Bolton et al. 2007). Alternatively, mortality due to crow predation could have been compensated by alternative predator species. On Grindøya, there was evidence of the effects of management failure, with new nesting pairs of crow moving into vacated territories and foraging by crow pairs from neighbouring islands. We could also not exclude the possibility of compensatory predation from large gulls on Grindøya as they are also common nest predators of eiders (Milne 1974, Götmark 1989). The results from Håkøya indicated that the effects of crow removal on nesting success can be seen after cessation of management in common with other removal studies (e.g. Parker 1985). The length of this effect is likely to be dependent on prey densities and immigration rates from neighbouring areas.

The results from study I also indicated consistent and contrasting nesting success at the two colonies during the study period, with consistently high nesting success on Håkøya and consistently low nesting success on Grindøya. This could be due to inter-colony differences in eider nesting density or habitat, affecting predation rates, or differences in predator species and/ or abundances at the two colonies. Alternatively, nest loss at Grindøya could be mediated by differences in human activity at the two colonies or inherent differences in eider body condition affecting rates of nest abandonment. In either case, predation would only be the proximate cause of nest loss. The results from study I highlight that proximate and ultimate causes of nest predation are context dependent and need to be investigated at the focal scale of interest, where focal scale refers both to scales of space and time. It also indicates the usefulness of before and after comparisons and experimental design in determining appropriate management.

Study II enabled investigation of the processes involved in nest predation in the 2 two eider colonies and the unravelling of sources of context dependency that could cause the contrasting nesting success. Furthermore, the results identified management actions that can increase nesting success at both colonies. The analysis of a 6-year time period reinforced the finding of Study I that the contrasting nesting success was indeed a characteristic of the two colonies with nesting success being significantly higher at Håkøya than at Grindøya. The frequency of nest disturbance was much higher at Grindøya than Håkøya and this led to a steeply increased risk of nest failure due to predation. Thus, the results are consistent with the hypothesis that the lower nesting success at Grindøya is ultimately due to a constantly higher rate of human disturbance of nests at this colony. Negative effects of human activity on nesting success are well documented (e.g. Bolduc and Guillemette 2003, Ibánez-Álamo et al. 2012) but not necessarily always occurring (e.g. Nisbet 2000). Thus, management of breeding populations exposed to human activity should include an assessment of effects of human activity on productivity. As the management aim of the two studies was to increase nesting success at the two colonies, the results from the two studies indicate that this can be achieved by reducing human disturbance and/ or after each disturbance event guarding of the nests until incubating females return. The subsequent step in management to achieve the goal of increasing nesting success would therefore be to trial these actions to see whether they are successful.

In addition to identifying plausible options for increasing nesting success in these two declining colonies of eider (i.e. decreasing disturbance and/ or implementing nest guarding) study II also indicated that observational studies with appropriate monitoring methods are relevant to indicate pertinent factors in processes. Conservation of declining species ideally involves not just halting the decline, but also increasing population size. The options from study II allow the testing of a hypothesis aimed at management action to increase colony size at these two specific colonies, that mortality at the nest stage is additive and therefore increasing nesting success will result in increased colony size via increased recruitment. This is a big supposition for a species with nidifugous young and a subsequent stage of delayed maturity that is exposed to many forms of mortality (Hario and Rintala 2006, Coulson 2010). However, a link between high nesting success and population increase is aided by the high natal philopatry of the species (Swennen 1991) and the high breeding philopatry which has been found at the Grindøya colony (Hanssen and Erikstad 2012). As the potential benefits of increasing the stability of the local distribution of the species are high, these management options should be tested. Thus, the stepwise learning from an experimental study (study I) and an observational study (study II) provide relevant management actions aimed at increasing the robustness of two local populations. Although the results are context dependent, the stepwise learning at local scale is an approach that is highly applicable to conservation management in general.

4.2. Results and discussion for paper III and IV

Studies III and IV demonstrate how a combination of systematic methods at different scales can be informative for management of focal conservation species. We found no support for the hypothesis that mink was a significant negative factor on breeding grebe in study III. An adaptive management framework allowed us to conclude this in a short time period from a start point of no knowledge about mink ecology in Norwegian lakes and no knowledge about the reasons for the regional decline in grebe. The study thus prevented the implementation of costly inefficient and/ or inadequate management aimed at removing negative factors on breeding success of grebe in the study area, even though the removal of mink *per se* is an appealing idea due to its invasive alien predator species status. The adaptive management framework is a powerful tool that should be standard protocol for investigating suitable management options for multiple sites. It is not a new concept, having being first formulated by Holling in 1978 (Holling 1978) and later advocated and developed by many others (e.g. Park 2004, Williams 2011). In particular, the development of the monitoring component of this framework appears to be an important addition (Lindenmayer and Likens 2009). However, adaptive management and monitoring have by no means become a standard tool for tackling conservation challenges (e.g. Brownstein et al. 2014, Williams and Brown 2014).

While study III by means of an adaptive management protocol allowed us to rule out mink as a salient factor limiting the breeding population of north Norwegian grebe, another approach is needed to investigate other sources of the reported population decline. The availability of breeding persistence data consisting of annual recording of a substantial number of breeding sites over a 22 year period allowed us to use an observational time series approach in Study IV. Although the monitoring was aimed at breeding success and not population trends, the scale of change in persistence suggested a large-scale change in factors affecting grebe on the breeding grounds or on their wintering grounds. The decline involved a decrease in both persistence and the number of grebe per active site over the period. None of the habitat variables explained the decline in persistence, however persistence was significantly greater with increasing number of pairs as measured at the start of monitoring in 1991. Similar declines have been recorded in adjacent populations of grebe in Scotland and Sweden without any pertinent factors being identified (Douhan 1998, Ewing et al. 2013, Pöysä et al. 2013).

Determining the reasons for decline is hampered by the lack of demographic data. Determination of standard methodology for counting has been developed (Stien unpub.) but remains to be tested over larger latitudinal gradients and with suitable sampling methodology. Future work should also focus on determining site faithfulness of breeding individuals to determine whether the decline is determined by mortality or movement to new breeding areas. As wintering grounds of individuals are unknown, tracking of individuals to their wintering grounds could also produce pertinent knowledge of factors that could act negatively on survival during the winter season (e.g. Bogdanova et al. 2011, Delmore et al. 2012, Tranquilla et al. 2014).

4.3. Results and discussion for paper V

The general level of interest in mink control programs is surprisingly low, given that the number of small game hunters in the NAHA was more than 80, 000 in 2012 (SSB 2013a). The low response compromised the strengths of using a questionnaire approach to investigating collaborative efforts to control mink populations at a national scale. Having considered this limitation, there were some clear results that came out of the study and that can be used to determine the appropriate organisation of mink control programs and are relevant to the planning of invasive alien species programs in general.

The majority of mink hunters believed that mink is a conservation concern and particularly to ground nesting birds. Most were interested in conservation of non-red listed birds, including eider and other non-specified red listed species and is likely to reflect both the past and present Norwegian culture involving subsistence of coastal economies from down and egg collection of eiders (Soot-Ryen 1941) as well as the strong interest for grouse and ptarmigan hunting (Kaltenborn et al. 2012). Awareness campaigns for mink and generally for invasive alien species may well benefit therefore, from discovering and highlighting appealing species in areas where red listed species are targeted, in order to achieve conservation goals.

We found support for the hypothesis that mink hunters that received bounty caught more mink than those not receiving bounty, suggesting that introducing bounty as an incentive may result in an increase in mink catch. Evidence shows that well planned control programs that include bounty can be successful in invasive species control (Gosling and Baker 1989, McLeod et al. 2011, Newsome et al. 2014). The planning phase is crucial to a successful control campaign and, should take into account the appropriate spatial and temporal scale to prevent harvesting (Einarsson et al. 2006a, Bonesi and Palazon 2007, Bodey et al. 2009, Bryce et al. 2011, Pasko et al. 2014).

Contrary to expectations regarding the importance of sociality in motivating small game hunters (Andersen et al. 2008), and for hunting participation in general, we found that hunters that do not need to hunt near their home or together with friends and family caught on average more mink than hunters motivated by local hunting and social benefits. Many volunteer studies indicate that social benefits are important for being involved in and long-term participation in volunteer conservation efforts (e.g. Ryan et al. 2001, Asah and Blahna 2012) suggesting a positive relationship between volunteer retention and a sense of belonging (Selinske et al. 2015). Effective mink hunters may well therefore be ‘loan wolves’ but in common with established invasive alien species are unlikely to be able to cover the scale required to control mink in many areas. Thus, the long-term stability of initiated control programs may be higher with an element of feedback that includes the whether the goal of large-scale control has been achieved. Mink hunters that were motivated by social interactions and local hunting caught significantly fewer mink. However, these hunters can also be highly relevant to successful control campaigns at landscape scale when organized into networks (e.g. Bryce et al. 2011).

The majority of mink hunters preferred governmental-led programs rather than citizen or landowner-initiated programs. Moreover, the hunters in our survey requested a more active role by the government for providing infrastructure, bounty, trapping equipment, organize landowner permissions to hunt, and to set up recruitment and education programs to increase participation in mink hunting. Favouring top down organisation may well be a direct result of the corporatist style of governance common to all Scandinavian countries and lack of conservation organisations and representation at the local level (Dryzek et al. 2002). It has also been seen to be crucial in achieving ecological and social objectives for invasive alien species management programs in Australia (Ford-Thompson et al. 2012). Given the low interest in mink removal and the history of low participation in previous programs, efforts should initially be concentrated around “conservation hotspots”, involving contract operators, bounty payments and awareness and recruitment programs.

5. Concluding remarks and recommendations

In this thesis I have used a variety of study methods at different spatial and temporal scales to explore population processes and management of 2 bird species of conservation concern, common eider and Slavonian grebe, focusing particularly on the role of nest predation in declining populations. I have demonstrated the role of proximate and ultimate causes of nest loss in eider at 2 declining colonies and highlighted the negative effects of human disturbance on nesting success and the potential role of disturbance in decline at one of the colonies. Furthermore, using the stepwise approach of elucidating proximate and ultimate factors has indicated management actions that are highly likely to improve nesting success and may also play a significant role in halting the decline of the eider colonies. I have demonstrated the usefulness of combining investigation of focal species of conservation and targeted invasive alien predator species in order to optimize management decisions when knowledge of both species is poor. I have further demonstrated the regional decline of Slavonian grebe at the northern range of its distribution. Finally, by investigating the level of mink hunting in Norway I have demonstrated that collaborative control programs that include volunteer mink hunters are best focused on hotspots of conservation concern. I view this thesis as an example of adaptive protocols for learning by doing. In contrast to common (mis)conceptions, I have demonstrated that this approach can be undertaken with relatively little funding and resource use and is simple in its design. Thus, conservation management in general, and game management particularly in Norway should be more willing to tackle management challenges using this adaptive protocol approach.

Acknowledgements

Having finished my Masters, I was free to write a report for the Norwegian Environment Agency (NEA) about the status and ecology of-, and control strategies against American mink, together with Rolf Ims and Nigel Yoccoz. This was favourably received by the NEA and led to me writing a successful application for funding of a PhD that focused on development of adaptive management protocols to enable large-scale control of mink in Northern Norway. The PhD was designed to give experience in both research and nature management in Norway. My PhD developed, to take in the wider theme of predation and declining populations of birds and investigating management alternatives for large-scale control of mink, as it became apparent that mink were not such a big issue in the study systems I was working in. I'd like to thank Rolf Ims for initiating my lead in writing the initial report and for guiding my research development thereafter. It has been a valuable experience to work with someone with such a focused and positive outlook on events and clarity in thought; thank you for injecting enthusiasm and support into the project and myself when required. I would also like to thank Vera Hausner for coming into the project well after it started and always providing enthusiasm, support and direction in a mind-baffling arena. My nature management work experience was carried out at the Department of Environmental Protection at the Troms County Governor offices. Thank you, Heidi-Marie for guiding me through the system and for your engagement and interest in developing my experience of working in Norwegian nature conservation.

Thanks to my work colleagues at both institutions and wider afield for your good company and many discussions over the years and to Nigel, Jane, Karl-Birger and Vigdis for collaboration on the articles. Thanks to the administrative staff at UiT, particularly Ann-Kirsti, Anne Karine and Gerd Anne for providing great logistic support and thanks to Renate for your good company and competent work in the field. Thank you also to Johan for the ease at which you carried ice ridden mink rafts and traps from A to B and Mathieu for your attempts to refine my crow trap carpentry skills. Audun, Frode and Eva, you solved quite a few boat logistic challenges. Thank you for minimising lost hours in the field due to temperamental engines / disintegrating parts. Thank you to Sveinn Are, for graciously letting me nose in on the Grindøya colony, being open with-, and sharing your data and being a wealth of knowledge about common eiders. I would particularly like to thank Jane, Eva, Janne G, Heidi-Marie, Ivar, Karianne, and Siw for support and motivation during different periods where my work-life balance got disrupted. For a long while, I wasn't sure whether I wanted to, or could finish this PhD. However, I have, and feel very pleased having seen it to its end. Special thanks to Hege, for being there, and not being a scientist. The list could be endless, and would of course have to include my dog. However, this thesis has gone on long enough. Last and biggest thanks go to Torbjørn, Hannah and Audun for your company, love and support.

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Paper I

Wildl. Biol. 16: 123-134 (2010)
DOI: 10.2981/09-060

www.wildlifebiology.com

Original article

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.

Key words: common eider, Corvus cornix, hooded crow, nest predation, population trends, Somateria mollissima

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Received 29 June 2009, accepted 24 November 2009

Associate Editor: Anthony D. Fox

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.

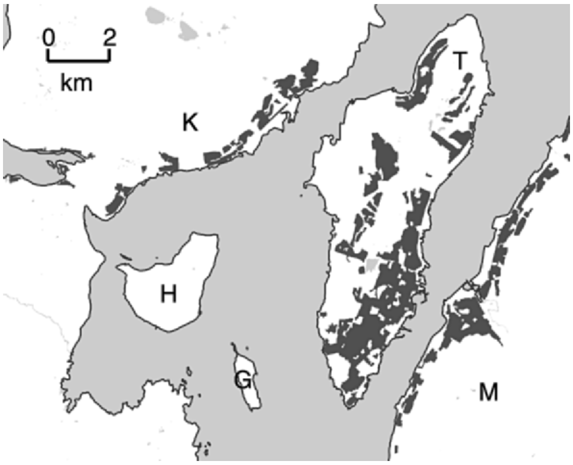

Figure 1. The study areas of Grindøya (G) and Håkøya (H) in relation to the growing city of Tromsø situated on the island of Tromsøy (T). Shaded areas on land refer to densely populated areas on Tromsøy, Kvaløy (K) and the Norwegian mainland (M).

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):

$$\begin{aligned} g(s_i) &= \log_e\left(\frac{s_i}{1-s_i}\right) \\ &= \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_k x_{ik} \qquad (1). \end{aligned}$$

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:

$$s_i(x) = \frac{e^{\beta_0+\beta_1 x_{i1}+\beta_2 x_{i2}+\cdots+\beta_k x_k}}{1+e^{\beta_0+\beta_1 x_{i1}+\beta_2 x_{i2}+\cdots+\beta_1 x_{i1}}} \qquad (2),$$

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 ($y_i = \text{binomial}\ (p = \theta_i, n = 1)$).

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 ± 2.09 (range: 1-9) and 4.25 ± 1.09 (range: 1-9), respectively. 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 ± 0.001 and for Håkøya 0.040 ± 0.002; day*year coefficient estimate was 0.036 ± 0.001 for 2007 and 0.038 ± 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.

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

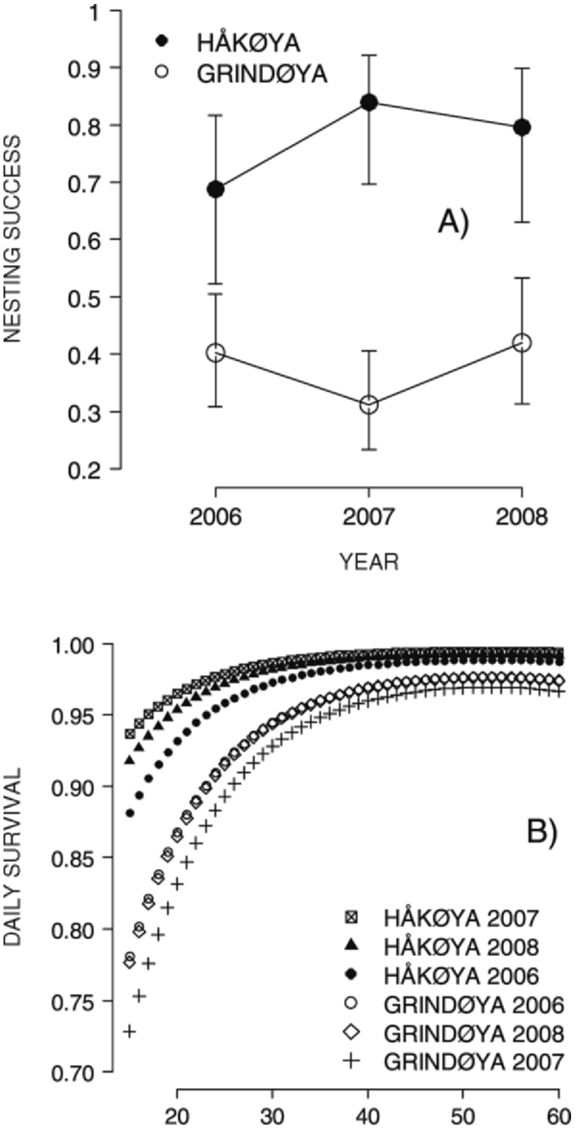

Figure 2. Predicted nesting success at Grindøya and Håkøya from the best logistic exposure model. A) shows the back-transformed coefficient estimates and 95% C.I. for the area*year effect with nesting success expressed as an average for the eider nesting period of 28 days (assumes average clutch size 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 negative 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.

Acknowledgements - we thank Sveinn Are Hanssen for providing much unpublished information on eider biology and historical background for Grindøya, and for assistance in gathering field data from Grindøya. Audun Stien provided considerable statistical and logistic support, whilst Frode Pettersen and Tom Jenssen's help simplified boating logistics. Thanks to Matthieu Roger for help in making Larsen Traps and to Tore Slagsvold for a useful discussion on crow censusing techniques. This study was supported by funding from the University of Tromsø's supplement for Master students and by the Directorate for Nature Management.

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Paper II

Human disturbance effects on nesting success in declining eider (*Somateria mollissima*) colonies

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Summary

Human disturbance in bird breeding colonies may cause reduced breeding success. It is therefore pertinent to assess the impact of disturbance, taking steps that minimise negative impacts where necessary. We carried out a study of nesting success at two contrasting adjacent colonies of common eider (*Somateria mollissima*) in Northern Norway between 2006 and 2011. Between 2009 and 2011 we employed camera monitoring of individual nests to identify causes and correlates of nest survival and predation. We focused in particular on the effect of disturbance, which differed between the colonies due to a long-term research project on Grindøya. Over the 6-year study period the nesting success was consistently higher on Håkøya (69 % - 82 %) compared to Grindøya (35 % - 60 %). We found that disturbance leading to absence of eiders increased the predation risk by a factor of 6.42 for an increase of one additional daily disturbance. Absence due to natural nest leaving did not increase nest losses. Contrasting levels of disturbance appeared to explain the difference in nesting success between the two colonies. Under high levels of disturbance, camera monitoring indicated that the main cause of breeding failure was predation, primarily by hooded crows (*Corvus cornix*), but also to some extent greater black-backed gulls (*Larus marinus*). Cameras did not increase the predation risk. We suggest management trials aimed at mitigating the effects of human disturbance on reproductive effort and further, to increase colony size.

Key-words:

Seabirds, researcher effects, nest predation, Corvus cornix, Larus argentatus

Introduction

A substantial effort has been put into research on marine birds during the breeding season with the result that we have a great deal of knowledge about their ecology, population dynamics and life history strategies. Most marine bird species are long-lived with a low average annual reproductive output (Sæther and Bakke 2000). Although population growth rates in long-lived species typically are most sensitive to adult survival (Gaillard et al. 2000), many successive years of low productivity (fledging rate) negatively impact on recruitment (Hario and Rintala 2006, Reiertsen et al. 2013) and ultimately may lead to declining populations.

Nest-loss due to predation can be a main cause of low offspring production in birds (Ricklefs 1969, Newton 1998). Its importance in determining population growth is debated (Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012, Gunnarsson et al. 2013), but management actions that increase nest survival may help halt population declines especially when populations are small and isolated.

Efficient management actions depend on understanding the main drivers of nest predation. Classical predator-prey theory focuses on predator numerical and functional responses as main causes of variation in predation rates, but many studies show that other factors may modify the impact of predators on nest survival (Taylor 1984, Gunnarsson et al. 2013). Disturbance is one such modifying factor as nests may be more prone to predation when the nest is unattended. Human activity can have significant impact on nest-loss, with human induced nest leaving resulting in predation of nest contents (e.g. reviews in Carney and Sydeman 1999, Martínez-Abraín et al. 2010, Ibánez-Álamo et al. 2012). In addition, the body condition and clutch size of breeding birds has also been shown to be important for the likelihood of continuation of nesting (Hanssen et al. 2003a). Other factors that may affect nest predation risk are nest habitat and in particular nest cover (Martin 1993, Ekroos et al. 2012, Seltmann et al. 2014).

