Paper II

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

2 **colonies**

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23 **Summary**

24 Human disturbance in bird breeding colonies may cause reduced breeding success. It is therefore

25 pertinent to assess the impact of disturbance, taking steps that minimise negative impacts where

26 necessary. We carried out a study of nesting success at two contrasting adjacent colonies of common

27 eider (*Somateria mollissima*) in Northern Norway between 2006 and 2011. Between 2009 and 2011

28 we employed camera monitoring of individual nests to identify causes and correlates of nest survival

29 and predation. We focused in particular on the effect of disturbance, which differed between the

30 colonies due to a long-term research project on Grindøya. Over the 6-year study period the nesting

31 success was consistently higher on Håkøya (69 % - 82 %) compared to Grindøya (35 % - 60 %). We

32 found that disturbance leading to absence of eiders increased the predation risk by a factor of 6.42

33 for an increase of one additional daily disturbance. Absence due to natural nest leaving did not

34 increase nest losses. Contrasting levels of disturbance appeared to explain the difference in nesting

35 success between the two colonies. Under high levels of disturbance, camera monitoring indicated

36 that the main cause of breeding failure was predation, primarily by hooded crows (*Corvus cornix*),

37 but also to some extent greater black-backed gulls (*Larus marinus*). Cameras did not increase the

38 predation risk. We suggest management trials aimed at mitigating the effects of human disturbance

39 on reproductive effort and further, to increase colony size.

40 Key-words:

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

42

43 **Introduction**

44 A substantial effort has been put into research on marine birds during the breeding season with the

45 result that we have a great deal of knowledge about their ecology, population dynamics and life

46 history strategies. Most marine bird species are long-lived with a low average annual reproductive

47 output (Sæther and Bakke 2000). Although population growth rates in long-lived species typically are

48 most sensitive to adult survival (Gaillard et al. 2000), many successive years of low productivity

49 (fledging rate) negatively impact on recruitment (Hario and Rintala 2006, Reiertsen et al. 2013) and

50 ultimately may lead to declining populations.

51 Nest-loss due to predation can be a main cause of low offspring production in birds (Ricklefs 1969,

52 Newton 1998). Its importance in determining population growth is debated (Hario and Rintala 2006,

53 Coulson 2010, Wilson et al. 2012, Gunnarsson et al. 2013), but management actions that increase

54 nest survival may help halt population declines especially when populations are small and isolated.

55 Efficient management actions depend on understanding the main drivers of nest predation. Classical

56 predator-prey theory focuses on predator numerical and functional responses as main causes of

57 variation in predation rates, but many studies show that other factors may modify the impact of

58 predators on nest survival (Taylor 1984, Gunnarsson et al. 2013). Disturbance is one such modifying

59 factor as nests may be more prone to predation when the nest is unattended. Human activity can

60 have significant impact on nest-loss, with human induced nest leaving resulting in predation of nest

61 contents (e.g. reviews in Carney and Sydeman 1999, Martínez-Abraín et al. 2010, Ibáñez-Álamo et al.

62 2012). In addition, the body condition and clutch size of breeding birds has also been shown to be

63 important for the likelihood of continuation of nesting (Hanssen et al. 2003a). Other factors that may

64 affect nest predation risk are nest habitat and in particular nest cover (Martin 1993, Ekroos et al.

65 2012, Seltmann et al. 2014).

66 Long-term research on marine birds is important because it both provides a basic understanding of

67 the biology of long-lived species (Clutton-Brock and Sheldon 2010) and important information

68 regarding how environmental pressures (e.g. pollution) affect marine ecosystems (Furness and

69 Camphuysen 1997). Much of this research involves invasive methods to acquire data on the

70 physiological and demographic parameters. Invasive research methods cause disturbance of nesting

71 birds with a potential for increased nest predation and thus reduced long-term performance of the

72 population. In bird populations subject to long-term research repeated assessment of researcher

73 effects may be necessary, in particular since the research-induced disturbance effect may be

74 contingent on temporally changing limiting and regulating factors that affect population dynamics

75 (e.g. Parmesan and Yohe 2003, Olito and Fukami 2009, Stien et al. 2012, Blois et al. 2013, Ferretti et

76 al. 2013).

77 A colony of the common eider (*Somateria mollissima*) at Grindøya in northern Norway has declined

78 during the period it has been subjected to long term research (Erikstad et al. 2009, 2010). This highly

79 philopatric sea duck has also experienced recent large-scale declines in much of its circumpolar range

80 (Desholm et al. 2002, Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Although

81 reproductive output at the Grindøya colony has been linked to large-scale climatic variation

82 (Descamps et al. 2010), local-scale impacts related to predation may also be influential (Erikstad et al.

83 2009, Hanssen and Erikstad 2012). Previous studies on Grindøya have indicated, that nest-loss due to

84 crow predation can be substantial (Erikstad and Tveraa 1995). To quantify the effect of crow

85 predation, Stien et al. (2010) carried out a crow removal experiment between 2006 and 2008 that

86 also included the adjacent Håkøya colony in a BACI design. In contrast to Grindøya, the Håkøya

87 colony had a lower level of research-induced disturbance and higher nesting success, but in common

88 with Grindøya the Håkøya colony was in a long-term decline (Stien *unpublished*). Crow removal

89 significantly increased nesting success at Håkøya but not at Grindøya. Without detailed data on the

90 processes of nest predation, Stien et al. (2010) could only hypothesise that the higher level of

91 research-induced disturbance and/or a more diverse community of nest predators could be the

92 reason for the consistently lower nesting success at Grindøya.

93   In the present study, we employed camera monitoring at individual nests over three nesting seasons

94 to more thoroughly investigate which factors were involved in determining eider nest predation

95 rates in the two colonies.   We expected the lower nesting success at Grindøya to be explained by the

96 higher frequency of nest disturbance at this colony. Specifically, we expected that nesting females

97 exposed to a high frequency of disturbance would have lower nesting success than those with low

98 disturbance and that absence from nests due to disturbance would be associated with a higher

99 predation risk than absence due to natural nest leaving. Finally, we evaluated whether the difference

100 between the two study colonies in nest predation rates could be explained by differences in the local

101 predator community.

102

103 **Materials and Methods**

104 **Research species**

105 The common eider (*Somateria mollissima*) is a well-studied sea-duck that has been at the focus of

106 many evolutionary, immunological and ecological studies throughout its circumpolar range (e.g.

107 Mehlum 1991, Erikstad et al. 1998, Desholm et al. 2002, Hanssen et al. 2003b, Hanssen et al. 2006,

108 Hario and Rintala 2006, Coulson 2010, Wilson et al. 2012). Adult survival is typically high, breeding is

109 delayed with first breeding from 2 years of age, and periodic non-breeding years occur due to high

110 energetic costs of breeding (Yoccoz et al. 2002, Hanssen et al. 2003a, Hario and Rintala 2006, Coulson

111 2010, Wilson et al. 2012). Nesting success may be highly variable between years and successive years

112 of low breeding success can cause population declines (Hario and Rintala 2006, Coulson 2010, Wilson

113 et al. 2012). These characteristics combined with high natal philopatry in first time breeders

114 (Swennen 1991) and general high philopatry of adult females (Bustnes and Erikstad 1993, Hanssen

115 and Erikstad 2012) may mean that increasing nesting success can be a relevant management action

116 to halt the decline of eider populations. Negative effects of researcher activity, resulting in nest-loss

117 have been demonstrated for common eider during egg laying and early incubation (