Long-term research on marine birds is important because it both provides a basic understanding of the biology of long-lived species (Clutton-Brock and Sheldon 2010) and important information regarding how environmental pressures (e.g. pollution) affect marine ecosystems (Furness and Camphuysen 1997). Much of this research involves invasive methods to acquire data on the physiological and demographic parameters. Invasive research methods cause disturbance of nesting birds with a potential for increased nest predation and thus reduced long-term performance of the population. In bird populations subject to long-term research repeated assessment of researcher effects may be necessary, in particular since the research-induced disturbance effect may be contingent on temporally changing limiting and regulating factors that affect population dynamics (e.g. Parmesan and Yohe 2003, Olito and Fukami 2009, Stien et al. 2012, Blois et al. 2013, Ferretti et al. 2013).

A colony of the common eider (*Somateria mollissima*) at Grindøya in northern Norway has declined during the period it has been subjected to long term research (Erikstad et al. 2009, 2010). This highly philopatric sea duck has also experienced recent large-scale declines in much of its circumpolar range (Desholm et al. 2002, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Although reproductive output at the Grindøya colony has been linked to large-scale climatic variation (Descamps et al. 2010), local-scale impacts related to predation may also be influential (Erikstad et al. 2009, Hanssen and Erikstad 2012). Previous studies on Grindøya have indicated, that nest-loss due to crow predation can be substantial (Erikstad and Tveraa 1995). To quantify the effect of crow predation, Stien et al. (2010) carried out a crow removal experiment between 2006 and 2008 that also included the adjacent Håkøya colony in a BACI design. In contrast to Grindøya, the Håkøya colony had a lower level of research-induced disturbance and higher nesting success, but in common with Grindøya the Håkøya colony was in a long-term decline (Stien *unpublished*). Crow removal significantly increased nesting success at Håkøya but not at Grindøya. Without detailed data on the processes of nest predation, Stien et al. (2010) could only hypothesise that the higher level of research-induced disturbance and/or a more diverse community of nest predators could be the reason for the consistently lower nesting success at Grindøya.

In the present study, we employed camera monitoring at individual nests over three nesting seasons to more thoroughly investigate which factors were involved in determining eider nest predation rates in the two colonies. We expected the lower nesting success at Grindøya to be explained by the higher frequency of nest disturbance at this colony. Specifically, we expected that nesting females exposed to a high frequency of disturbance would have lower nesting success than those with low disturbance and that absence from nests due to disturbance would be associated with a higher predation risk than absence due to natural nest leaving. Finally, we evaluated whether the difference between the two study colonies in nest predation rates could be explained by differences in the local predator community.

Materials and Methods

Research species

The common eider (*Somateria mollissima*) is a well-studied sea-duck that has been at the focus of many evolutionary, immunological and ecological studies throughout its circumpolar range (e.g. Mehlum 1991, Erikstad et al. 1998, Desholm et al. 2002, Hanssen et al. 2003b, Hanssen et al. 2006, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Adult survival is typically high, breeding is delayed with first breeding from 2 years of age, and periodic non-breeding years occur due to high energetic costs of breeding (Yoccoz et al. 2002, Hanssen et al. 2003a, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Nesting success may be highly variable between years and successive years of low breeding success can cause population declines (Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). These characteristics combined with high natal philopatry in first time breeders (Swennen 1991) and general high philopatry of adult females (Bustnes and Erikstad 1993, Hanssen and Erikstad 2012) may mean that increasing nesting success can be a relevant management action to halt the decline of eider populations. Negative effects of researcher activity, resulting in nest-loss have been demonstrated for common eider during egg laying and early incubation (Bolduc and Guillemette 2003, Wilson et al. 2012), and heterogeneity in nesting habitat has been found to cause variable nesting success where avian predation dominates and nests are left exposed (e.g. Götmark and Åhlund 1984, Noel et al. 2005).

The common eider has low clutch size for a duck species (mean of 4 eggs) with mean complete nest attendance from the second or third laid egg for females with 4 and 5 egg clutches respectively (Hanssen et al. 2003a). Complete nest attendance results in up to 40 % loss of body mass during incubation and decreased egg predation (Parker and Holm 1990, Swennen et al. 1993, Hanssen et al. 2002, Andersson and Waldeck 2006). A wide range of nest loss rates have been documented from less than 10 % to more than 90 % within and between eider colonies (e.g. Mehlum 1991, Noel et al. 2005, Coulson 2010, Wilson et al. 2012). Clutch size, egg size, clutch investment, duckling size and duckling survival depend on female condition before the onset of egg laying (Erikstad et al. 1993, Erikstad and Tveraa 1995, Hanssen et al. 2003a). Long-term studies indicate both presence and absence of density-dependent effects acting on different populations (e.g. Desholm et al. 2002, Hario and Rintala 2006, Coulson 2010). Mortality of young due to adverse weather, food availability and food-transmitted infections is particularly prevalent during the first two weeks of duckling stage (Milne 1974, Hario and Rintala 2006) and large-scale mortality of young has been linked to population decline (e.g. Desholm et al. 2002). Furthermore, large-scale variation in climate correlates with adult reproductive success (e.g. D'Alba et al. 2010, Descamps et al. 2010).

Study colonies

Grindøya and Håkøya colonies are adjacent low-lying islands approximately 2 km from each other at 69˚38 ′N, 18˚52 ′E and 69˚39 ′N, 18˚49 ′ E. There were approximately 150 pairs and 50 pairs of common eider in respectively the Grindøya and Håkøya colony in 2006. Habitat and the egg predator communities are described in Stien et al. (2010). Eider is the main ground nesting bird on the islands and their eggs are a main source of terrestrial food for predators in late May on Grindøya. On Håkøya a fluctuating population of tundra voles (*Microtus oeconomus*) exceeds the biomass of eider eggs in most years (Ims unpublished). Grazing of sheep has occurred on Grindøya during the breeding season since 2007.

The eider colony on Grindøya has been used for annual long-term monitoring and research since 1985 (Erikstad et al. 2009). Individual incubating females have been exposed to varying intensities and frequencies of disturbance for research purposes, including counting and measurement of eggs during laying, capturing of individuals for life history studies and handling of individual females for manipulations of plumage and parasite levels (e.g. Erikstad et al. 1993, Bustnes 1996, Hanssen et al. 2005, Hanssen et al. 2006). Disturbance from other human sources is limited due to public access restrictions at the colony. Nest failure is as high as 62 % (Stien et al. 2010). The colony has decreased steeply from over 500 pairs in 1995 to c.150 pairs in 2009 onwards (Erikstad et al. 2010). Adult female survival decreased from > 80 % between 1986 – 2002 to a low of 53% in 2005 with the decrease in 2002 and continued low survival being attributed to mink predation of incubating females (Erikstad et al. 2009, Erikstad et al. 2010). Between 2005 and present, survival has been variable but increasing, with an estimate of 80 % in 2011 (Hanssen unpublished).

Håkøya colony has been the focus of low intensity annual nest monitoring since 2006. The colony is a remnant of an active eider down colony with an estimated population of over 600 nesting individuals (Olsen pers. comm.) in the middle of last century. The study area contained at least 49 nesting individuals in 2006, which decreased to 26 in 2011. Individual nest fates are followed but not individual females. Disturbance from other human activity is limited as the colony area was little used during the study period 2006 - 2011. Nest failure is up to 39 % (Stien et al. 2010).

Study design

During 6 consecutive breeding seasons (2006 - 2011) we monitored 1003 common eider nests by discrete observational time intervals to estimate nesting success in the two study colonies (Stien et al. 2010). In the 3 last seasons (2009 - 2011) we camera-monitored 203 of the nests (Table 1). Of the camera-monitored nests, 184 yielded data suitable for establishing the causes of individual nest failures, including identity of predator species, while the effects of disturbance on nesting success were estimated from a subset of 103 camera-monitored nests that had complete histories of nest leaving identifiable as due to either disturbance or natural (Table 1). Forty-one matched pairs of camera monitored and non-camera monitored nests were used to estimate effects of cameras on nesting success at both colonies in 2009. Finally, the number of breeding pairs of nesting avian predators at both colonies were recorded by means of transect counts for crows or counts while searching for eider nests for large gulls.

Monitoring of colony level nest survival

The outcome of 1003 nests was followed on Grindøya and Håkøya between 2006 and 2011 (Table 1). At both colonies searches for nests were conducted covering the main laying period. Nests were found from the onset of eider breeding between 15 and 22 May (the onset differed slightly between years) and 5 June. Nests were marked by fixing a piece of plastic tape around nearby vegetation. Nest outcomes were monitored until between 28 and 30 June with nest fate being registered as success or failed on each subsequent visit. After laying was complete, nest activity was observed at the same frequency as for camera monitored birds (see below) in order to expose the 2 matched groups of the camera impact assessment to equal researcher visitation. Clutch size upon nest discovery (hereafter referred to as initial clutch size) and maximum clutch size were recorded at both colonies. The recording of maximum clutch size involved disturbing each individual from the nest and was undertaken using different methods at the two colonies in order to have low research related disturbance at Håkøya. On Håkøya, maximum clutch size was recorded by one subsequent visit to nests after discovery, allowing for a full clutch of maximum 6 eggs to be observed. As eiders lay one egg at approximately 1-day intervals (Watson et al. 1993, Hanssen et al. 2002), the interval depended on the initial clutch size. On Grindøya, nests for the current study were also part of the parallel long-term studies carried out over the same period as the current project and so monitoring followed the procedures of the parallel long-term project. These involved disturbing females from nests every second or third day to count and measure subsequently laid eggs until no new eggs were laid on 2 successive visits to record maximum clutch size (Erikstad et al. 1993), catching females of still active nests during incubation and disturbing females from nests in late incubation to check for hatching success. Catching of females occurred on day 5 and 20 of incubation for nests with known onset of incubation (i.e. for nests with subsequent laid eggs observed during egg laying monitoring), and once for females of unknown onset of incubation in order to read leg rings or apply leg rings to non-ringed individuals. Where initial capture of females was unsuccessful, several attempts were made on subsequent days to catch targeted females. From day 20 of incubation until females and chicks left the nest, nests were revisited in order to check for hatching success. Nest monitoring was co-ordinated between the present study and the long-term monitoring project in order to limit extra disturbance. All nests disturbed due to research and monitoring were covered with down or vegetation where nests were not lined with down after researcher visits.

Camera monitoring of individual nest

RECONYX cameras were deployed at time of nest discovery at 158 nests on Grindøya and 45 nests on Håkøya between 17 May and 5 June between 2009 and 2011 (Table 1). On Grindøya, an additional 34 (10 in 2009 and 12 in both 2011 and 2012) cameras were laid out on nests in the first week of June that had been found during the parallel long-term monitoring project between 7 and 13 days previously. We aimed to set out 10 cameras on each nest-finding day in order to take account of seasonal effects on nesting success (Stien et al. 2010). We covered open, wooded and thicket habitat within searches in order to take account of possible habitat effects on nesting success. In 2010 and 2011, cameras were laid out at the first 10 nests we found due to variation in the daily frequencies of nest initiation. In 2009, cameras were laid out on alternately found nests to enable the effects of cameras to be estimated. Cameras were deployed at nests with both known and unknown incubation date as lay date could not always be determined on the first visit.

Nest habitat was initially categorised into the three broad categories open, wood and thicket but these were not considered further as a measurement of cover at the nest captured well the difference between these categories. This *nest cover* variable was scored at an ordinal scale between 0 and 5 at time of nest discovery and time of failure. As cover did not vary substantially between time of nest initiation and time of failure, we used cover at nest discovery in the analysis. We estimated a 30 cm^2 cube cage over each nest and using the photos taken by the automatic camera scored the nest cover as 1 if more than ≥ 50 % of the cube was covered by vegetation or man-made structures and 0 if < 50 % of the face was covered. Thus the minimum score, zero would occur if there was < 50 % cover on all 5 faces and the maximum score, 5 would occur if there was > 50 % cover on all 5 sides. *Nearest neighbour distance* (between nests) was calculated from GPS nest co-ordinate positions in order to check for density-dependent predation. *Distance to the sea* was measured in Map Source (Garmin) as the shortest distance in metres from each nest to the high water line.

Camera settings were set to motion sensor, where the change in focal point temperature in relation to background temperature triggers the shutter. Cameras were placed 2 – 3 m from nests and positioned between 30 and 50 cm above the ground to allow a clear view of the nest contents. They were secured to tree trunks or to a weathered stake hammered in to the ground where suitable trees were not available. In 2009, 2 GB memory cards were used, while in 2010 and 2011 larger capacity cards of 4GB were used to reduce the number of visits to nests. In 2009, cards were changed once a week, whereas in 2010 and 2011 cards were changed once every 10 days to reduce disturbance. This overlapped visitation due to catching of incubating females on Grindøya, but did not necessarily result in the incubating bird leaving the nest.

Nest leaving recorded from camera monitoring was identified as either *natural* (hereafter referred to as natural) or *disturbed* (hereafter referred to as disturbance). The category natural was recorded when individuals covered their eggs with vegetation or down before leaving the nest and the category disturbance was recorded when individuals left their eggs uncovered and moved quickly off their nest. One hundred and four of the 184 nests with environmental variables had both uninterrupted camera monitoring from initial deployment of cameras at nest finding and all nest leaving events identifiable as disturbance or natural. These nests with complete nest-leaving histories were used to account for possible effects of previous nest leaving on nesting outcome. The remaining 82 nests had either periods of non-monitoring due to memory cards being filled and / or unidentifiable nest leaving cause.

Of the original 203 deployed cameras, data was not used from 17. Eight cameras malfunctioned at deployment and GPS location and / or nest cover was not recorded 9 nests. The reduction is unlikely to bias the results as these omissions were spread over all years of the study period and at both colonies (Table 2).

Effect of nest cameras on eider nesting success

Previous studies have shown that nesting success can be influenced positively or negatively by the presence of a camera at bird nests (e.g. Richardson et al. 2009). We tested whether cameras affected nesting success in this study by following the fate of 32 and 10 nest pairs with and without nest cameras on Grindøya and Håkøya respectively between 19 May and 4 June in 2009. Each pair consisted of chronologically found odd numbered nests being deployed with a camera and chronologically found even number nests receiving no camera. To control for the previously demonstrated season effect on nesting success at both colonies (Stien et al. 2010), paired nests were found on the same day. Camera deployed nests were visited on the same day as their non-camera monitored pairs, thus ensuring comparison of effects even in cases of camera malfunction. No females left their nests during these visits.

Monitoring of nest predator density

The number of territorial crows (*Corvus cornix*) present at both colonies was counted from transect lines covering the study areas 100 m apart, 65 ha on Grindøya and 64 ha on Håkøya. The location of nests and territorial behaviour were recorded between 12 and 19 May each year. The approximate number of large gull (greater black-backed (*Larus marinus*) and herring gull (*L. argentatus*)) breeding pairs were recorded each year during the searches for eider nests.

Statistical analysis

Colony level differences

We used 4492 nest visitation intervals to estimated nest survival for all 1003 monitored nests using a logistic exposure model (see Stien et al. 2010). This type of model gives reliable estimates of daily nesting success when nest visitation intervals vary between nests (Shaffer 2004). Predictor variables used were, colony, year, Julian day and clutch size. Preliminary exploration of models comparing AIC values revealed that Julian day was best fitted as a 3rd order polynomial whilst clutch size was best fitted as a linear variable. The most complicated model considered contained the interactions between area and year fitted as a categorical predictors and area and clutch size at nest discovery. These models were included to evaluate the possibility that differences in survival were due to differences between colony clutch size at nest discovery rather than differences in disturbance, and to see whether differences in nest survival were significantly different between colonies within the same year.

Effect of nest disturbance on individual nests

We used Cox proportional hazards models to estimate the effect of disturbance on the success of the 103 nests for which complete nest leaving histories were available. The proportional hazard model estimates the instantaneous risk of failure at time *t* for an individual nest given its success (i.e. survival) up to that time and allows the inclusion of covariates to correct for biases. It also takes account of incomplete event histories in the sampled population at the end of sampling time (i.e. right censoring in case of incomplete covering of nest outcomes due to malfunctioning cameras). The frequencies of disturbance and natural were calculated as the average daily number of disturbance or natural nest leaving events over the period the nest was monitored (i.e. number of events per nest day). In addition to the focal disturbance effects, the most complicated statistical model considered included the following covariates: frequency of natural nest leaving, colony, year (categorical), Julian day, initial clutch size, cover, distance to the sea and nearest neighbour distance. The initial clutch size was used as a proxy for the amount of investment females had used at time of nest finding and is referred to as clutch size hereafter. Maximum clutch size was not used as it was not possible to determine all egg laying events at camera-monitored nests. Preliminary investigation indicated that Julian day, clutch size and cover could be added as continuous untransformed variables. Distance to the sea and nearest neighbour distance were square root transformed to centralise their distributions as this improved the fit of the models. The simplest model included the effect of disturbance.

Effect of photo boxes on eider nesting success

We estimated nest survival for camera-monitored and control paired non-camera-monitored nests using a logistic exposure model (see above). Three hundred and fifty-five nest visitation intervals were used to estimate the effects of camera deployment on daily nesting success. A model with an additive effect of camera presence, area (Grindøya and Håkøya) and the covariates day and clutch size were used to evaluate the effects of cameras on nesting success.

Results

Colony level differences

The nesting success of common eider at the colony level was significantly higher at Håkøya than at Grindøya for the entire 6-year time series (Figure 1). The best logistic exposure model contained the effects of colony, year, Julian day and initial clutch size (Appendix A). This model showed some evidence for lack of fit (le Cessie-van Houwelingen-Copas-Hosmer goodness of fit test $z = 10.887$, $P < 0.001$) as the model overestimated nesting success when observed daily nesting success probability was less than 0.45. This bias does however not affect the strongly contrasting nesting success between the two colonies (Figure 1).

For the camera monitored nests, initial clutch size tended to be smaller on Håkøya than on Grindøya (Table 2, ANOVA with Welch's correction for variance non-homogeneity $F_{(1,56.26)} = 6.89$, $P = 0.01$) indicating that the nests were found somewhat sooner at Håkøya. The scores of cover at the nest sites were overall similar in the two colonies ($F_{(1,65.80)} = 3.39$, $P = 0.07$), as were distance to the sea ($F_{(1,115.67)} = 0.73$, $P = 0.40$) and nearest neighbour distance ($F_{(1, 65.65)} = 3.04$, $P = 0.09$) (Table 2).

Effect of nest disturbance

The best Cox proportional hazard model for the estimation of the disturbance effect contained the following covariates in decreasing order of importance; Julian day, initial clutch size and average daily frequency of natural nest leaving (Appendix B). Overall fit for the best model was good $P = 0.25$ and none of the variables violated the assumption of proportionality ($P > 0.12$). Disturbance had a strong positive effect on the risk of failure, increasing the risk by a factor of 6.42 for an increase of one additional daily disturbance ($P < 0.001$). Julian day had a small negative effect on risk of nest failure, decreasing the risk by a factor of 0.07 ($P = 0.02$). Clutch size also had a negative effect on the risk of failure that was weakly statistically significant, decreasing the risk of failure by 0.19 ($P = 0.05$). Natural nest leaving had a negative effect on the risk of failure that was however not statistically significant, decreasing the risk of nest failure by a factor of 0.35 ($P = 0.19$). A graphical depiction of the nest survival as function of disturbance and the significant covariates is given in Figure 2. Nest survival is less than 100 % at t_0 as 23 nests failed on the day of nest discovery. This included 10 nests of 4 eggs or more i.e. when the female is in full attendance at the nest. Nest survival was constant from day 8 to 21 before showing a small decrease at around day 22. These decreases in estimated nest survival correspond approximately to periods of increased nest leaving frequency during egg laying and between late incubation and early hatching. There were no partially significant colony or year effects on nest survival and none of the habitat variables entered the proportional hazard rate model. This result even applied to a model applied to all nests (n=184) with functioning cameras.

On average disturbance frequencies were 2.26 times higher on Grindøya than Håkøya ($F_{(1,24.97)}$= 16.04, P < 0.001, Table 2) and natural frequencies were 3.15 times higher on Håkøya than Grindøya ($F_{(1,24.91)}$ = 13.39, P = 0.001). Disturbance accounted for 61 % of recorded nest leaving on Grindøya and 30 % on Håkøya. There was a weak negative correlation between the frequency of disturbance and natural (r = - 0.19, P = 0.09). The photographic evidence showed that the majority of females returned to the nest after disturbance or natural events. On the 12 occasions females did not return, disturbance accounted for 11 of the 12 nest leavings and all 12 nests were predated. Absences varied from one minute to 1.79 days with 75% of absences less than 63 minutes and median absence of 28 minutes (mean = 2.43 hours). There were no significant colony differences between length of absence for disturbed or natural events ($F_{(1,\ 35.79)}$ = 0.35, P = 0.55). Mean absence length for nest leaving due to disturbance was 2.87 (se ± 0.72) hours and was significantly longer than the mean value of 1.81 (se ± 0.45) hours due to natural leaving ($F_{(1,527.44)}$ = 4.56, P = 0.03). When absence was split into early laying (associated with low attendance and referred to as pre-incubation) and incubation (associated with almost 100 % attendance) periods, mean absence for pre-incubation was 7.62 ± 0.98 to 12.61 ± 1.93 hours for incubation defined as attendance from the second egg and third egg respectively. Mean absence time during incubation was 1.52 ± 0.13 to 1.72 ± 0.13 hours for incubation from the second and third egg. Pre-incubation absences were significantly longer than absences during incubation ($F_{(1,\ 31.44)}$ = 31.83, P < 0.001 and $F_{(1,\ 107.40)}$ F = 36.47, P < 0.001, for second and third egg incubation respectively). There was no effect of change in natural nest leaving time during incubation phase (4 eggs or more) for birds with clutches between 4 and 6 eggs ($F_{(2,\ 158.12)}$) = 0.20, P = 0.81).

Time to predation varied between 1 minute and 48 hours with a median of 1.9 hours and was not statistically different between nest leaving due to disturbance and natural causes ($F_{(1,\ 19.57)}$ = 2.60, P = 0.12). Analysis of the 41 paired camera-monitored and control nests (without cameras) in 2009 indicated that there was no effect of cameras on nesting success (Figure 2). The best logistic exposure model included effects of day, area and clutch size (Appendix C).

Abundance and identity of nest predators

On both Grindøya and Håkøya the number of crow territories remained constant during the study period with 4 and 1 territory respectively between 2009 and 2011 (Table 3). The number of nesting large gulls (mostly herring gull) increased between 2009/2010 and 2011 at Grindøya from approximately 30 to over 80 pairs. On Håkøya, the number of greater blacked back gull and herring gull territories remained low (4 – 6 pairs). Among the 184 nests that had functioning cameras there were 85 events of camera-monitored predation (Table 3). On Grindøya crows were clearly the most important predators followed by greater blacked-backed gulls, while mammalian predation was negligible. The few predation events on Håkøya were quite evenly distributed among the predator species identified from camera-monitored nests. The majority of predation resulted in loss of the entire clutch (nest loss) (Table 3). All predation events occurred in the absence of the females and 81% of these events when the nest had been disturbed. Of these disturbed nests, 37 were due to researcher disturbance (i.e. eggs were covered after visiting), while the causes of nest leaving of the remaining 29 disturbance events could not be determined.

Discussion

The results from this study are consistent with the hypothesis that the lower nesting success at Grindøya is due to a constantly higher rate of disturbance of nests at this colony. That is, the frequency of nest disturbance was much higher at Grindøya than Håkøya and this led to a steeply increased risk of nest failure due to predation. There was no evidence of any additional colony effect in the hazard model when the disturbance effect was included, implying that the overall difference in nesting success between the two colonies could be accounted for by the contrasting disturbance rates. This also implies that we did not find evidence for the alternative hypothesis that the general predation pressure differed between the two colonies, which should have amounted to an independent colony effect. For the hooded crow, the predator species that inflicted most of the predation events, there were more crow territories on Grindøya than on Håkøya. However, the ratios of crow territories to eider nests were very similar for the two colonies, 0.03 and 0.04 at Grindøya and Håkøya respectively. Erikstad et al. (2009, 2010) suggested that predation by American mink (*Neovison neovison*) on incubating birds was important for the recent decline in the population. However, here we have shown that mink predation was not at all important over the 3 breeding seasons of camera monitoring between 2009 and 2011.

As far as we are aware, this is the first study that has been able to relate complete nest leaving histories that included both natural causes and disturbance to nest losses in order to investigate the role of disturbance on the nesting success of common eider. This allowed us to show that in contrast to absences from nests due to disturbance, a high frequency of natural nest leaving was not associated with increased nest losses. Moreover, we found that disturbance leads to breeding failure through nest predation rather than nest abandonment as the majority of females returned to nests after disturbance events. The camera monitoring also allowed us to establish which predators were most important. Both crows and large gulls are known to be common nest predators in eider colonies (e.g. Gerell 1985, Götmark 1989, Mehlum 1991, Swennen et al. 1993). However, although large gulls were much more abundant than crows at Grindøya, crow had a disproportionately higher nest predation rate. The consistent high rate of nest predation by crows supports earlier studies indicating that this visual predator is particularly good at homing in on, and remembering novel cues and human activity (Milne 1974, Picozzi 1975, Sonerud and Fjeld 1987, Marzluff and Neatherlin 2006), especially if they are within crow territories (Erikstad et al. 1982). Indication of homing in on human cues in the present study comes from the rapidity of predation and domination of predation of nests that have been visited by researchers. Since the contents of disturbed nest were covered by the researchers in the same manner as birds themselves do in connection with natural nest leaving, crows may have been observing the disturbance events. The use of cues may well be a reason for the lack of strong positive effect of clutch size on nesting success and the lack of effect of clutch size on absence length, which would have supported the clutch investment hypothesis (Coleman et al. 1985, Andersson and Waldeck 2006). Disturbed, vacated nests are made apparent to predators and available to predation, thus maintaining a high risk of nest loss regardless of the stage of the nesting attempt.

Nest-loss rates due to disturbance do not necessarily translate into lower life time reproductive success as the reproductive rate of this long-lived sea duck is low (acting through high nesting failure) and as such we cannot attribute the human related disturbance of eiders at Grindøya to an ongoing population decline of this colony. An unknown proportion of disturbance mediated predated nests may have failed later in the breeding period due to poor female body condition (Hanssen et al. 2003a). However, an experimental study undertaken between 1997 and 2001 at the same colony (Hanssen and Erikstad 2012) found long-term negative effects of nest failure due to nest predation on future reproductive output . They found that fifty percent of females that failed during egg laying did not relay during the same season and furthermore, females that lost their first clutch due to predation regardless of whether they re-nested or not, had a lower number of breeding attempts during the following 4 seasons than females that successfully hatched young (Hanssen and Erikstad 2012). Also, Hario and Rintala (2006) indicated that repeated reproductive failure (fledging rate) can be enough to cause a decline in an eider population in Southern Finland. For populations experiencing sharp declines such as is apparent at Grindøya and Håkøya (possibly mainly owing to high female mortality [Erikstad et al. 2009]), the human induced breeding failures over multiple years may suppress fledging rates, thereby adding to the decline.

To what extent any given population is resilient to disturbance will depend on the extent of density-dependent population regulation (Sinclair 1989). Long-term studies of eider suggest both presence, and absence of density dependence in eider populations (Hario and Rintala 2006, Coulson 2010). To what extent density-dependent factors were acting on any demographic factor in the two study colonies in Northern Norway is unknown. We did not find however, any evidence for density-dependent predation as nearest-neighbour distance did not predict predation rates.

Long-term research is important to increase knowledge of ecological functioning, behaviour and evolution of species (Clutton-Brock and Sheldon 2010). However, potential negative effects of research activity should regularly be quantified and evaluated, especially as many common species (including eider) are in decline (e.g. Inger et al. 2015). In addition, the study shows the potential negative effects on nesting success from general human disturbance in areas that are newly exposed to increasing frequencies of human recreation. Using camera monitoring of individual nests, we have shown that the intensity of activities undertaken during the study period at Grindøya clearly inflicted high nest losses. We suggest that nest loss should be reduced at the Grindøya and Håkøya colonies, by reducing nest predation. Stien et al. (2010) demonstrated that removal of territorial crows on Grindøya alone had no effect on nest predation rates, possibly due to crows on nearby islands compensating for predation carried out by removed crows (Stien unpublished). Thus, disturbance leading to nest leaving could be reduced by the use of less invasive study protocols or disturbed nests could be subjected to some kind of nest guarding until females return. In association with the reduced nest predation, a longitudinal study should be implemented in order to investigate whether high nesting success can lead to increased recruitment and halt the decline in the population of breeding common eiders.

Acknowledgements

We would like to thank Renate Lohne for help during fieldwork and Sveinn Are Hanssen for sharing data on nesting success of eider on Grindøya and for commenting on the manuscript. Funding was provided by the Norwegian Environment Agency, The County Governor of Troms and The University of Tromsø, Norway's Arctic University. Permission to work on Grindøya was provided by The County Governor of Troms.

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Appendix

Appendix A

Table 1A. The five logistic exposure models of daily nesting survival of 1003 nests on Grindøya and Håkøya between 15 May and 30 June, 2006 – 2011 ranked according to Akaike's Information Criteria (AICc and ΔAIC) and Akaike's weights (w_i) The ΔAIC values are expressed in relation to the best fitting model. K is the number of parameters in the models. Clutch is the initial clutch size at nest discovery and day is Julian day.

Rank	Modell	K	AICc	ΔAIC	w_i
1	Colony + year + poly day^3 + clutch	16	2844.78	0.00	0.59
2	Colony + year + poly day^3 + clutch + Colony* clutch	17	2845.59	0.81	1
3	Colony + year + poly day^3	15	2877.99	33.21	1
4	Colony + year	12	3033.48	188.69	1
5	Intercept	1	3099.38	254.60	1

Appendix B

Table A2. The three best Cox proportional hazard models for the effect of disturbance on nest survival of 103 camera monitored nests on Grindøya and Håkøya ranked according to Akaike's Information Criteria (AICc and ΔAIC) and Akaike's weights (*w*ᵢ) The ΔAIC values are expressed in relation to the best fitting model. K is the number of parameters in the models. Clutch is the initial clutch size at nest discovery and day is Julian day.

Rank	Model	K	AICc	ΔAIC	w_i
1	Day + clutch + disturbance + natural	4	355.20	0.00	0.71
2	Disturbance	1	358.24	3.04	0.86
3	Colony + year + day + clutch + cover + sea + neighbour + disturbance + natural	10	358.55	3.35	0.13

Appendix C

Table A3. The three best logistic expoure models for the effect of cameras on daily nesting survival of 82 nests consisting of 41 camera and non – camera pairs ranked according to Akaike's Information Criteria (AICc and ΔAIC) and Akaike's weights (w_i) The ΔAIC values are expressed in relation to the best fitting model. K is the number of parameters in the models. Clutch is the initial clutch size at nest discovery and day is Julian day.

Rank	Model	K	AICc	ΔAIC	w_i
1	Camera + area + day + clutch	5	226.17	0	0.85
2	Camera + area + poly day^3 + clutch	7	229.74	3.56	1.00
3	Camera	2	253.54	27.36	1.00

Table 1. Number of nests followed for monitoring of nesting success on Grindøya and Håkøya colonies between 17 May and 30 June 2006 – 2011. Observational monitoring refers to nests followed to estimate nesting success of the two colonies during the entire monitoring period. Camera monitoring refers to the subset of nests equipped with cameras and for which the success of individual nest level could be related to nest covariates and nest leaving histories. Sample size for estimation of effects of cameras on nesting success is shown in parenthesis, which is a subset of the total number of camera-monitored nests in 2009.

Colony Year	**Camera monitoring**			**Observational monitoring**
	Complete nest leaving histories	**Nest covariates**	**Camera deployed**	
Grindøy				
2006			-	165
2007			-	162
2008			-	123
2009	25	42	45 (32)	81
2010	32	50	54	127
2011	26	54	59	133
Håkøy				
2006			-	49
2007			-	49
2008			-	41
2009	8	11	13 (10)	26
2010	9	15	15	23
2011	3	12	17	24
Total	103	184	203	1003

Table 2. Summary of colony-specific characteristics of camera monitored eider nests and predator abundance on Grindøya and Håkøya. Clutch size at nest finding (initial clutch size) and habitat characteristics (nest cover, distance to the sea and nearest neighbouring nest) are given for all 184 camera monitored nests found between 17 May and 5 June 2009 -2011. Annual and overall disturbance and natural nest leaving rates (mean number of events per day) are given for 103 nest with complete nest leaving histories (see Table 1 for year- and colony-specific sample sizes). Means, standard deviations and ranges are shown for all continuous variables.

Colony Year	**Initial Clutch size**	**Nest cover**	**Distance to sea (m)**	**Neighbour distance (m)**	**Disturbance rate**	**Natural rate**	**Predators**	
							Crows	**Gulls**
Grindøy					0.78 ± 0.58 (0.09 – 2.00)	0.20 ± 0.34 (0 – 2.00)		
2009	3.19 ± 1.23 (1 - 5)	2.19 ± 1.27 (0 – 5)	40.02 ± 40.99 (1 – 151)	29.08 ± 23.38 (2.23 – 92.96)	0.81 ± 0.64 (0.16 – 2.00)	0.16 ± 0.41 (0 – 2.00)	4	≈30
2010	3.30 ± 1.51 (1 – 6)	2.94 ± 1.44 (0 – 5)	39.58 ± 38.17 (1 – 187)	26.29 ± 25.70 (1 – 114	0.73 ± 0.62 (0.09 – 2.00)	0.25 ± 0.29 (0 – 1.00)	4	≈30
2011	3.05 ± 1.50 (1 – 6)	2.83 ± 1.16 (1 – 5)	37.55 ± 42.37 (1 – 139)	28.22 ± 27.10 (2 – 154)	0.82 ± 0.46 (0.14 – 2.00)	0.17 ± 0.34 (0 – 1.5)	4	≈80
Håkøy					0.34 ± 0.52 (0 – 2.00)	0.64 ± 0.66 (0 – 2.33)		
2009	2.16 ± 1.16 (1 – 4)	1.81 ± 1.16 (1 – 4)	28.63 ± 20.49 (5 - 75)	20.58 ± 19.37 (2.82 – 69.87)	0.48 ± 0.44 (0.00 – 1.00)	0.78 ± 0.47 (0 – 1.5)	1	6
2010	2.60 ± 1.50 (1 – 6)	2.33 ± 1.23 (1 – 5)	25.06 ± 17.99 (13 - 74)	21.74 ± 27.67 (5 – 118)	0.06 ± 0.09 (0.00 – 0.28)	0.68 ± 0.84 (0.14 – 2.33)	1	4
2011	2.91 ± 1.62 (1 - 5)	2.66 ± 0.88 (1 – 4)	32.08 ± 18.92 (11 - 64)	18.91 ± 15.14 (2 – 48)	0.82 ± 1.02 (0.13 – 2.00)	0.13 ± 0.23 (0 – 0.40)	1	4

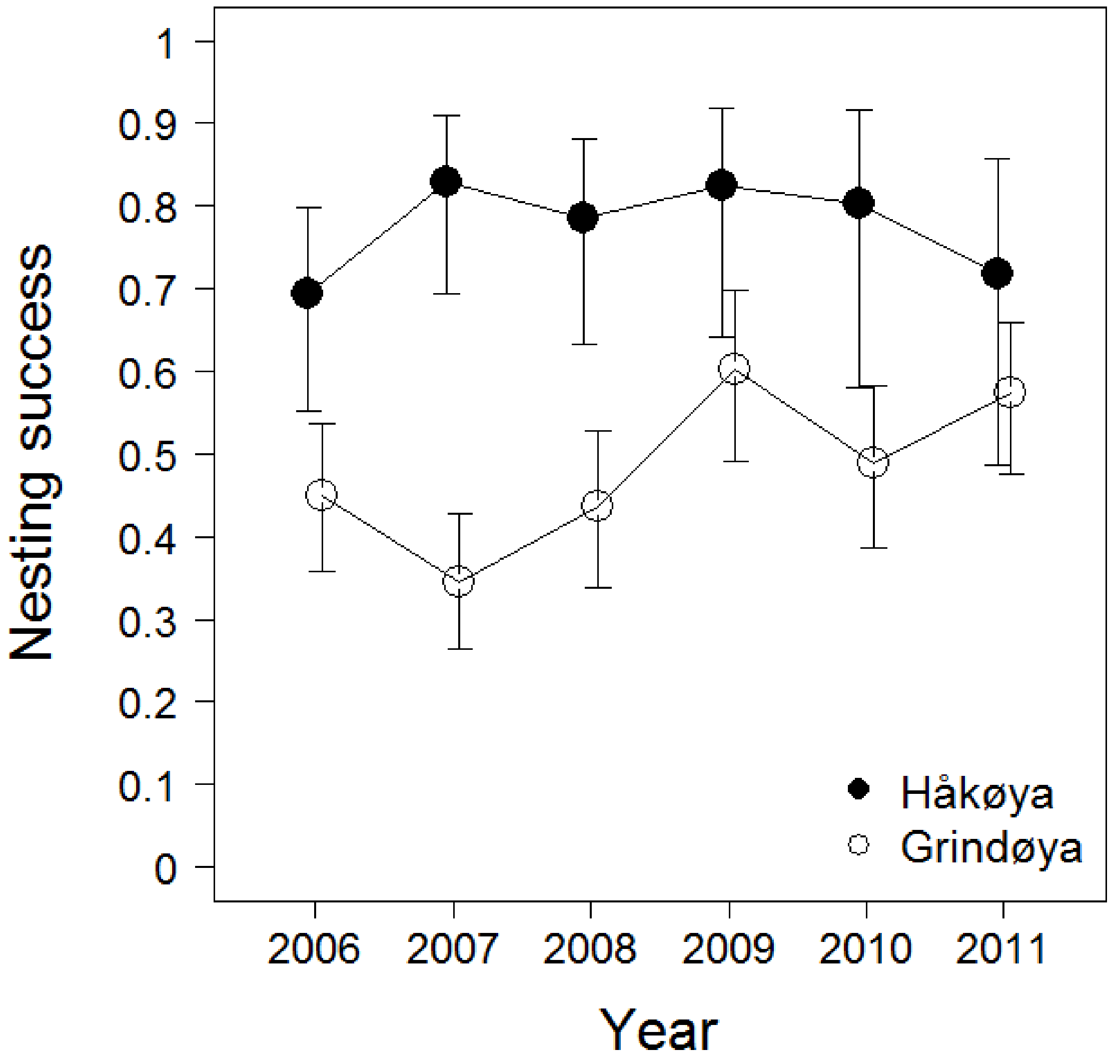
Table 3. Predator species responsible for full (nest loss) and partial predation of camera monitored nests on Grindøya and Håkøya between 17 May and 30 June 2009 – 2011.

Colony	**Partial predation**	**Nest loss**	**Predator species**
Grindøya	4	36	Hooded crow
	4	17	Greater black–back gull
	0	4	Herring gull
	2	3	Raven
	0	1	Mink
Håkøya	2	1	Hooded crow
	0	4	Greater black–back gull
	1	2	Raven
	0	2	Stoat
	0	1	Unknown

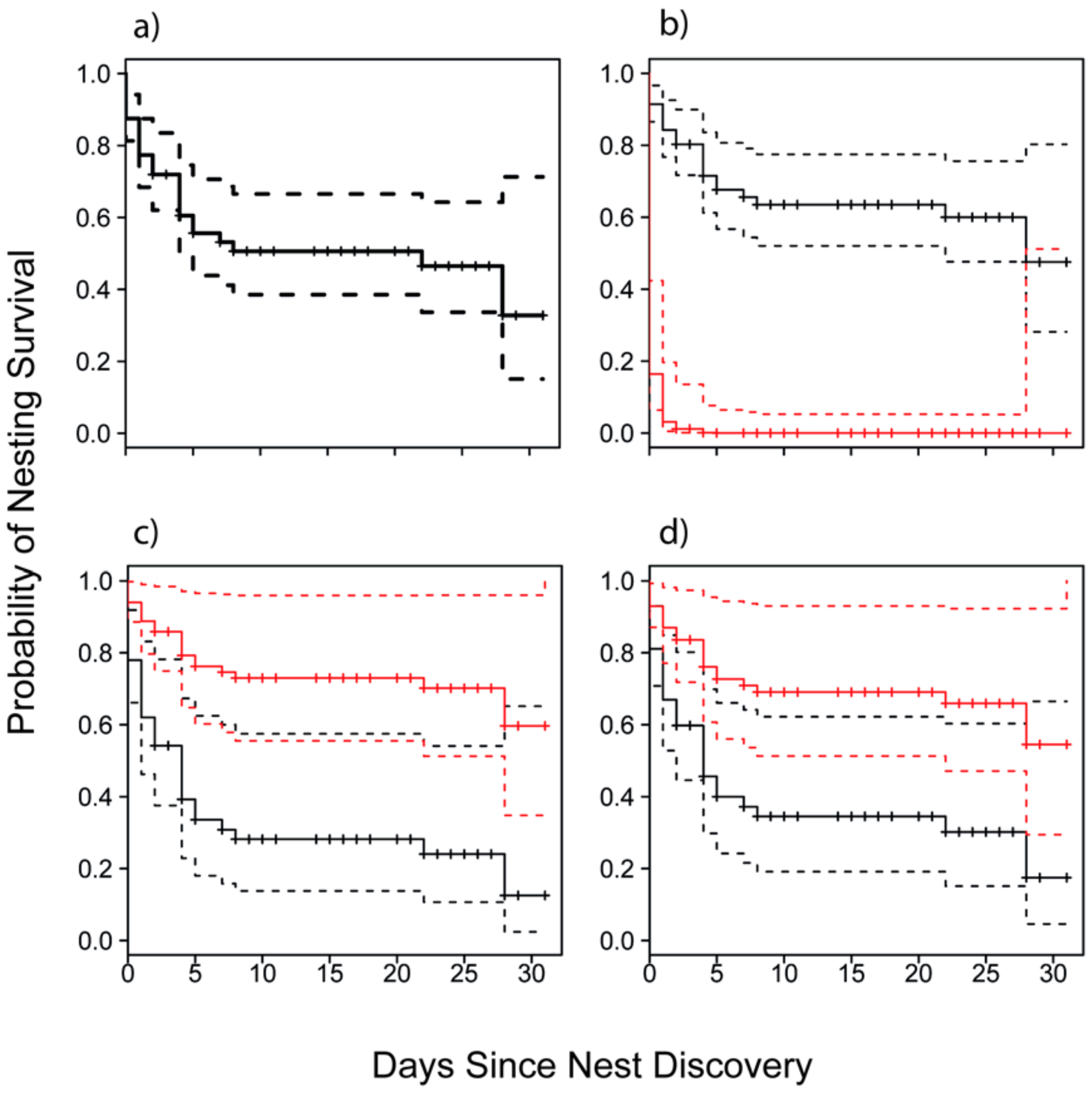
Figure 1. Predicted common eider nesting success at Grindøya and Håkøya from a logistic exposure model. The predictions are obtained from back-transformed coefficient estimates and 95% C.I. for the area*year effect with nesting success expressed as an average for the eider nesting period of 28 days (assumes average clutch size of four and average incubation period of 24 days; adapted from Erikstad et al. 1993).

Figure 2.a) Predictions (solid lines with 95 % C.I. shown by broken lines) of nest survival rate as a function of number of days since nest detection obtained from the best Cox proportional hazard model for 103 camera monitored nests on Grindøya and Håkøya. a) Mean effects of all covariates included in the model while b - d) gives predictions for contrasting levels of covariates. b) disturbance (P = < 0.001), where lower solid line is a maximum rate of disturbances per nest life day (2 disturbances) and upper solid line is a rate of 0.5 disturbances per nest day life; c) Julian day (P = 0.02), where lower solid line is 17 May and upper solid line is 27 May; d) clutch size (P = 0.05), where lower solid line is 1 egg and upper solid line is 6 eggs.

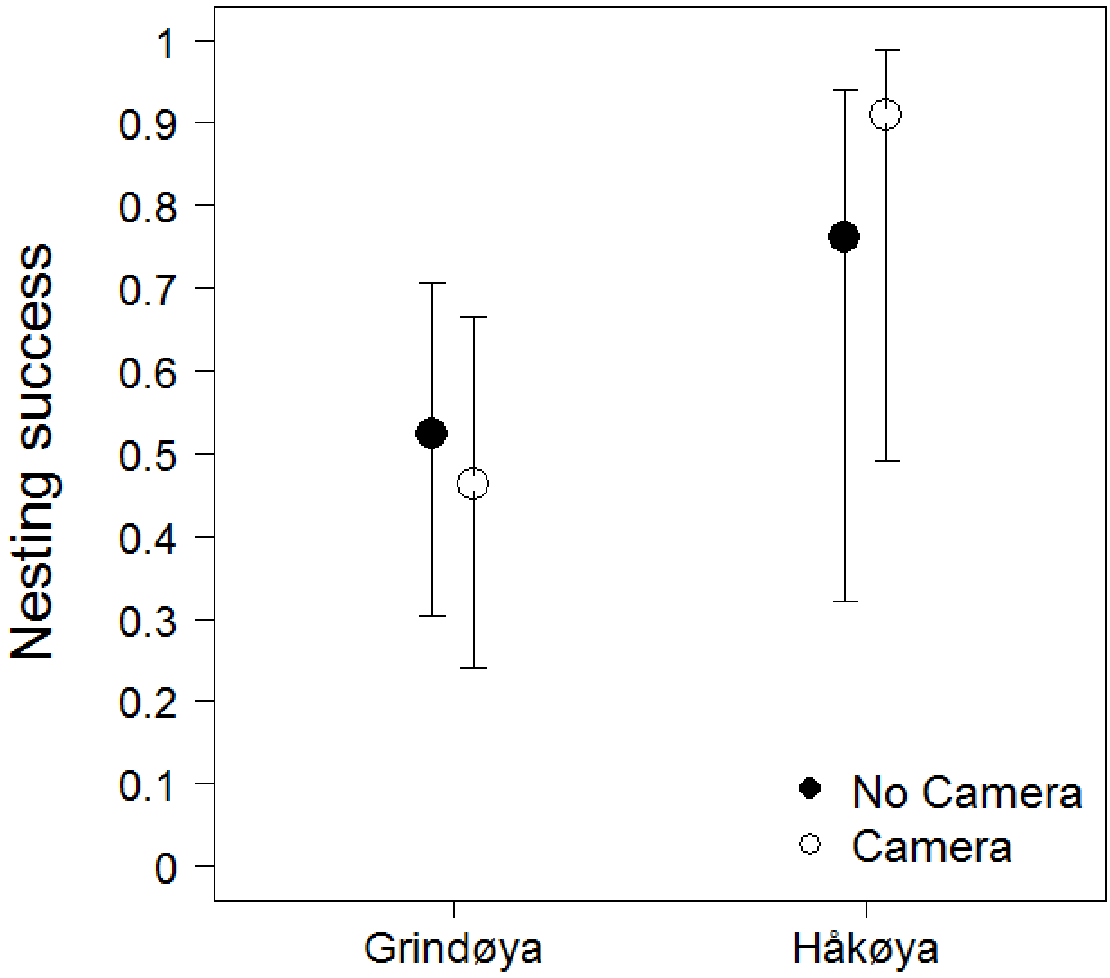
Figure 3. Effect of cameras from best exposure model on the nesting success of 42 pairs of eider on Grindøya and Håkøya monitored between 19 May and 30 June 2009. Daily interval estimates from the model have been raised to the power of 7 and clutch is set to mean clutch size (3) to estimate average weekly nesting success. Estimates are shown with 95 % C.I.


Nesting success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
2006
2007
2008
2009
2010
2011
Year
● Håkøya
○ Grindøya

744


a)
b)
c)
d)
Probability of Nesting Survival
1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
25
30
Days Since Nest Discovery

745


Nesting success
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
● No Camera
○ Camera
Grindøya
Håkøya

Paper III

Wildlife Biology 21: 44–50, 2015
doi: 10.2981/wlb.00026

Subject Editor: Aurélien Besnard. Editor-in-Chief: Ilse Storch. Accepted 5 November 2014

Management decisions and knowledge gaps: learning by doing in a case of a declining population of Slavonian grebe *Podiceps auritus*

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Species of national conservation concern require management action to reduce the threat of extinction. As part of its obligations to reduce national loss of biodiversity, the Norwegian authority for nature management (The Norwegian Environment Agency) published an action plan in 2010 for one of these species, the Slavonian grebe *Podiceps auritus*. The American mink *Neovison vison*, a non-native, invasive species with wide spread negative effects on native fauna, was highlighted as a major potential treat. We used an adaptive management approach that included management trials with the aim to assess whether mink predation is likely to be affecting grebe numbers significantly. We monitored mink activity, and put in place mink control measures at three of our seven study lakes. We then used 35 pairs of artificial nests, with one of each pair equipped with cameras, to measure predation at all seven lakes. The combined use of progressive experiments in an adaptive management/monitoring framework showed that mink activity was generally low with a mean activity at raft stations of between 0.41–1.22 per lake (n = 5), a range of zero to three excavations executed as a result of hunting (n = 3), and no incidences of mink nest predation (n = 35). Hence we conclude that mink is presently not likely to be a significant negative factor on grebe breeding success in the targeted lakes. We found a high nest predation rate by hooded crow with 18 of 21 identified predation events being identified to this species. Future effort should investigate non mink related threats to the Slavonian grebe such as the role of hooded crow in nest predation. This case study exemplifies the usefulness of the adaptive management/monitoring framework as a powerful means of testing hypotheses and to inform management, especially when knowledge of the focal system is poor.

All signatory countries to the Convention on Biodiversity (CBD) agreed to significantly reduce the rate of biodiversity loss by 2010 (Secretariat of the Convention on Biological Diversity 2010). Conservation measures to achieve this target include implementation of management to allow population growth of targeted species vulnerable to extinction and control of invasive species which can have a strong negative effect on vulnerable populations (Bonesi and Palazon 2007, Lentini et al. 2013). The Red List of species conservation (IUCN) is internationally recognised as the source for assessing the vulnerability of populations to extinction. It is the source which state nature management authorities use when compiling management strategies (action plans) to halt species biodiversity loss and therefore results in a large number of species which require some kind of management. However, for very many of these species it is unclear what kind of action is needed. An adaptive management framework is suitable for improving knowledge about system state as well as for assessing the relevance and effectiveness of potential management actions (Lindenmayer and Likens 2009, 2010, Williams 2011). Adaptive management may be carried out using an active or passive approach. The effects of multiple scenarios of perturbations on the response are tested in active management whereas the effect of a single perturbation is tested in passive adaptive management. Surprisingly, few studies utilise an adaptive management approach even though the idea has been around since the 1980s (Walters and Holling 1990, Williams 2011, Westgate et al. 2013).

Norway is a signatory to the CBD and as part of its obligations produced an action plan to increase the breeding population of Slavonian grebe *Podiceps auritus* (hereafter grebe) which was initially red listed in 2006 (Kålås et al. 2006) and currently has a small population with unknown trend. In Norway, Slavonian grebe breeds on inland water bodies between May and September (Cramp and Simmons 1977, Fjeldså 1973, 2004, but see Ulfvens 1988). Nests consist of a floating raft made from dead plant material situated in waterside vegetation. The action plan names 10 factors which are proposed to affect grebe negatively with all except one relating to factors at the species' breeding grounds (Fig. 1). However, direct evidence for these effects is lacking. It further expressed the need for increasing information about proposed, but untested, negative factors affecting the grebe at its breeding sites and implementing appropriate management (Direktoratet for Naturforvaltning 2009). We

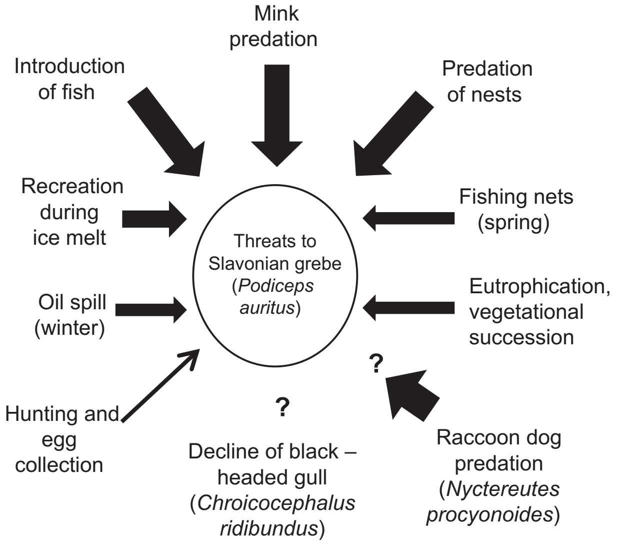

Figure 1. Study design showing factors perceived to have negative impacts on the Norwegian breeding population of grebe according to the Norwegian national action plan. Arrow thickness represents action plan assessed importance of the risk of a negative effect with thick arrows representing highest risk. Importance of risk is assessed as unknown for black – headed gull and potentially high for raccoon dog.

used an adaptive management framework to focus on one proposed high risk factor, the invasive American mink *Neovison vison*. Our target system was a core area for the grebe in northern Norway where the breeding population during the last decade has been subjected to a dramatic decline (Strann et al. 2014). We proceeded with management and monitoring trials in a sequential fashion in order to assess the usefulness of implementing mink removal as a management action to increase the grebe population in the target system. Each trial consisted of an experiment whose outcome informed the direction of each subsequent trial.

Material and methods

Experimental lakes and their grebes

Our focal *Podiceps auritus* conservation area, consisting of 7 lakes, is situated in Troms county, northern Norway which is an historical core area for the national population (Direktoratet for Naturforvaltning 2009). The grebe population in this area has been subject to a sharp decline in recent years (Fig. 2, Strann et al. 2014). The seven lakes are low lying (between 7 and 162 m above sea level with a mean area of 3.1 km^2, range 0.3–13.1 km^2) and oligotrophic with patches of shallow water vegetation consisting of water horsetail *Equisetum fluviatile* and common bog sedge *Carex limosa*. All lakes were relatively close to the sea (mean distance was 6.7 km, range 0.48–21.4 km). Lakes were in the same region and near each other so as to represent a single management area. They were expected to be independent with respect to individual mink during their breeding season, with Euclidean distance (range 5–43 km) between study lakes being greater than reported mean home range for territorial males during the breeding season in freshwater habitats (Gerell 1970, Dunstone and Davies 1993). Three lakes had connecting riparian ways of between 14.7 and 21.3 km. Estimates of number of breeding pairs of grebe per lake during the period 2001–2011 were obtained from Strann and Frivoll (2010) and Strann et al. (2010, 2012).

Management design and actions

Three sequential experiments were undertaken. The first involved a paired treatment and control BACI design at five lakes, whereby the activity of mink before and after trapping events was compared to the activity of mink at monitored control lakes in order to assess the effectiveness of mink passive trapping throughout the ice-free period in 2010 (Fig. 2). The second experiment proceeded in the same treatment and control lakes. Dogs were used to track mink on snow in early spring of 2011, while lakes were still frozen and before the arrival of the grebes. The third experiment focused on assessing the predation risk on grebe nests in the following breeding season in 2011.

Experiment 1. Mink removal and activity assessment with rafts and traps

Six mink raft stations consisting of a floating monitoring footprint plate and removable trap were deployed at each lake (Reynolds et al. 2004, Anonymous 2007, Bryce et al. 2011). Distance between each trap was 1 km allowing multiple detection possibilities within active mink territories at each checking period (Gerell 1970, Birks and Linn 1982, Reynolds et al. 2010). Stations were monitored every seven days to comply with the wildlife laws and to be a sufficient time interval to both remove individuals from a treatment area and record activity in control areas (Moore et al. 2003, Asakskogen 2010, Lambin pers. comm.). Stations were active during two periods during the ice-free season, with deployment between 26 May and 2 June as soon as ice melt began, until 21 July, and from 4 August until onset of first winter ice on October 20. This frequency of monitoring also ensured multiple sampling and trapping opportunities for mink in the study area. The start point for lake-raft deployment order was made by flipping a coin. All rafts were initially deployed in monitoring state (i.e. the tracking plate but not the trap was deployed). Traps were deployed at treatment site rafts only when tracks were registered on the monitoring plates. Lethal traps were used in order to further minimalize manpower required to check traps. Conibear 120 spring traps (<www.fangstmann.no/>) were used until 2 September, thereafter all treatment lakes monitored activity for 3 weeks while we waited for delivery of new traps. From 23 September Syningsfella (<www.syningfella.no/>) traps were used for the remaining four weeks until October 20.

As the objective of the study was to test the management action of mink removal, the first lake where mink activity was recorded became the first treatment lake (i.e. a lake where traps were deployed and activated in addition to monitoring). Thereafter the adjacent lake became a paired control lake where only monitoring of activity occurred. The next pair of lakes was similarly chosen whilst the remaining lake became a third treatment. Where activity had occurred, tracks were registered at each station and at treatment

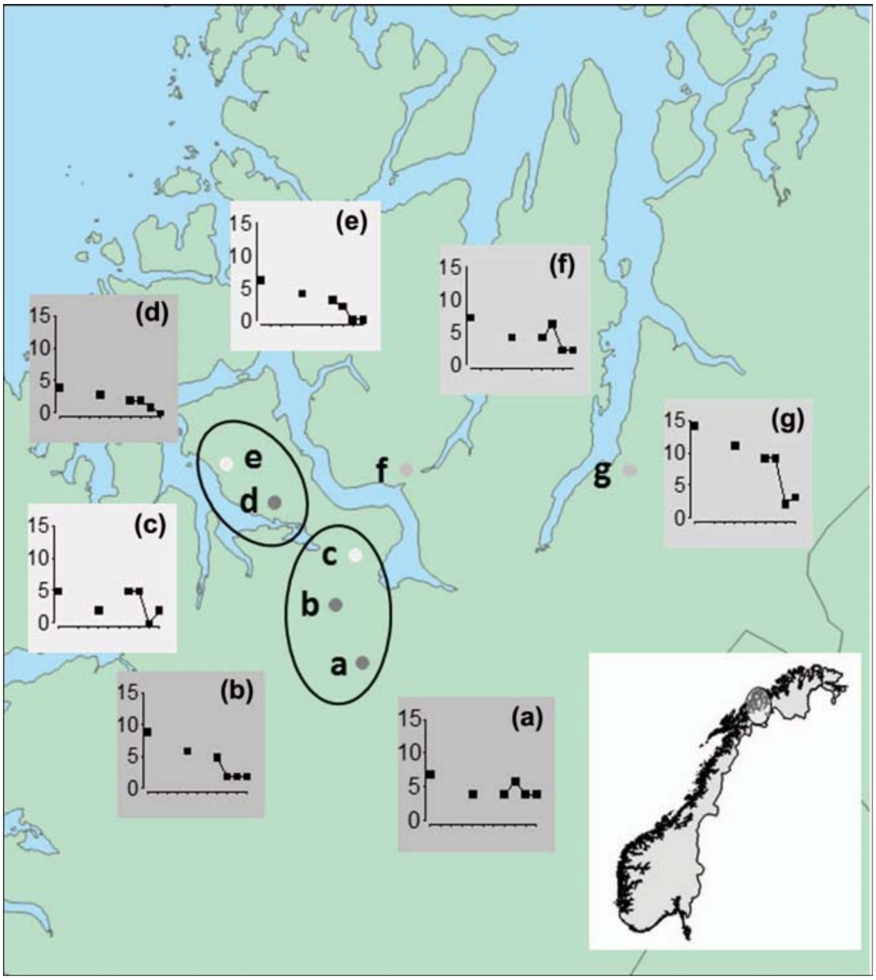

Figure 2. Site design and number of breeding pairs of grebe at study sites. Individual lakes are shown with dots. Colouring of dots relates to treatment (dark grey), control (pale grey) and additional (mid grey) lakes used for artificial nest experiment. Oval rings show the replicate treatment and control lake groups. Study lakes are (a) Langvatn, (b) Sagelvvatn, (c) Josefvatn, (d) Nordbyvatn and (e) Sandsvatn, (f) Laksvatn and (g) Øvervatn. Number of pairs is from 2001–2011, taken from Strann and Frivoll (2010) and Strann et al. (2010, 2012). Colouring of graph backgrounds is the same as for the dots. Inset map shows the study location area within Norway.

lakes a trap was deployed. At the next station round, traps and any caught mink were removed and footplates were returned. State of the trapping attempt (successful or not) was registered and resulting dead individuals were collected for later analysis. By-catch was also registered. After seven weeks of low activity and capture of only one individual all traps at treatment lakes were deployed permanently together with their respective tracking plates in order to maximize the chance of trapping transitory individuals between station rounds. Monitoring of mink at control lakes remained unchanged.

Experiment 2. Mink removal and activity assessment with snow tracking and dogs

The second experiment involved active searching and trapping (or tracking in control areas) of mink in the time window between establishment of mink territories and return of breeding birds. Active hunting works well when mink activity (and therefore the chance of mink entering a trap) is low (Nordström et al. 2003, Macleod, pers. comm.). Furthermore, the timing of mink removal provides temporary mink free areas during the breeding season and avoids disturbance of nesting birds (Craik 1995). A team of one biologist and two experienced hunters with two trained fox terrier dogs walked a transect line along each lake between 2 and 4 April 2011. Snow conditions were recorded during each transect as 'good' when a track could be easily identified and 'poor' when identification was not possible. Transects (mean = 6.12, range = 4.3–7.9 km) either circumvented small lakes or covered the area relevant to grebe nesting at larger lakes and was recorded as tracks on handheld GPS. Mink tracks crossing the transect line were logged with GPS as an index of activity. Active mink areas were located by dogs and also recorded on GPS. At treatment lakes an attempt was then made to remove the mink. Syningsfella traps were set in treatment areas where activity was registered but no mink was found. These were checked at the end of the week.

Experiment 3. Assessing predation risk with artificial nest

The third experiment followed the two trials of mink removals (experiment 1 and 2) and coincided with incubation and hatching of the earliest clutches of grebe. It was carried out at all seven lakes. It involved camera monitoring of artificial nests in grebe nesting habitat and was designed to assess egg predation risk due mink. We recorded by means of Garmin Map source habitat features which potentially could predict the variation in mink egg predation between lakes; specifically lake area and perimeter, altitude, distance from the coast and length of river tributary from the coast. Within the lakes we measured for each artificial nest the distance to closest incoming or outgoing waterways. Previous studies show that mink densities are higher in coastal than inland regions and also that mink mostly utilise waterways (Dunstone and Davies 1993).

Artificial nests of similar size and appearance to those built by grebe were made by binding lake vegetation around a small polystyrene raft. A quail egg was put in each nest to simulate an unattended nest during incubation phase. Nests were anchored using plastic coated gardening wire weighted by a stone. Five pairs of nests were deployed between 22–23 June and 14 July 2011 at each lake along a 1 km transect in grebe nesting habitat. Deviations occurred from 1 km when vegetation was patchy (mean 1.14 km, range 0.83–1.46 km). Transects were chosen to cross a major inflow or outflow maximizing the chance that mink would cross the area. Where several waterways existed, the transect line was chosen randomly. Mean distance between nest pairs was 284 m (range 151–469 m) and mean intra pair nest distance was 16 m (range 8–90 m). The first nest of each pair was deployed with a 14 × 9 × 6 cm game camera. The camera was fastened to a thin stake 30 cm above the water line and approximately 3 m from the nest. Picture settings were set to motion in order to record movement at the nest. The second nest in each pair had no camera and functioned as a control for camera effects on nest survival (Richardson et al. 2009). We assumed that non camera monitored nests were subject to the same predator species and to the same predator behaviour as the camera monitored nests. The state of the nest, predated or not predated was recorded at the end of the period. Variation in predation rate between the seven lakes was analysed with simple logistic regression model in R with binomial distribution. The predictor variables area, altitude, river length and distance to nearest stream were entered singularly.

Ethical standards

All experiments comply with the current laws in which they were performed.

Results

Experiment 1

Activity of mink on the rafts was low in particular during spring and early summer when grebes are nesting and increased at all lakes during late summer (Fig. 3). Only two mink were captured from 259 trapping possibilities (i.e. at non malfunctioning stations on each of the treatment lakes) over a total of 89 trapping days, giving a frequency of 0.02 mink per trap day. There was one occurrence of by-catch of a waterfowl.

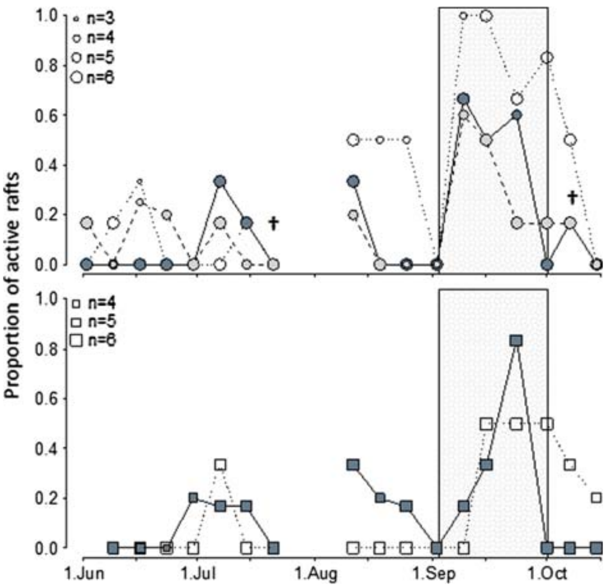

Figure 3. Mink activity shown as the proportion of mink raft stations with mink tracks recorded at seven day intervals in five lakes in Troms county between 26 May and 20 October 2010. Treatment lakes are shown by shaded symbols and control lakes by open symbols. Size of symbol shows the number of functioning rafts during trapping and recording of mink activity. Shaded rectangles depict periods of only monitoring in trapping lakes (see text for details). Lakes are Langvatn: dark grey circle, Sagelvvatn: light grey circle, and Josefvatn: open circle. Timing of capture of trapped mink at Langvatn is depicted by †; Sandsvatn: dark grey square, Nordbyvatn: open square.

Experiment 2

Snow conditions for tracking with dogs were good for all lakes except Sandsvatn where they were moderate as snow had begun to melt. Snow conditions for human visual tracking were poor at Sandsvatn. Mink activity assessed by means of dogs was low (Table 1). No mink were present in recently used holes and no individuals were caught by setting traps at places where mink activity was indicated by the dogs.

Experiment 3

Predation rate was high occurring at 56 of 70 artificial nests. At camera equipped nests, 27 out of 35 nests were predated. Predator species was detectable on 21 of these occurrences (Table 2). No mink egg predation was recorded. In addition, no pictures of mink were recorded in the vicinity of the nest.

Hooded crow *Corvus corone* was responsible for the majority of predation whilst jay *Garrulus glandarius* and common gull *Larus canus* were occasionally recorded. There was a significant heterogeneity among lakes in total predation rate (Fig. 4) with Nordbyvatn clearly deviating from the other lakes in terms of lower predation rate. Logistic regression on the proportion of surviving nests showed that none of the site scale predictors or distance to nearest stream were relevant ($p > 0.43$ for all models). Moreover, there was no difference in egg predation rates between camera or control nests (co-efficient estimate –0.35, ± 0.60, $p = 0.55$, $DF = 68$).

Table 1. Mink activity and trapping effort at study lakes between 2 and 4 April 2011. Transect length, snow conditions, number of times mink tracks crossed each transect line, number of mink holes found by dogs and number of times mink holes were excavated due to recent activity based on dog behaviour are shown. In addition the number of traps set inside the study area and in river outflows (outside of the study area), and number of days traps were active are also shown. Snow conditions were assessed as the same for both dog tracking and human visual tracking apart from at Sandsvatn where human visual tracking is shown in parenthesis.

Treatment /control	Lake	Date	Transect (km)	Snow conditions	Tracks (freq)	Holes (freq)	Excavations (freq)	Traps set (freq)	Traps set in outflow (freq)	Trap days (freq)	Mink killed (freq)
Treatment	Langvatn	2 April	7.9	Good	8	5	3	6	0	5	0
	Sagelvvatn	2 April	4.3	Good	0	0	0	0	2	4	0
	Nordbyvatn	3 April	5.1	Good	3	2	2	0	2	3	0
Control	Josefvatn	3 April		Good	0	0	–	–	–	–	–
	Sandsvatn	4 April		Moderate (poor)	4	0	–	–	–	–	–

Table 2. Artificial nest survival and frequency of egg predation by egg predator species for camera equipped nest and control nests (without cameras) between 22 and 23 June and 14 July 2011.

		Predator species at camera nests						
Lake	No. of camera equipped nests	Hooded crow	Jay	Common gull	Unknown	Survival at camera nests	No. of control nests	Control nests Survival
Josefvatn	5	4			1	0	5	0
Langvatn	5	3		1	1	0	5	0
Laksvatn	5	3			1	1	5	1
Nordbyvatn	5				1	4	5	4
Øvervatn	5	2	2			1	5	0
Sagelvvatn	5	5				0	5	0
Sandsvatn	5	1			2	2	5	1
Total	35	18	2	1	6	8	35	6

Discussion

The results are not consistent with the hypothesis that mink predation is the cause of decline in breeding numbers of Slavonian grebe in the region targeted by the present study. Monitoring of mink activity was generally low despite there being multiple possibilities for mink detection at each trapping and monitoring round. Activity was particularly low during the grebe nesting season. Furthermore, no predation event due to mink was recorded on the simulated grebe nests. Despite intensive trapping at 3 sites only two mink were caught. This is a low rate compared to other studies (Craik 2008, Harrington et al. 2008) even allowing for differences in capture methodology. Craik (2008) used non baited live traps, and caught an average of 3 mink year^{-1} per trap site during daily trapping sessions between June and the end of September at coastal sites. Harrington et al. (2008) used baited live traps and caught an average of 4.8 mink year^{-1} per trap site over a five-day trapping period in July and September at inland sites. These figures give a respective trapping rate per day of 0.73 and 0.64 in contrast to the trapping rate in this study of 0.02. We are not aware of any studies that compare live trapping capture rates with lethal traps or of studies that compare non baited traps to food baited. One study that compared the use of scent gland lure had mixed results (Moore et al. 2003).

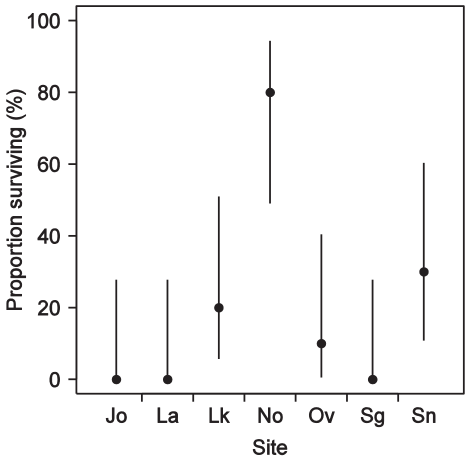

Figure 4. Survival estimates from logistic regression model with 95% CI for artificial nests at seven sites in Troms between 22 (Sandsvatn, Nordbyvatn, Josefvatn, Sagelvvatn) and 23 June (Langvatn, Øvervatn, Laksvatn) and 14 July (all sites) 2011.

Predation rate on artificial nests needs to be interpreted with care (Moore and Robinson 2004) and pertinent to the nesting behaviour of grebe may underestimate the risk of predation during intensive nest feeding activity during the first few days after hatching (Dillon et al. 2008). However, the high incidence rate of crow predation is in line with results from studies of crow diet (Coombs 1978, Zduniak 2006), studies of predation of natural nests on land during incubation (Stien et al. 2010) and hatching (Stien unpubl.), as well as studies of artificial nest predation in the Troms region (Pedersen et al. 2009, Klaussen et al. 2010). Furthermore, Summers et al. (2009) found a negative correlation between crow abundance and both grebe clutch survival and productivity. Crow and raven are included in the grebe action plan (Fig. 1) but without any empirical underpinning. Using an adaptive management approach, the next step would be to investigate crow predation of grebe nests. Camera monitoring at natural nests (Perkins et al. 2005, Richardson et al. 2009) could be used to test the hypothesis that nest predation is a key factor behind the decline of the grebe with crow being the most significant driver.

Our study indicates how an adaptive management framework can be implemented in order to increase knowledge for two species at opposing sides of conservation concern. Whereas grebe is vulnerable to extinction, American mink is seen as a key cause of local extinction of many ground nesting birds (Nordström et al. 2003, Bonesi and Palazon 2007). Our study provides previously lacking knowledge about mink activity in Norwegian lake systems as well the interaction between mink predation pressure and grebe nesting numbers and success. Thus, although mink is perceived as a cause of population decline for this species, implementing mink control as a management action aimed at preventing the decline of grebe in these areas is likely to be ineffective. Heterogeneity in predation pressure and predation species is seen in other studies of ground nesting birds (Chalfoun et al. 2002, Bolton et al. 2007, Stien et al. 2010) and is important to identify at sites targeted for management in order for the implemented management to be effective. Furthermore, utilising this progressive learning approach, which in our study involved three sequential experiments in the core area of grebe decline enabled us to rule out mink control as a management option within 1.5 years of initiation of the study. Thus the time lag between identification of need to act and appropriate action is minimalized. Finally, our study enabled us to identify crow nest predation as a more probable driver of grebe population declines in the study area.

Where several factors are proposed as being drivers of target species dynamics, active adaptive management is often more appropriate as multiple hypotheses are tested concurrently (according to an active management scheme; Williams 2011). However, there is seldom funding for this approach within nature management. This study shows that passive adaptive management as defined by Westgate et al. (2013) also has value within the nature management setting. Using the passive adaptive management approach, factors in the model would be tested sequentially.

Although countries have committed themselves to implement measures to reduce the loss of biodiversity, there will always be a lag in identification of species to be targeted and initiation of management. Poor knowledge of causes of declines hinders our ability to restore populations; adaptive management provides a framework for resolving this issue. It involves first making a conceptual model of potential drivers of population decline. These are then tested one at a time, improving our knowledge of their relative importance, and ultimately helping us focus conservation efforts (Lindenmayer and Likens 2010). It uses a framework which is simple to understand and highly relevant to the management goal for the conservation of the species. It is strange that the adaptive management approach has not been more widely adopted in conservation management (Westgate et al. 2013). We echo Westgate and Likens and advocate a call for a revival of this approach.

Acknowledgements – We thank Malangen-, Vestre Balsfjord-, Laksvatn-, Takvatn- and Sagelvatn- landowner associations and Statskog S.F. for permission to deploy mink traps on their land, and to Renathe Lohne for assistance in the field. Funding was provided by the Norwegian Environment Agency, Troms County Governor and the University of Tromsø.

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Paper IV

Breeding persistence of Slavonian Grebe (*Podiceps auritus*) at long-term monitoring sites: Predictors of a steep decline at the northern European range limit

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Abstract

The Slavonian Grebe (*Podiceps auritus*) has its European northern range limit in northern Norway and is a species of national conservation concern due to its small population size and unknown population trend. Long-term monitoring at the range limit suggests breeding site use is in decline. We used annual occupancy data from 104 breeding lakes monitored since 1991 in northern Norway to investigate correlates of change in occupancy. Persistence was 100 % until 1999, but thereafter decreased to 25 % (26 lakes with breeding pairs). A particular steep decrease occurred between 2010 and 2012. Persistence increased with the number of pairs present in each lake in the initial monitoring year of 1991. The number of grebe pairs also decreased in the lakes that had continous breeding persistence over the entire 22-year monitoring period, suggesting a large-scale factor caused the population decline. Over the last year of the monitoring series, lake altitude was negatively related to the probability of persistence, indicative that harsh climate played some role. The temporal pattern of persistence was not related to mean winter temperature, however the decrease between 2010 and 2011 coincided with a late ice melt in 2010. Monitoring that includes a larger area of the species' range is required to conclude whether the observed decline indicates an overall decline in population size or range fluctuations at the edge of the species' range. However, investigating the processes that determine population range borders can give insights into important limiting factors pertinent to the conservation of species in the long term.

Key-words:

range change, red list, conservation, proportional hazard models, long-term monitoring

Introduction

Identification and management of species of conservation concern is hampered by a lack of knowledge about the population trends of the target species. Knowledge is often dependent on species' popularity with both knowledge of population trends and conservation management being most prevalent for birds, butterflies and mammals and less so for other insects and amphibians (Lecis and Norris 2004, van Swaay et al. 2008). Even for charismatic species, monitoring to capture spatial variation in population trends and ranges is often lacking. However, in recent years more robust monitoring programs have been established that allow estimation of change in nation or continent-wide population ranges (e.g. Newson et al. 2005, van Swaay et al. 2008, Thomas 2010).

Site and/or habitat occupancy may vary temporally and spatially, with occupancy at range edges especially prone to change over time as the ecological conditions are at the limits of those under which the species is adapted to exist (White 2008, Sexton et al. 2009, Gilman et al. 2010, Rius and Darling 2014). Thus, (sub-)populations at species range edges are often transitory (Lawton 1993), existing in metapopulations or source-sink populations (Hanski and Gaggiotti 2004) which can be reduced to extinction state when conditions become less favourable.

Investigating causes of change in species range has received much attention in the scientific literature particularly with respect to climate change and its implications for vulnerable species (e.g. Chen et al. 2011, McClure et al. 2012). Physical factors (e.g. climate) are recognised as being the principal drivers of species ranges at regional and larger scales, whereas biological interactions are more important at local scales (Araújo and Luoto 2007). In addition, physical factors are considered to be of primary importance at northern species' ranges, although some advocates of climatic envelope models state the need for the inclusion of demographic factors such as dispersal and intra/interspecific interactions (e.g. Davis et al. 1998). Demographic factors may be of particular relevance for species characteristically breeding in small numbers in discrete habitat patches across their range with the small unit size making patches prone to extinction due to founder effects and demographic stochasticity (Traill et al. 2007, Moran and Alexander 2014, Rius and Darling 2014). Species that migrate between breeding and non-breeding grounds may moderate the risk of patch extinction by forming seasonal re-colonising waves (Moran and Alexander 2014). As such, migratory species have the potential to exist in suboptimal breeding areas.

Empirical studies involving both physical and biotic correlates of range change can result in important insights into decisive factors underlying range shift (e.g. Lecis and Norris 2003, McClure et al. 2012) and are therefore an essential component for guiding effective management for species of conservation concern. Much data is readily available from existing databases regarding site characteristics of high biological significance for species. Combined with existing temporal site persistence data, this can be used to investigate decisive factors for range shifts.

Slavonian Grebe (*Podiceps auritus*), is a species of national conservation concern (Kålås and Viken 2006, Direktoratet for naturforvaltning 2009), however there is currently no systematic monitoring at the national scale (Øien and Aarvak 2008). The Slavonian Grebe is a seasonally migratory species, overwintering in coastal regions and breeding in small numbers mostly on small inland lakes (Faaborg 1976, Sonntag et al. 2009, Summers et al. 2011). Present in Northern Norway at the northern end of its European range for over a century, the species experienced an apparent increase in numbers between the 1970's and 1990's (Fjeldså 1973a, Strann and Frivoll 2010). However, monitoring of active northern breeding sites from the 1990's to present shows a decrease in number of pairs and site use (Strann et al. 2014). At the southern end of its Norwegian range it is becoming more abundant and it appears to be spreading southwards (Øien and Aarvak 2008). Proposed but largely untested factors responsible for the decline of the Slavonian Grebe have been identified in an action plan for the species (Direktoratet for naturforvaltning 2009) and include predation by mink (Stien and Ims 2015), predation by corvids and food resource competition with fish. However, additional factors including several habitat characteristics expected to have biological significance as drivers of site persistence and indeed range change were not included.

We investigated the breeding site persistence of Slavonian Grebe at 104 lakes at the northern edge of its population range between 1991 and 2012 in order to evaluate the relationship between pertinent physical and biological factors and the population decline. We expected lakes with small populations, unproductive habitat and harsh climate to be more prone to perish. We discuss the implications for management of this targeted species from the study.

Materials and Methods

Study species and area

Study species

The Slavonian Grebe, hereafter referred to as grebe, has a circumpolar distribution mainly at 50 – 65 ˚N in the boreal climatic zone, breeding in North America, Europe and with isolated populations in Iceland, Færoes and Scotland (Bird Life International 2011). In Norway, the species extends between 60˚ 52' and 69˚ 30' and so forms one of the most northerly ranges for the species internationally (Fjeldså 1973a, Fournier and Hines 1999). Occasional breeding has been recorded further north in

Norway in eastern Finnmark and adjacent districts in Finland and Kola Peninsula (Fjeldså 1973a). The populations of Norway, Iceland and Scotland are described as a subspecies *P.a.arcticus*, being morphometrically semi-distinct and are thought to have different origins from the rest of the Western European population (Fjeldså 1973a).

The grebe spends most of the year in marine habitat but migrates inland to breed between May and September. Breeding can occur in both freshwater and brackish water and in a wide range of lakes sizes, with sites (< 10 ha) common in north America and the Baltic and a larger range of site area used in northern Norway and Iceland (Fjeldså 1973b, Faaborg 1976, Ulfvens 1988, Ewing et al. 2013). Sites commonly have between 1-2 pairs and seldom more than 20 pairs per lake (Fjeldså 1973c, Faaborg 1976). In Norway, winter habitat is in coastal archipelago and outer fjord systems (Fjeldså 2004, Strann and Frivoll 2010) with part of the population migrating as far south as the Scottish coast (Øien and Aarvak 2009). Inland observations during winter are rare and are normally before ice has formed on lakes or on ice free lakes close to the coast (Cramp et al. 1977, Øien and Aarvak 2008). Onset of nest building is determined by ice melt and varies considerably with latitude, altitude and season (Cramp et al. 1977, Fjeldså 2004). Nests consist of floating rafts of dead plant material, constructed in shore vegetation. Diet during the breeding season consists mostly of fish by biomass but also of aerial and aquatic invertebrates (Fjeldså 1973b, Dillon et al. 2010). Young and adults migrate to the coast in September.

The species has a circumpolar population of 140,000 - 1,100,000 individuals (Bird Life International 2011). The general trend for the population is declining e.g. 75 % decline in North America over the last 40 years (Bird Life International 2011), but due to the size and geographical extent of the population, the species is categorised as 'least concern' on the IUCNs red list. In Western Europe and Scandinavia, historical records indicate a range expansion westward into southern and middle Sweden during the late 1800's and early 1900's. The populations in northern Norway and Iceland have been in existence for at least 2 centuries while the population in Scotland established itself during the first half of the 20th century (Fjeldså 1973a, Douhan 1998). In Norway (Figure 1), historical records indicate that the core area in the 1970's was between Bodø and mid Troms and was estimated to be c. 400 pairs (Fjeldså 1980).

Although no systematic monitoring of grebe occurs on a national scale, regional scale monitoring of core sites in Troms and bordering Nordland reveals a decrease in the use of breeding sites compared to when monitoring began in 1991 (Strann and Frivoll 2010, Strann et al. 2014). National declines have been reported in neighbouring countries with an estimated 54% decline between 1972 and 1996 in Sweden (Douhan 1998) and strong negative population change index since 1997 in Finland

(Pöysä et al. 2013). In Sweden, the population appears to have increased again and in 2011 was estimated to be close to the 1972 estimate of 2200 pairs (Norevik 2014). This increase has been an accompanied by an apparent eastward shift in its range away from inland areas to areas along the Swedish Baltic coast (Norevik 2014).

Study area

We report data from 104 study sites located in Troms and northern Nordland regions, between 68˚30’ and 69˚43’ N and 16˚39’ and 22˚09’ E. Sites were chosen for monitoring annual breeding success and were therefore all occupied in 1991. Six sites were omitted from the analysis as they had very different habitat characteristics than those of lakes; five occurred in “lombolas” which are small widenings of river sections and one opened directly into the sea. The 104 study sites were all inland and fed by streams or rivers and/or had rivers as outflows. Average (mean) water body area was 93 ha (median 19.18, range 0.34 – 1521 ha) and mean altitude was 90.98 m (median 91.00, range 0-269 m). Immediate surrounding vegetation was dominated by mosaics of mountain birch (*Betula pubescens*), Scots pine (*Pinus sylvestris*), mire, heath and grassland. Agricultural grassland also existed around some lowland lakes. Lake bedrock consisted of mostly calcareous rock types including mica, mica slate, meta-sandstone and amphibolite, with smaller frequencies of marble rock types including calcareous mica and marble. Granite rock types including dioritic to granitic rocks and conglomerate and breccia occurred less often. Lakes were mostly oligotrophic with several mesotrophic and eutrophic lakes. Dominant shallow water vegetation included bottle sedge (*Carex rostrata*) and to a lesser extent bogbean (*Menyanthes trifoliata*), and provided nesting habitat for the grebe. Lake vegetation was sparse in oligotrophic lakes forming small pockets of nesting habitat, and more or less continuous in eutrophic lakes, providing continuous nesting habitat around the lake edge perimeter. Mean distance from lake centroids to nearest road, ranging from district to European road, was 0.53 km (median 0.44, range 0.25 – 1.99 km).

Data

Grebe monitoring

Monitoring was based on two visits each year in the period 1991-2012. The first visit was around 22 June, roughly 3 weeks after ice melt and the second between 10 and 20 July (exceptionally the end of July). Number of nesting pairs, territorial pairs and non-territorial individuals were counted in both visits from standardised observation points using binoculars and telescope. The counts of nesting pairs were used in the analysis and were expressed as a single unit of observed number of breeding pairs per lake in the analysis.

Habitat

Habitat variables were extracted using ArcMap 10.0. Lake bedrock was categorised into three bedrock categories, calcium, granite and marble to reflect water pH and hence be a proxy for lake ecosystem productivity determining nesting habitat and food resource availability. Marble category was used where marble derived bedrock was present, calcium category where calcareous bedrock was present in the absence of marble, and granite category where bedrock was derived of granite without the presence of marble or calcium. Vegetation around each lake was classified based on a national vegetation map developed from Landsat imagery (Satveg, Johansen 2009). From this map the original 25 vegetated classes were grouped into 6 initial habitat types: coniferous forest, deciduous forest, mire, alpine, herb and agriculture and further into three broad landscape types: forest, open lowlands (mires, herb and agriculture) and alpine. The proportion of the different habitat types were calculated in two buffers surrounding each lake with a radius of 100 m and 200 m respectively. Visual inspection of the resulting proportions revealed no difference between the two buffer radii and a 100m buffer was therefore chosen to represent the proportional coverage of habitat and landscape types around each lake. Proportion of agricultural land was used as a proxy of eutrophication which has been shown to be associated with colonisation of previously unused breeding areas (Douhan 1998). Distance between individual lakes and nearest road was used as a proxy of disturbance.

As no data existed for the date of ice melt of individual lakes, we explored the use of air surface temperature and snow depth data as possible proxies (Borgstrøm et al. 2010, Kvambekk and Melvold 2010, Godiksen et al. 2012). Values were extracted from national air temperature and snow depth models with a 1 km grid resolution (https://met.no). Where lakes crossed two grid squares, the value from one of the grid squares was used, selected at random. Mean temperature and total cumulative positive temperature (˚C) were expressed as yearly mean and yearly summed temperature > 0 ˚C respectively for time-dependent analysis (see below) and total mean and total positive cumulative temperature for the time-independent analysis. Snow depth was expressed as yearly mean snow depth or total mean snow depth. Exploration of three winter time periods 1st November – 31st May, 1st January – 31st May and 1st April – 30th June indicated that ice melt was best indicated by positive cumulative temperature and that there was no statistical difference between time periods (AICc, Burnham and Anderson 2002). The period January – end of May was used with a sample size of 99 lakes for the time dependent-analysis of ice melt as five lakes shared meteorological data grid squares.

Statistical analysis

The key response variable was grebe site persistence (hereafter persistence). This variable was taken as the number of years from the onset of the monitoring to the year grebes disappeared from the site or until the end of the monitoring series in case grebes continued to be recorded during the entire 22 year monitoring period (i.e. until 2012). The presence-absence records indicated that detection rates were very high as continued presence were interrupted by one (n=11) to two years (n=2) in only 13 of the 104 lakes. Thus detection rate could be assumed to be close to unity (and thus omitted from the analysis) which allowed for more flexible and powerful analyses by semi-parametric Cox proportional hazards models (R library survival). For the 13 lakes with pseudo-extinctions the intermittent zeros (absences) where replaced with ones (presence) in those data records. The Cox proportional hazards model estimates the instantaneous risk of an event happening, in this case cessation of use of lake as breeding habitat and takes the form

$$\log h_i(t) = \alpha(t) + \beta_1 x_{i1} + \beta_2 x_{ik} + \cdots + \beta_k x_{ik}$$

where $h_i(t)$ is the hazard function i.e. the instantaneous risk of loss of breeding lake at time t, given the survival to that time, $\alpha(t)$ is an unspecified baseline hazard function and $\beta_k x_{ik}$ are the covariates entered into the model linearly (Fox 2002).

The full model contained additive effects of the continuous predictors altitude, lake area, number of breeding pairs at t_0 (i.e. 1991), distance to nearest road (road) and proportion of agricultural land (vegetation) and the 3 level factor bedrock with classes marble, calcareous and granite. The number of breeding pairs was used as a proxy for susceptibility to demographic stochasticity which could be expressed as total mean, total maximum and number at start of monitoring in 1991 (t_0). These indices of local population size were highly correlated but investigation showed that number of pairs at t_0 was the best predictor. Ice melt was initially explored as a time-dependent variable but the coefficient estimate was not significant. Ice melt was therefore entered as a time-independent variable in time-independent Cox proportional hazard model. As ice melt and altitude were highly correlated, the two were entered in separate models. All continuous variables were transformed to centralise their distributions and increase linearity, with square root transformation for altitude, number of breeding pairs (t_0), road and agricultural land. Lake area was log-transformed. Analyses were carried out in software package R (R Core Team 2014) and best model chosen by AICc. Goodness of fit of the selected models were assessed by Chi square test on Schoenfield residuals.

Results

The model including effects of altitude, lake area and number of breeding pairs at t_0 best predicted the persistence of breeding sites. However, this model showed violation of the assumption of proportional hazards for both altitude (Schoenfield residuals $\chi^2 = 6.19$, $P = 0.01$) and number of breeding pairs at t_0 (Schoenfield residuals $\chi^2 = 10.56$, $P = 0.0001$). Examination of the residual plots suggested that the hazard ratios increased abruptly for these predictors between 2011 and 2012. We therefore split the data into 2 groups to be analysed in separate models with the same covariates; the first model for the period 1991-2011 and the second for 2011-2012. As the second period had had one time interval, the analysis could be simplified to a binary logistic regression of the probability of one further year persistence of those lakes with breeding pairs still present in 2011. The fit for proportional hazard model containing effects of altitude, lake area and number of breeding pairs at t_0 was good when leaving out the last year of the time series (2012) (Schoenfield residuals 1991 - 2012: $\chi^2 = 5.72$, $P = 0.12$). Only the coefficient for the predictor *number of pairs at* t_0 was statistically significant (Figure 2). The estimate of this coefficient shows that an additional increase of 1 in the square root of number of breeding pairs at time t_0, reduced the hazard rate for loss of breeding lake by 90.2 % ($\exp[-2.31] = 0.098$, $P < 0.001$). The proportional hazard rate model for the period 1991 - 2011 explained 44 % of the variation and had good predictive power with an AUC of 81 % (95 % C.I. 71 - 89). Mean predicted probability of individual lake persistence after 21 years (in 2011) was 0.36 (95% C.I. 0.28 – 0.47). The loss of breeding sites began after 8 years (1999) (Figure 2) with a pronounced additional drop in the probability curve after 20 years (between 2010 and 2011). In the logistic regression model for the period 2011 – 2012 only the coefficient for altitude was significant (-0.23 ± 0.10, $P = 0.02$, area = -0.20 ± 0.28, $P = 0.48$, number of pairs at t_0 = -0.07 ± 0.87, $P = 0.93$, df = 34; Fig. 3). Between 2011 and 2012, mean predicted probability of individual lake persistence decreased by 31.6 %.

None of the habitat variables except altitude and lake area predicted the persistence of grebe in individual lakes. There was a small significant negative correlation between number of breeders at t_0 and proportion of mire (- 0.27, $P = 0.005$) and small significant positive correlation between number of breeders at t_0 and the proportion of herbs (0.31, $P = 0.001$), which to some extent might have concealed their effects. Goodness of fit test revealed that the overall model containing ice melt showed some indication of violation of the assumption of constant proportional hazard of predictor variables ($\chi^2 = 15.00$, $P = 0.03$), with both number of pairs at t_0 and ice melt showing indications of being non-proportional in predicting hazard rate ($P < 0.05$). As model selection using AICc showed no difference between the use of altitude or ice melt, altitude was used, enabling the use of all 104 sites in the analysis.

Discussion

The present 21-year monitoring series of breeding Slavonian Grebe in the northernmost part of its distribution range in Europe showed clear evidence of a decline. The onset of the decline in grebe breeding site occupancy began in 1999 and by 2012 the number of lakes with breeding pairs steeply declined to one quarter of those lakes that had breeding grebes 13 years earlier. The results support our predictions that lakes with small breeding populations, and to some extent poor environmental conditions (high altitude), have lower persistence but do not support our prediction that unproductive habitats lead to lower persistence. Persistence of breeding status was predicted well for the majority of the monitoring period by the inclusion of the variables number of breeding pairs and in the final year of monitoring by altitude. The number of pairs per site at the onset of monitoring in 1991 was also an excellent representation of the maximum number of pairs per site ($r = 0.90$). Thus, sites with small breeding populations were highly vulnerable to extinction, and the number of breeding pairs in the initial monitoring year explained the majority of the variation in persistence, potentially due to demographic stochastic processes (Caughley 1994). Whether persistence was maintained by site faithfulness by the same individuals over successive breeding seasons or replacement of individuals to the same sites via source-sink dynamics is not known as individuals were not followed in this study. However, evidence from other studies suggests that recruitment from within the regional population at least in part by returning females may well play a role in population persistence. Ferguson et al. (1981) found that individuals return to breeding sites in successive breeding seasons resulting in a certain level of both lake faithfulness and a wider local area faithfulness (Ferguson 1981), while Fournier and Hines (1999) and Ewing et al. (2013) found a positive association between breeding success on population growth rates in the following year. It can be noted that in our study the dominant pattern of lake occupancy was not represented by stochastic extinction- re-colonising dynamics at site level, indicative of classical meta-population dynamics. Rather the situation appears to be more in line with a “declining population paradigm” due to some deterministic driver (*sensu* Caughley 1994). Indeed, an overall steady decline in number of breeding pairs was even evident for those lakes that maintained continuous presence of breeding grebes over the 21 years (Figure 4). A similar declining trend (which has been ongoing since 1993) has occurred in the Scottish population of Slavonian Grebe (Ewing et al. 2013). While this population forms a southern range boundary for the species and may be expected to be sensitive to other processes such as range contraction due to climatic warming (Green et al. 2008), low breeding success appears to be partly responsible for the decline in the Scottish population. Identification of factors that can fully explain the decline have so far eluded research efforts (Ewing et al. 2013). Reasons for the change in numbers and eastern movement of the Swedish population are also currently unknown (Douhan 1998, Norevik 2014).

The lack of relationship between breeding site persistence and the meteorological variables (air temperature and snow depth) used here as proxies for ice melt dates may have been due to small-scale topographical variation in temperature and catchment effects (Kvambekk and Melvold 2010) not captured in the meteorological data. It would be useful to have better knowledge regarding the extent to which these variables capture the variation in ice melt times at individual lakes. Site persistence was also not correlated with mean winter temperature. However, the drop in persistence between 2010 and 2011 occurred after an exceptionally late ice melt in 2010. The resulting shortening of the breeding season may have resulted in the observed reduced site use the following year. Lagged effects on reproductive performance are apparent in several avian studies and include site avoidance after poor performance (e.g. Stacey and Robinson 2012, Hanssen et al. 2013). As grebes are income breeders (Kuczynski and Paszkowski 2010), the late breeding onset may have limited quality of eggs and/or offspring resulting in low productivity. Poor body condition combined with migration to wintering grounds, or non-related but correlated factors in wintering areas such as poor weather could have resulted in reduced over wintering survival (Newton 1998, Golet et al. 2004, Sandvik et al. 2005, Frederiksen et al. 2008). Altitude also negatively affected grebe persistence but significantly so only between 2011 and 2012. Altitude affects temperature and precipitation and modulates lake productivity and grebe breeding season length (Summers and Mavor 1995). Snow and ice cover delay return dates of individuals breeding at higher latitudes as they do not return to their breeding sites before there is open water (Fournier and Hines 1999, Øien et al. 2008). Presumably, the variation in ice melt day in this study was not sufficient to prevent grebe from initiating a breeding attempt apart from in 2010. In 2012, low altitude sites may have been available to most breeders as site occupancy had become so low. Alternatively, high altitude breeders may have been of poorer quality and so not attempted to breed in 2012.

We found no effects of habitat productivity, as indicated by bedrock, or presence of agricultural grassland indicating eutrophication. The majority of lakes in this study had either neutral or alkaline water characteristics based on bedrock classification, thus a water chemistry that should not limit fish growth or invertebrate abundance (Eriksson 1986). In addition, aerial insects make up a large proportion of grebe diet and are unlikely to be limited (Fjeldså 1973b, Dillon et al. 2010). In this study, only 19 of the 104 sites were less than 5 ha. This is in contrast to studies from the Baltic and

North America that have reported that the majority of sites were less than 5 ha but in common to earlier studies in northern Norway (Fjeldså 1973c, Faaborg 1976, Summers et al. 2011). The lack of relationship between lake area and breeding number in year t_0 may be modified by variation in patch quality making overall lake area a poor predictor of breeding population size (Hanski and Gaggiotti 2004, Lenda and Skórka 2010, Williams 2011). In many of the lakes, overall nesting habitat is patchy and not proportional to lake area. The relationship is further modified by territorial behaviour of the grebe, making high densities unlikely unless vegetation suitable for breeding is abundant (Fjeldså 1973c, Faaborg 1976).

The distribution and numbers of grebe present in the initial monitoring year (1991) suggests a possible recent northern increase in the species range compared to historical accounts gathered between the 1950's and early 1970's (Fjeldså 1980, Strann et al. 2014, Fjeldså pers. comm.). Although the mechanisms behind this shift are unknown, the present study indicates that range expansion further north has probably been limited by climatic conditions even though there is plenty of available habitat. We are not aware of any published data on the range dynamics at the northern end of the North American range during the same period, however a study of grebe towards the current North American range edge by Fournier and Hines (1999) shows a clear pattern of population growth with both temperature, precipitation and ice free days. The amount of mixing between the Swedish population and the Norwegian population is unknown but thought to be little (Fjeldså 1973a). Future investigation of the existing study population's overwintering movements may help determine whether the change is due to reduced mortality or use of alternative breeding sites.

The grebe is suffering decline in both its North American and western European range. In Norway, it now appears to be declining at the northern end of its range. This decline is mostly associated with a low number of pairs at most sites making the grebe very vulnerable to site extinction, in particular in harsher (higher altitude) environments. In order to say whether this reduction is indicative of a wider decline in the population, it is necessary to expand monitoring to cover a spatial extent that allows estimation of grebe population trends. Optimally, combining spatial data together with data on vital rates, site faithfulness, individual dates of ice melt and habitat characteristics measured at site scale, will allow us to come closer to understanding the main population drivers are in the grebe population and whether they are manageable by human intervention.

Acknowledgements

We are grateful to Matias Hagtvedt and Jan Heggås for helping to collect data in the field and to Torkild Tveraa for providing meteorological data. Funding was provided by The Norwegian Environment Agency, The County Governor of Troms and The University of Tromsø – Norway's Arctic University.

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Figure 1. The historical Norwegian distribution of Slavonian grebe between 1950 and 1970 adapted from Fjeldså (1973a) and the distribution for the present study between 1991 and 201. The historical distribution is located in northern Nordland and Troms (A), Helgeland coast (B) and North Trøndelag (C) and the sites used in the present study are shown by dots.

Figure 2. Predictions (solid lines) of probability of grebe breeding persistence with 95% C. I. (dotted lines) from the best model for Cox proportional hazard model for 104 lakes in Troms and northern Nordland for the period 1991-2011 a) mean of all co-efficient estimates, and predictions for different levels of b) number of pairs (t_0), c) lake altitude and d) lake area. P-values are derived from z-test of the coefficients of the predictor variables.

Figure 3. Predicted effect of altitude in time-period 2011 and 2012. The estimate is derived from a logistic regression model with altitude as the back-transformed predictor of site persistence. 95 % C.I. are shown with dotted lines and the observed survival for lakes over the range of altitudes are shown with open circles. The figure is shown with the full range of altitude values.

Figure 4. Mean number of breeding pairs per site and their standard deviations for the 26 sites that still had presence of breeding pairs in 2012.

Figure 1.

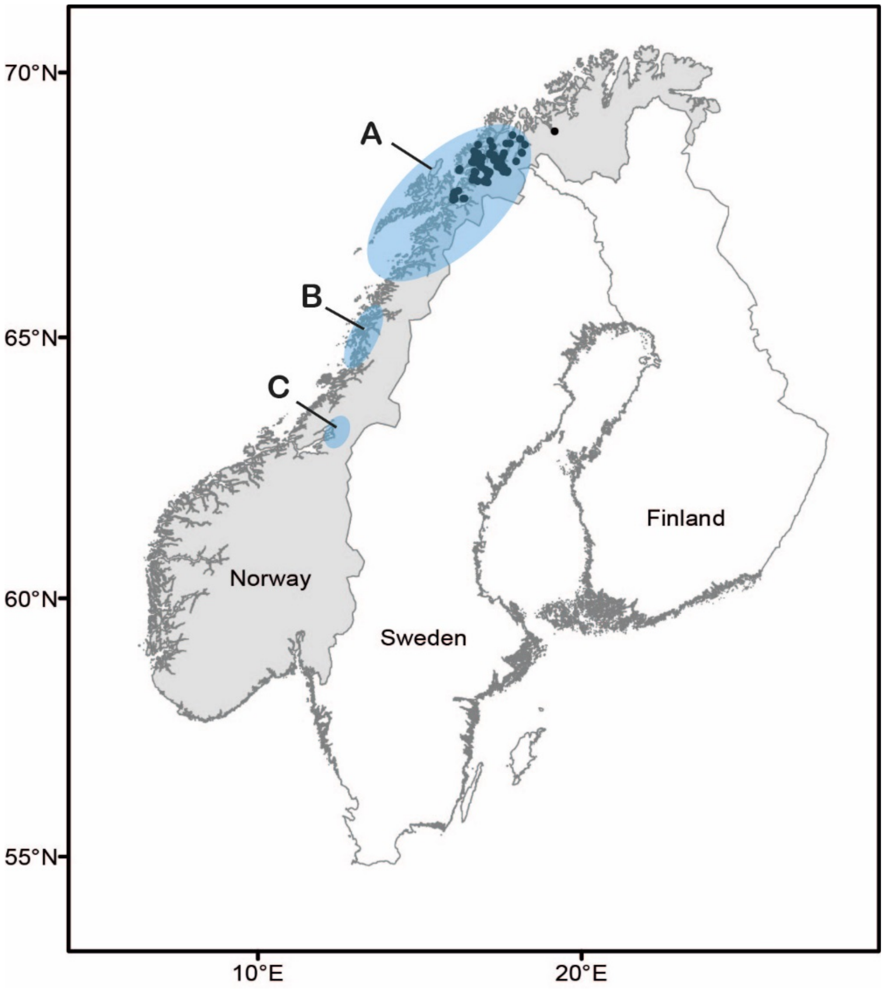
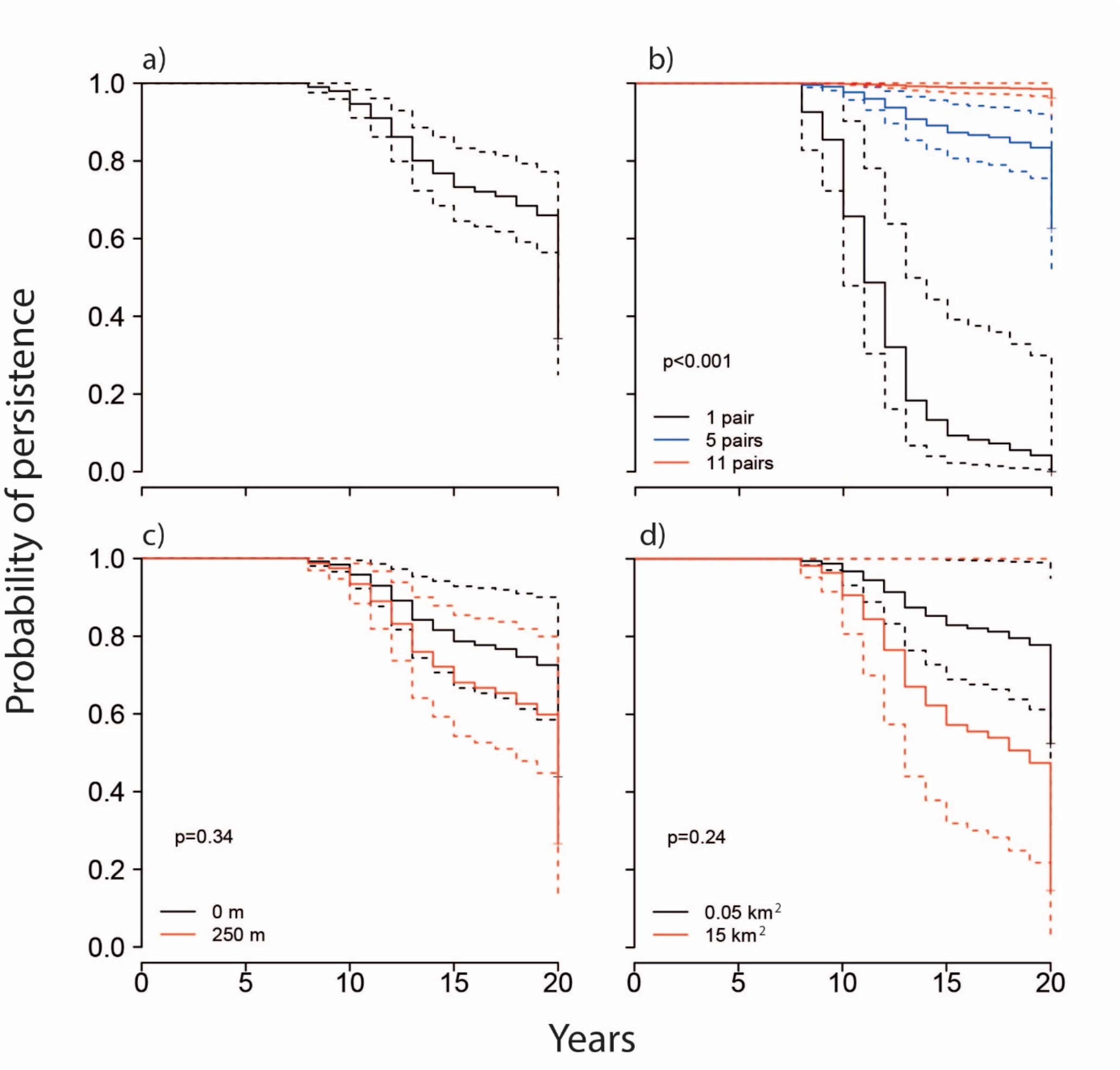


Figure 2.



a)
b)
c)
d)
Probability of persistence
1.0
0.8
0.6
0.4
0.2
0.0
p<0.001
1 pair
5 pairs
11 pairs
p=0.34
0 m
250 m
p=0.24
0.05 km^2
15 km^2
0
5
10
15
20
Years

Figure 3.

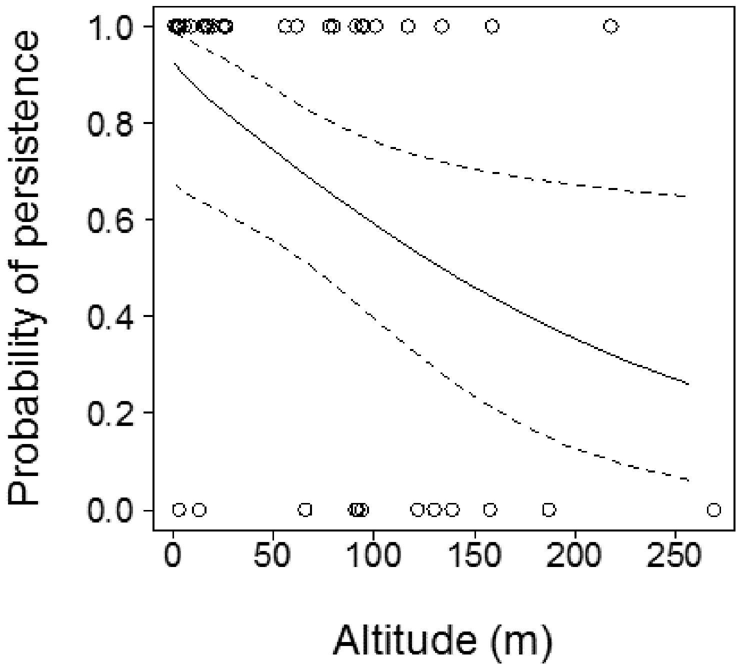
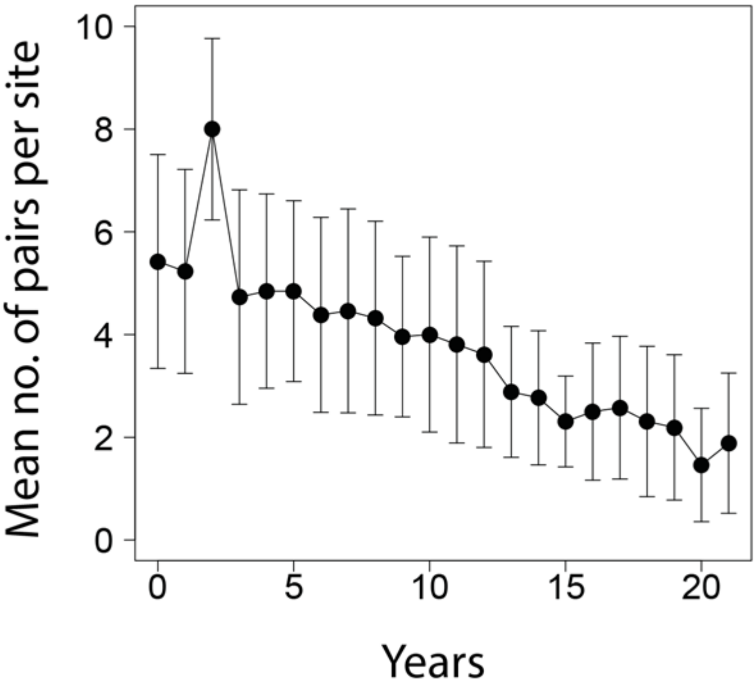

Probability of persistence
1.0
0.8
0.6
0.4
0.2
0.0
0
50
100
150
200
250
Altitude (m)

Figure 4.



Paper V

Volunteer hunter motivation and engagement to control the invasive alien American mink (Neovison vison) in Norway.

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Abstract

Invasive alien species (IAS) can have widespread negative effects on native biodiversity. We investigated the prospects of engaging hunters in large scale and collaborative efforts to control non-native mink populations in Norway. We made a questionnaire available to all members of the Norwegian Association of Hunters and Anglers (NAHA) to examine the conservation support and the level of efforts to remove mink in relation to wildlife value orientation, hunting motivations and bounty payments. We find that the general level of interest in mink control programs is low, but the few participating believe that mink is a conservation concern and particularly to ground nesting birds. Mink catches were best predicted by municipal bounty payments that caught on average 5.07 more mink than those who did not receive bounty. Contrary to expectations we found that mink hunters that prefer to hunt alone and that had no preference to hunt locally caught on average 2.89 more mink than those that hunted due to social benefits and preferred hunting close to where they lived. The majority of mink hunters prefer governmental-led programs (47%), 33% confer to NGO-led campaigns whereas 20% believe that mink hunting should be self-initiated by individuals or landowners. Their main recommendation is to invest in bounty programs (52%), but more organized efforts were also supported such as raising awareness and recruitment campaigns (33%) and providing equipment and covering costs for mink trapping (29%). Given the low interest in mink removal, we recommend to concentrate efforts around “conservation hotspots” as a start, involving contract operators, bounty payments and awareness and recruitment programs.

Introduction

Invasive species are responsible for the loss of species diversity that in turn can lead to alteration and degradation of ecosystems (Baillie et al. 2004, Poorter et al. 2007, Simberloff et al. 2013) and are estimated to cost Europe at least 12.5 billion euros per year (Kettungen et al. 2008). Invasive alien species (IAS), such as mammalian predators, can exert negative effects via novel predation strategies on native prey species that have not had time to evolve successful predator avoidance strategies, which in many cases eventually have caused local extinctions (e.g. Atkinson 2001, Didham et al. 2005). Signatory states to the Convention on Biological Diversity (CBD) recognize the wider threat of IAS to native species and have adopted a three-stage hierarchical approach to IAS: prevention; early detection and rapid eradication; and finally control and long-term containment of non-native species which are already established (CBD 2002). These CBD guidelines are also supported in the new regulatory framework for member states which are currently under development in the European Union (EU) (Beninde et al. 2014).

Control and eradication campaigns of non-native invasive species have usually been governmental-led and executed by professional conservation staffs (e.g. Bester et al. 2002, Moore et al. 2003, Nordström et al. 2003, Lorvelec and Pascal 2005, Cranswick and Hall 2010). However, time and financial constraints often limit such campaigns to smaller scales. Alternatively, the government may invest in harvest incentives to encourage a broader participation in removal campaign. These may include i) *bounty programs* that give participants monetary rewards based on sufficient evidence of removal; ii) *contract operators* in which public or private organization are directly paid to remove or harvest the invasive species; iii) *recreational harvest* facilitated by training, education and outreach programs or by iv) encouraging harvest of the targeted species by *regulatory modifications* such as changing hunting seasons, licensing practices or bag limits. Finally, governments could also play a role by supporting the development of *commercial markets* for increasing harvests of non-native invasive species. Pasko et al. (2014) show that few studies investigate the use of harvest incentives in invasive species management and best practice for control or eradication of IAS has yet to coalesce.

Inclusion of non-professional volunteers in a coordinated campaign could significantly improve IAS removal on a larger scale (DEFRA 2006, Bremner and Park 2007, Bryce et al. 2011). For example Bryce et al. (2011) successfully organised a campaign including gamekeepers, fisheries staff, wildlife conservation professionals, land managers and local residents to eradicate breeding mink to protect native species in an areas covering 10,570 km^2 in Eastern Scotland. The campaign is now covering larger parts of the Scottish mainland and a recent scoping study shows the potential of including ecotourism tour operators for eradicating mink around seabird colonies in coastal west Scotland (Fraser et al. 2014). Insights from red fox eradication programs in Australia confirm the significance of a well-organised and coordinated landscape approach for successful control and eradication of IAS (McLeod et al. 2011, Newsome et al. 2014). Bounty programs that are based on shooting, have generally been perceived as an ineffective method for controlling fox populations having suffered from the lack of persistent, planned and collaborative group effort (McLeod et al. 2011, Kirkwood et al. 2014). While such collaborative initiatives could be initiated by local communities, hunters, landowners or other organizations, a review of 34 participatory invasive-vertebrate programs in Australia show that active support from the government is a crucial element in most effective control programs (Ford-Thompson et al. 2012).

Incentives – or voluntary management programs are dependent on the willingness of people to donate time and energy on such initiatives. It is therefore crucial to investigate the motivation of potential participants before choosing the right mechanisms to achieve the goals. Ryan et al. (2001) identified concerns for the environment, personal growth and social learning as important for initial participation in volunteer activities in 148 programs in Michigan. Volunteers did not perceive themselves as free labour, but were deeply engaged in their work and needed to know how their efforts have helped the environment. On the other hand, social benefits such as meeting other people and socialising, may be crucial for volunteer commitment over time and therefore for the continuity of the program (Ryan et al. 2001, Asah and Blahna 2012). Ford-Thompson et al. (2012) found environmental motives as the strongest motivator in IAS programs, but economic effects were the most salient reasons for campaigns initiated by citizens who were typically landowners and agricultural communities. Other studies have shown that place attachment consisting of volunteer work near participant's homes or other areas they feel strongly about ensures a stronger commitment to the program (e.g. Selinske et al. 2015).

Diverse motives may explain the willingness to participate in volunteering, but deeper held beliefs and values may also influence successful IAS management (Sharp et al. 2011, Fischer et al. 2014). Wildlife value orientations may influence the hunting behavior through their impacts on more specific conservation beliefs and attitudes (Fulton et al. 1996) Wildlife value orientation could for instance explain differences in preferences for trapping (e.g. Manfredo et al. 1999) or divergence in views about lethal control in wildlife management (e.g. Manfredo et al. 2009). A difference in wildlife value orientations along a continuum from domination to mutualism appear to exist across western countries and are important for explaining differences in acceptability of lethal control in particular (Jacobs et al. 2014). Based on divergent value orientations we could assume that IAS which involves lethal control and trapping may recruit volunteers with different motives than in other conservation stewardship programs.

The purpose of this study is to investigate the potential for establishing harvest incentive – or volunteer-based mink control programs in Norway. Until recently there have been no coordinated programs for control or eradication of mink except for sporadic captures by recreational hunters or small-scale bounty programs which have been established in some municipalities. As local environmental NGO's are not so prevalent in Norway, a collaborative and coordinated program to remove mink is likely to depend on more organized involvement of recreational hunters, salmon fishers, or coastal populations dependent on fisheries and aquaculture. Hunters and anglers may have the motive for mink removal which may or may not be consistent with the need to protect red-listed species or seabird colonies. However, a targeted program that combines eradication of mink from nature reserves or other hotspot areas by professional staff with recreational hunters and bounty programs could allow for larger scale initiatives on a landscape scale. Potential participants are to a large extent organized by the Norwegian Association of Hunters and Anglers (NAHA) who organize 120,000 of the 190 000 licensed hunters in Norway (Kaltenborn et al. 2012). Understanding hunters' and anglers' motivations and value orientation, as well as their response to bounty programs is a first step for exploring volunteer based control programs.

We start this paper by summarising the government-led mink control programs which have been initiated so far. There are neither previous studies to refer to nor evaluation reports of these initiatives so we base this summary primarily on documents and knowledge acquired by working with this issue for several years. Next, we used a questionnaire to survey the perceptions, motives and value orientations regarding actual removal of mink hunters and trappers in the NAHA, and to examine the support for the leadership of such programs to understand how a collaborative incentive – or volunteer program best could be organised. The questionnaire also included a question regarding whether hunters received bounty payments. Previous studies show that a high percentage of hunters generally express utilitarian wildlife value orientations (Fulton et al. 1996) but Norwegian small game hunters vary extensively both in value orientations and in their motivation to hunt (Kaltenborn et al. 2012). We expected mink hunters with more utilitarian values and who hunt primarily for consumptive reasons to be more oriented towards the protection of fish and game species. Consumptive oriented hunters are also hypothesized to maximise catch to a larger extent than those with more appreciative motives (sensu Kaltenborn et al. 2012). Mink hunters expressing stronger caring beliefs for animals are expected to shoot or trap mink primarily because of biodiversity protection (i.e. red-listed species and protected areas). We also hypothesized that hunters receiving bounty payments would catch more mink than those not receiving bounty payments due to economic reward. Since the retention of hunters is important for long-term mink control we explored whether social benefits or hunting near their homes affects the catch rates and support to conservation actions. Finally, we discuss our results together with the preferred leadership s and open comments regarding ways to improve mink hunting and compare it to the experiences with large-scale IAS programs elsewhere.

Mink control programs in Norway

As with many countries, state organized hunting bounties were the main method of pest control in Norway during the last century (Pohja-Mykrä et al. 2005). These were disbanded in Norway in 1975, with organisation of bounty and size of economic reward being devolved to individual municipalities. Although payment of bounty for mink hunting varies with municipality, there is no overall knowledge of the number of municipalities involved or the amounts paid. An email survey of coastal municipalities from the 5 highest ranked counties for mink caught revealed that 27.78 % paid bounties ranging from 20 – 400 NOK (€ 2.36 – 47.33). Financial incentives from the Norwegian Environmental Agency were also potentially available to hunters through competitive application for county level distributed funds that were open to all individuals with game management interests. The Norwegian Environmental Agency made efforts to raise the profile of mink hunting within the NAHA by coordinating the production of hunting method manuals, media coverage and a number of written articles. However, no financial or logistical incentives were introduced, or research into understanding the dynamics of mink hunting within the NAHA. There was also no knowledge within the NAHA itself regarding the number of mink hunters in its association.

In 2010, the Norwegian Environmental Agency commissioned a status report of mink ecology and control in Norway and other European countries (Stien et al. unpub.) and began to gather information about mink control initiatives. As part of the information collation, there was a common meeting with participants of a successful citizen initiated mink control program at the World Heritage Site (WHS) on Vega island, in Nordland County and residents interested in mink control in areas adjacent to the WHS. The goal was to hear and report to the Norwegian Environmental Agency their experiences of mink control to protect several colonies of eider that enabled the traditional coastal eider down culture to be maintained, which in turn was the reason for the WHS status. The meeting revealed that the control program was citizen orientated with support from the municipality. The WHS committee had found and hired 2 proficient hunters with tracking dogs who were on call to remove ‘problem mink’ from eider down colonies i.e. mink not caught by colony owner initiated trapping campaigns. These hunters also undertook in their spare time, independent and fairly systematic mink hunting on the chains of islands to the south and north of the WHS. The hunters were partly motivated by receiving municipal bounty, which in turn had been initiated to aid the success of the WHS but also had a strong desire to eradicate mink in order to aid conservation of ground nesting seabirds. Results from the rest of Norway indicated that few mink control initiatives existed and that no systematic monitoring of the effect of mink capture on mink numbers or monitoring of sea birds existed. These additional efforts consisted of group citizen initiatives in a few areas in southern Norway and in addition, the contractual operators of the Norwegian Environmental Agency, the Norwegian Nature Inspectorate operated seasonal removal of mink from a small number of nature reserves where mink predation of ground nesting sea birds was observed to be high. This involved hiring a few individual mink hunters with tracking dogs to remove mink from individual reserves before the breeding season began. Otherwise, there were small-scale actions by Norwegian Nature Inspectorate staff including an attempt by staff to recruit local residents to participate in mink control around a nature reserve. Concurrently, county environment protection officials were required to report to the Norwegian Environmental Agency the status of coastal and island nature reserves in terms of threat to breeding seabirds from mink. The Norwegian Environmental Agency drew up a short list of prioritised reserves for mink removal and chose training of professional staff in the Norwegian Nature Inspectorate to undertake the mink removal.

Methods

Survey Sampling and recruitment

Our study was largely exploratory and intended to provide knowledge for the design and elucidation of alternative strategies for a targeted volunteer – and incentive program. As there is no arena for recruiting mink hunters directly, we decided to recruit broadly through the NAHA. We advertised the questionnaire in co-operation with NAHA as a news item in September 2013, on both the organisation’s internet home page and monthly magazine with a link to the electronic questionnaire. This was followed 6 weeks later by direct e-mail contact with all NAHA at county level (n=19) and municipality (n=509) groups and further, the 152 municipalities for the five counties with highest mink returns in the 2012 hunting season. The e-mails explained the goals of the project and asked for contact information for potential respondents. The e-mail to NAHA groups also asked for promotion of the survey at county and municipality level. We spent considerable time on the telephone following up contacts and participated in local radio to increase recruitment to our study.

Survey questionnaire

We designed an internet survey in Questback directed to mink hunters. The questionnaire was trialed on a small subset of eight respondents and employees in the NAHA and altered slightly based on their feedback before being available to respondents. The questionnaire consisted of 47 questions and included questions about the number of mink caught-, and general hunting effort in the 2012 hunting season. We included questions to investigate respondents’ wildlife value orientations, motivation for mink hunting and payment of bounty (Fulton et al. 1996) . The variable bounty was collapsed into the 2 categories received or not received. To explore possible forms of leadership of mink control programs we included a question about whom hunters thought should be responsible for mink control. Questions reflecting the motivation to hunt included stating the relative importance of personal, social and environmental benefits for motivating hunters in general (Asah and Blahna 2013). We built on the standardized questions developed to measure wildlife value orientations (e.g. Manfredo et al. 2009) and included a category in subsistence hunting to capture the motivation to hunt for game and fish in Norway. Similar to Manfredo et al. (2009) we used a 7-point scales ranging from −3 (strongly disagree) to +3 (strongly agree) with zero as a mid-point. The utilitarian value orientation was based on four belief items in which 2 reflect priority of humans over wildlife and 2 threats to life and property. We also included two items reflecting caring beliefs. For hunting motivations, respondents were asked to check one or more statements describing why they hunt or fish. We supported these general questions on wildlife value orientations, motivation, and bounty with more specific questions directed to indicate attitudes and intent to participate in conservation aimed at mink control. These included questions about perceived threats of mink to fish, game and red-listed species as well as the importance of removal of mink within protected areas (PA´s). ‘Removal from PA’s’ included nature reserves, national parks, world heritage sites and other specially protected areas. The variable ‘red list species of bird’ was aggregated for those who checked that mink is a threat for black and white guillemot (*Cephus grylle*), puffin (*Fratercula arctica*), black throated diver (*Gavia arctica*) and common scoter (*Melanita nigra*) according to the Norwegian Species Red List for 2010 (Kålås et al. 2010). The variable ‘ground nesting species not red listed’ refers to common eider (*Somateria mollissima*) and ‘other ground nesting birds’. Finally, we included threat to ‘salmon and other salmonids’ as a separate variable. Mink hunting behavior was surveyed by three questions (Table 1) to investigate how beliefs, motivations and conservation attitudes affected the number of mink caught and the effort invested in mink hunting. We analysed number of days hunted and intentions to remove mink the next 3 years, but we only retained mink catches in the 2012 season as our analyses showed a significant association among those three variables.

For the purpose of setting up a conservation program targeted towards removing mink we also asked who they thought should be in charge of the program. Since this is the first study targeted towards mink hunters in Norway, we wanted to make sure that we identified a broad range of challenges and alternatives for initiating control programs. We therefore included an open question inviting respondents to contribute suggestions that could improve mink hunting.

The questionnaire and ethics were reviewed and approved by the Norwegian Social Sciences Services (NSD), project number 34676.

Data analysis

Exploratory factor analysis is generally not recommended for small sample sizes, but could be meaningful if interpretable factors can be identified (Pearson and Mundform 2010). We first used principle component analysis and correspondence analysis to investigate the main structure of our data, but decided to use agglomerative hierarchical cluster analyses to classify hunters into groups, which is recommended when sample size is small. Variables were standardized and centralised before conducting Principal Components Analysis (PCA) on belief variables, while Multiple Correspondence Analysis (MCA) was used to explore the categorical data on motivation and leadership variables. We then created classes of the wildlife value orientation, motivation and leadership data by using Hierarchical Clustering on results from the MCA and PCA. Clusters were determined using a Euclidean distance metric for co-ordinate distances and Ward's method to define optimum clusters (Ward Jr 1963, Husson et al. 2010). All of these analyses were carried out in the R package FactoMineR (Husson et al. 2015).

We used generalised linear regression (glm) assuming a poisson error distribution to model the effects of bounty, value orientation and motivation on the number of mink caught. For the categorical data we used cumulative logistic models to predict conservation attitudes and leadership from the wildlife value orientation and motivation using the clm function with a probit link in R package ordinal (Christensen 2015). Best models were chosen using AICc for small sample sizes (Burnham and Anderson 2002).

Results

One hundred and four respondents from 18 counties answered the questionnaire, of whom 96 were NAHA members. While the sample size is statistically small, it represents hunters responsible for a high number of mink caught in Norway. Their total catch of mink was 1053 (mean 12.84, [1 – 80]) which accounts for 19.87 % of the national mink total for the 2012 season (SSB). More than 60% caught less than 5 mink during the 2012 season, which means that a few hunters are catching a large share of the mink in Norway (Figure 1). Most respondents were male (96%), mean age 41.29 [16 – 76] years, lived in coastal municipalities (86 %) and hunted in their residential or neighbouring municipality (91 %, n = 90).

The effect of bounty, belief, motivation and hunting effort on the number of mink caught

Cluster analysis of wildlife value orientations identified one class associated with utilitarian values (28%), one associated with caring beliefs (32%), and one with intermediary values but with higher scores on acceptability to kill wildlife that poses a threat to property or humans (40%)(Table 2). The 3 motivation classes identified are defined by 2 variables: whether they like to hunt with family and friends (social) or if they like to hunt close to where they live (local) (Table 3). The best model for predicting the number of mink caught included the effects of value orientation, motivation and bounty (Figure 2, Appendix Table A1). Significant effects in decreasing order of effect size included a positive effect of receiving bounty, a positive effect of the non-social and non-local hunting class (NSNL), and a negative effect of caring beliefs. Receiving bounty increased the average number of mink caught from the reference value of 6.45 ± 1.08 mink to 11.52 ± 1.10, while hunters that enjoyed hunting alone and not necessarily close to where they lived (NSNL) hunted on average 9.34 ± 1.09 mink compared to the reference value. Hunters with stronger care for animal values caught on average 4.75 ± 1.10 mink, which is slightly less than those who expressed utilitarian orientations. Three outliers that had a large effect on the co-efficient estimates were removed. Inspection of the model residuals indicated that standard deviations were larger than expected when theoretical quantiles were > or < 1. Neither wildlife value orientation nor motivations were significant in predicting conservation attitudes.

Most hunters were interested in removing mink to aid conservation management (Table 4), agreeing strongly that mink was a threat to Norwegian biodiversity and that mink should be removed from PA's. Hunters believed it was more important to remove mink to conserve ground nesting species rather than specific red listed ground nesting species (Table 4). The respondents were divided with regards to protection of Salmonid fishes.

Leadership and recommendations for conservation targeted towards mink control programs?

There was no significant effect of wildlife value orientation or motivation on leadership class. Leadership class was best defined by 3 clusters (Table 5). Cluster one consisted of 47 % of the hunters that had a preference for governmental leadership, cluster 2 indicated a preference for NGO leadership (33 %) and were the most reluctant to municipal leadership and cluster 3 consisted of hunters (20 %) who preferred self-initiated and landowner actions to hunt and were against any hierarchical led actions.

The majority of hunters (86 %) recommended one or more ways that mink hunting could be made more appealing. Recommendations fell into 5 common areas with bounty (52 %) and raising awareness of the negative effects of mink together with recruitment of more mink hunters (36 %)

being common to all leadership classes (S1, Table 1). The recommendation of more logistic and financial support in terms of undertaking mink hunting (29 %) was supported equally by those in favour of governmental and NGO led mink control programs, but not by hunters favouring landowner or self-inititated mink removal (S1, Table 1). The recommendation of organising landowner permissions was only supported by those emphasising governmental-led programs (S1, Table 1). Most recommendations were not explicitly directed to a specific leadership class (S1, Table 2). A third of hunters recommended that bounty should be increased to attract mink hunters.

Discussion

The overall insight gained from this study is that the recruitment to, and interest in mink control programs is low in Norway. The previous attempts to set up such programs and our extensive efforts to recruit participants in our study suggest a low potential for collaborative volunteer programs at present. The few mink hunters that participated in our study accounted for 19.9% of the reported mink catches for the 2012 hunting season, which implies that a few hunters were responsible for a significant part of the mink harvest in Norway. We found support for our hypothesis that mink hunters receiving bounty caught more mink than those that did not. Increasing the bounty payments was also one of the main recommendations provided by hunters to improve mink control programs. Bounty programs may be a way of increasing the number of mink caught. However, increasing number of mink caught per se does not result in successful control due to their high dispersal capacity and probable density dependent response (Einarsson et al. 2006, Bonesi and Palazon 2007, Bodey et al. 2009, Bryce et al. 2011). Indeed, Pasko and Goldberg (2014) indicate that uncoordinated measures have a low success rate for the control of IAS in general, resulting in harvesting, or in some cases conservation of the target species due to changing perceptions of value. Albeit these considerations bounty payments could be a part of a carefully planned programs to control IAS as in the case of the coypu eradication program Gosling and Baker (1989). Bounty was also successfully used in a coordinated landscape approach to red fox eradication in Australia (McLeod et al. 2011, Newsome et al. 2014).

While the mink hunters generally agree that mink is a threat to biodiversity and protected areas, they appear less concerned about the red-listed species that are prioritised by the Norwegian Environmental Agency. Rather the conservation targets of mink hunters appear to be ground nesting birds which are important for recreational hunting (e.g. grouse) or which have previously been economically important (e.g. eider). The willingness to remove mink to protect ground nesting birds is not surprising given the strong support to recreational grouse hunting in Norway (Kaltenborn et al.

2012). Mink on the other hand has no value as food, pelt or for conservation of edible game so that mink hunting for the majority is likely to be a small-scale hobby or by-catch activity rather than a targeted hunting effort. Awareness campaigns that aim at increasing the hunters' interests to harvest mink may be more successful if there is a perceived threat to popular harvestable species such as ptarmigan and salmonid species. The case study from Vega WHS indicates that people living in coastal communities could self-initiate mink removal programs to protect seabird colonies. In Vega, the strong interest in mink removal reflects a strong cultural history as coastal communities were economically substituted by eider down industry up until the 1940's (e.g. Soot-Ryen 1941).

Conservation support to mink control was not clearly reflected by the motivation and value measures included here. We cannot dismiss that the lack of evident relationships are due to the measures used or the low sample size, but literature suggests that hunters and anglers in Norway represents a diversity of interests and values and therefore may deviate from other settings where a more tight relationship between value orientation, conservation beliefs and support to management actions could be found among hunters (Manfredo et al. 2009, Sharp et al. 2011, Jacobs et al. 2014). Appreciative, therapeutic, conservation and consumptive benefits were all expressed as important to hunters and confirms the diverse interest in small game hunting found by Bjerke et al. (2006) and Kaltenborn et al. (2012). The most surprising result is that among a group of hunters there is a distinct class with strong caring beliefs and that invest less in IAS removal.

Many volunteer studies indicate that social benefits are important for being involved in and long-term participation in volunteer conservation efforts (e.g. Ryan et al. 2001, Asah and Blahna 2012). These studies point to a positive relationship between volunteer retention and a sense of belonging either by hunting together with friends and family or by being a member of local cultures and volunteer work near participant's homes (Selinske et al. 2015). We found the opposite for mink hunters. Social benefits and local hunting were among the lowest ranked motivations by mink hunters, and hunters belonging to this class catch more mink than others. Our results also run contrary to what has previously been found for small game hunters (Andersen et al. 2008), and for hunting participation in general. Lack of social motives is further supported by the lack of mentioning of hunting teams in the general recommendation to improve mink control programs, and reflects that there are a few devoted hunters or trappers who have the personal motivation and skills to hunt mink. As much as 43% of the hunters are primarily motivated by social benefits and mink control programs need to encourage also this segment to hunt more. Locally organised control programs may inject a social motivation to hunt and ensure continuity in initiated programs. Such co-ordination may also result in successful control at the landscape scale, even when individual mink hunter catch is low as shown by (Bryce et al. 2011).

Bottom-up initiatives may be easier to facilitate in some cultures and for some conservation purposes than others (Fischer et al. 2014). Conservation volunteer organisations are largely utilised in Britain, the USA and Australia (Silvertown et al. 2013), and most of the examples on volunteer-based programs related to IAS comes from these regions. In Norway, environmental conservation is organised differently, deriving from the corporatist style of governance common to all Scandinavian countries (Dryzek et al. 2002). Organisations are perceived as the arms of the state, and contribute to the formulation of conservation policies as well as the implementation of them by receiving financial and logistic support by the government. It is therefore no surprise that hunters prefer more top-down initiatives led by the government or NAHA rather than citizen or landowner initiated programs. Organising mink control programs as collaboration between the government, municipalities and the NAHA is sensible given the number of local organisations NAHA represents and the financial and the logistic support the government could provide. In comparison, conservation organisations in Norway have fewer members also than the other Scandinavian countries (Dryzek et al. 2002), and are poorly represented at the local level. The crucial role of the government to achieve ecological and social objectives is also confirmed by a review of IAS management programs in Australia (Ford-Thompson et al. 2012). Similarly the hunters in our survey request a more active role by the government for providing infrastructure, bounty, trapping equipment, organize landowner permissions to hunt, and to set up recruitment and education programs to increase participation in mink hunting.

Conclusions and recommendations

We can conclude that there is currently little interest in mink hunting in Norway. The Norwegian Environmental Agency has tried to increase interest in mink hunting through motivating hunters to hunt without supplying economic or logistic support. Whether there has been an increase in mink hunting as a result is not possible to say as the number of mink hunters within the NAHA is unknown. However, the hunting statistics indicate that there has been little change in mink hunted during the 2013 and 2014 seasons. It is clear any future effort involving volunteer mink hunting will require significant investment by the state. This would include provision of finances, direct and/ or facilitation of carefully coordinated plans in collaboration with municipalities, organisation of landowner permissions, and payment of bounty. In addition, the state would need to organise networks of hunters in “conservation hotspots” that can reduce the rate of recolonisation in reserves targeted by state employed professionals. Collaborative efforts involving hunters to control red fox in Norway suggest that effective control of other species could be feasible by combining contractual operators (i.e Statens Naturoppsyn), hunting organizations and bounty payment (which in this case was remarkably higher than in any mink control programs). Coordinating networks of low catch hunters giving low returns could then complement the effect of relatively few high catch hunters willing and able to catch high numbers of mink over a relatively large area. Furthermore, efforts must be adaptable to cope with changing focus when control results in the decline of mink numbers (e.g. Bodey et al. 2009). Any trial projects should be carefully designed. Not least, the effectivity of mink hunting in such projects must be assessed and should include both an assessment of mink capture on both mink re-colonisation and whether mink catch results in can increase in the target species of conservation.

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Table 1. Variables used in analysis of mink hunter perceptions based on survey questions sent to Norwegian mink hunters regarding the 2012 hunting season.

Variable	Question
Wildlife value orientation	On a scale of 1 to 7, where 1 is total disagreement and 7 is total agreement, how much do you agree with the following statements? 1. Humans should manage fish and wildlife populations so that humans benefit 2. The needs of human should take priority over fish and wildlife protection 3. It is acceptable for people to kill wildlife if they think it poses a threat to their life 4. It is acceptable for people to kill wildlife if they think it poses a threat to their property 5. I care about animals as much as I do about people 6. I value the sense of companionship I receive from animals
Motivation	Check one or more statements that are appropriate for you. I like to hunt or fish because… 1. family or friends hunt (social) 2. it gives me a sense of belonging to a group I wanted to be part of (social) 3. it gives me exciting experiences (appreciative) 4. I think it is important to harvest from nature(consumptive) 5. it increases my knowledge about quarry species (appreciative) 6. I like to eat fresh fish and/ or game that come directly from nature (consumptive) 7. it is an outdoor hobby that is close to where I live (local) 8. it gives me the opportunity to experience impressive nature (appreciative) 9. it is a good form of relaxation (therapeutic) 10. it gives me physical activity (therapeutic) 11. I can contribute to good conservation and/ or management of nature (conservation)
Leadership	Who do you think should lead programs aimed at controlling mink? 1. The Norwegian Environment Agency (national government) 2. The County Government Offices (regional government) 3. The Municipalities 4. Landowners 5. The Norwegian Hunting and Fishing Association / other NGO's 6. Individuals must take responsibility for controlling mink
Bounty	Do you receive funding from the municipality (and how much)? 1. NOK 0 2. 1 – 99 3. 100 – 199 4. 200 – 399 5. 400 – 499 6. > 500
Conservation attitudes	Presence/absence of the following conservation attitudes (combined from several questions as described in the text). 1. Mink is a threat to Norwegian biodiversity 2. It is important to remove mink from protected areas 3. It is important to remove mink to protect red list species of birds

	4. It is important to remove mink to protect ground nesting species 5. It is important to remove mink to protect salmonid fish
Mink hunting	1. How many mink did you trap or shoot during the 2012 season?
	2. Do you intend to trap or shoot mink during the next three years?
	3. How many days did you hunt during the 2012 season?
Recommendations	Can you suggest some ways to motivate or make it easier for hunters to remove mink?

Table 2. Descriptive values of classes for the beliefs expressed by 104 Norwegian mink hunters. The percentage of hunters in each cluster class is shown in parenthesis. Cluster classes were found by hierarchical agglomerative clustering (see text for details). Values of > 2 for the v.test are significant at the P < 0.05 level with positive sign indicating that the group mean is larger than the overall mean and negative sign indicating that the group mean is smaller than the group mean. The global mean for each variable is indicated in the column MEAN.

Belief variables	**Utilitarian (28%) (dominance)**			**Caring (32%) (mutalism)**			**Intermediary (40%) (dominance mutualism)**			**MEAN**
	Mean	**SD**	**v.test**	**Mean**	**SD**	**v.test**	**Mean**	**SD**	**v.test**	
Humans should manage fish and wildlife populations so that humans benefit	5.17	1.94	-4.26	-	-	NS	6.78	0.55	3.47	6.18
The needs of human should take priority over fish and wildlife protection	3.17	1.44	3.17	1.38	0.73	-4.81	-	-	NS	2.40
It is acceptable for people to kill wildlife if they think it poses a threat to their life	-	-	NS	3.88	1.68	-6.22	6.52	0.82	5.16	5.43
It is acceptable for people to kill wildlife if they think it poses a threat to their property	-	-	NS	2.35	1.23	-6.41	5.21	1.28	6.31	3.91
I care about animals as much as I do about people	2.10	1.26	-6.17	4.94	1.73	2.45	5.02	1.84	3.22	4.21
I value the sense of companionship I receive from animals	3.00	1.28	-6.57	5.41	1.33	2.11	5.71	1.38	3.92	4.88

Table 3. Descriptive values of classes for motivation. The percentage of hunters in each cluster class is shown in parenthesis. Motivation clusters Local = motivated by local hunting, NSNL = non-social and non-local hunting, Social = social motivations for hunting. Cluster classes were found by hierarchical agglomerative clustering using the ward method. Values of > 2 for the v.test are significant at the P < 0.05 level with positive sign indicating that the group mean is larger than the overall mean and negative sign indicating that the group mean is smaller than the group mean. N = mean frequency of hunters responding to motivational variable.

Motivation variables	**Local (32%)**	**v.test**	**NSNL (26%)**	**v.test**	**Social (43%)**	**v.test**	**N**
It gives me exciting experiences	-	NS	-	NS	-	NS	93
I think it is important to harvest from nature	-	NS	-	NS	-	NS	92
It gives me the opportunity to experience impressive nature	-	NS	-	NS	-	NS	91
I can contribute to good conservation and/ or management of nature	-	NS	-	NS	-	NS	88
It is a good form of relaxation	-	NS	-	NS	-	NS	87
It gives me physical activity	-	NS	-	NS	-	NS	84
I like to eat fresh fish and/ or game that come directly from nature	-	NS	-	NS	-	NS	84
It gives me a sense of belonging to a group I wanted to be part of	-	NS	-	NS	-	NS	79
It is an outdoor hobby that is close to where I live	33	3.59	0	-5.19	-	NS	64
It increases my knowledge about quarry species	-	NS	-	NS	-	NS	63
Family or friends hunt	0	-5.23	0	-4.13	44	7.76	44

Table 4. Percentage of conservation attitudes expressed by wildlife value orientation and motivation classes. We found no significant differences among classes.

Conservation values	**Utilitarian**		**Caring**		**Intermediary**		**Local**		**NSNL**		**Social**	
	Yes	**No**	**Yes**	**No**	**Yes**	**No**	**Yes**	**No**	**Yes**	**No**	**Yes**	**No**
Mink is a threat to Norwegian biodiversity?	25	3	29	3	38	3	28	4	35	1	39	4
It is important to remove mink from protected areas?	24	4	27	5	39	2	31	1	24	2	35	8
It is important to remove mink to protect red list species of birds.	7	21	12	20	13	28	8	24	5	21	19	24
It is important to remove mink to protect ground nesting species	22	6	31	1	25	6	26	6	34	2	28	5
It is important to remove mink to protect salmonid fish	13	15	14	18	22	19	21	11	7	19	21	22

Table 5. Descriptive values of classes for the variable leadership. Leadership clusters Government = state and municipal agencies; NGO = non-government organisation and not municipalities, Individual = individual hunters and landowners. Cluster classes were found by hierarchical agglomerative clustering using the ward method. Values of > 2 for the v.test are significant at the P < 0.05 level with positive sign indicating that the group mean is larger than the overall mean and negative sign indicating that the group mean is smaller than the group mean. N = mean frequency of hunters responding to leadership variable.

Leadership variables	**Government (47%)**	**v.test**	**NGO (33%)**	**v.test**	**Individual (20%)**	**v.test**	**N**
1. The Norwegian Environment Agency	33	2.75	-	NS	2	-2.81	57
2. The County Government Offices	23	2.11	-	NS	0	-3.17	40
3. The Municipalities	37	3.24	16	-3.16	-	NS	62
4. Landowners	-	-	-	NS	11	2.25	37
5. The Norwegian Hunting and Fishing Association / other NGO's	0	-5.69	33	7.36	0	-2.75	33
6. Individuals must take responsibility for controlling mink	8	-3.64	-	NS	20	4.97	47

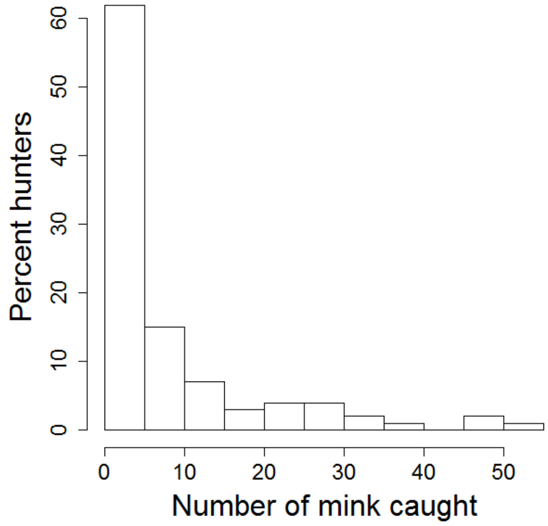

Figure 1. The percentage of hunters catching mink during the 2012 hunting season.

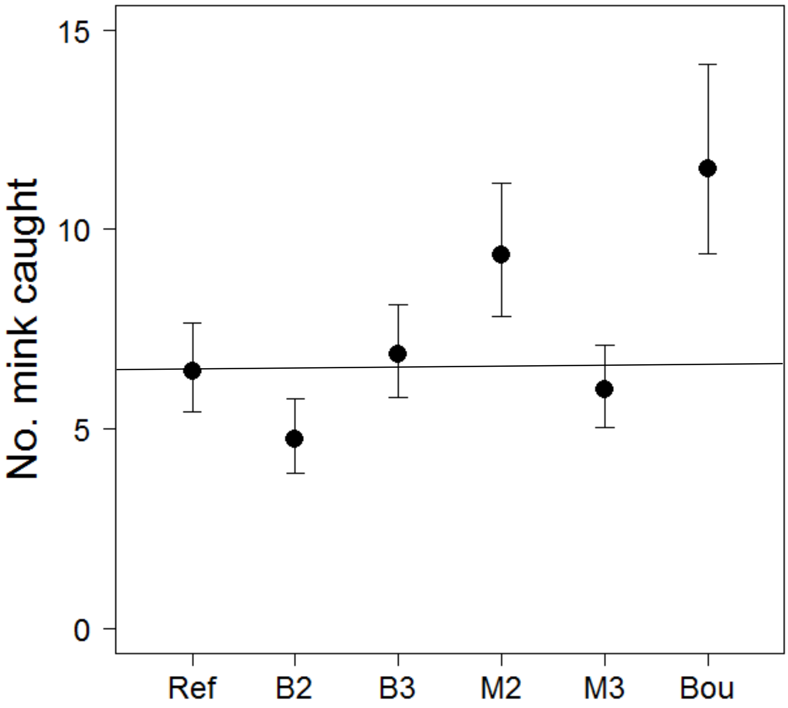

Figure 2. The effects of wildlife value orientation (B), motivation (M) and bounty (Bou) on the number of mink caught by 101 mink hunters during the 2012 hunting season. Ref refers to the reference level given by hunters characterised by utilitarian beliefs, local hunting motivations and no bounty payments and is shown by the horizontal line, B2 = caring beliefs and B3 = intermediary. M2 = non-social and non-local hunters, and M3 = social hunters. Bou = municipal bounty was received. Estimates are given as the exponential of the poisson error regression estimates.

Appendix

Table A1. The three best regression models for the effects of belief, motivation and bounty on the number of mink caught by 104 hunters in the 2012 hunting season ranked according to Akaike's Information Criteria (AICc and ΔAIC) and Akaike's weights (w_i) The ΔAIC values are expressed in relation to the best fitting model. K is the number of parameters in the models.

Rank	Model	K	AICc	ΔAIC	w_i
1	Belief + motivation + bounty	6	1480.66	0.00	1
2	Motivation + bounty	4	1496.67	16.01	0
3	Belief + bounty	4	1505.88	25.23	0

Supplementary Material

Table S1. Recommendations to make mink hunting more appealing displayed by desired leadership class for 86 mink hunters active during the 2012 hunting season.

Recommendation	**Leadership Class**		
	Government	**NGO**	**Individual**
Bounty	19	16	10
Awareness and recruitment	13	12	6
Equipment and costs	12	12	1
Organisation of landowner permission	9	1	1
Changes in law	4	5	2

Table S2. Examples of statements in the 5 recommendation categories made by 86 mink hunters hunting in the 2012 season.

Recommendation	**Statement**
Bounty	‘Bounty for mink would have helped a lot I think’
	‘Higher bounty’
Awareness and recruitment	‘Local groups buy in traps for young hunters and others interested ‘
	‘Instruction and [the possibility for] increasing skills’
	‘Raise awareness what a scourge mink is ‘
	‘More focus on publicising the consequences of mink predation‘
	‘Increase understanding of the destruction that mink does on natural wildlife that belongs here’
	‘Better information regarding where it is possible to hunt’
	‘Better information to landowners so that it is easier to get permission’
Equipment and costs	‘Easier access to traps’
	‘Grant to cover traps and / ammunition’
	‘It would have been nice to be given some traps’
	‘Economical support and free traps’
	‘It would have been nice with economical support…because ammunition and fuel for boats has become so expensive’
Organisation of landowner permission	‘Easier to get permission from landowners’
	‘Organization of landowners [access]’
	‘Landowners that allow access to hunting’
	‘That more landowners let us set up traps or hunt’
Changes in existing hunting laws	‘It should be possible to shoot from a motor boat’
	‘There should be free hunting of mink on uninhabited islands along coast with holms and islands’
	‘Remove landowner permission’
	‘Lawful to use 22 caliber ammunition as in Sweden’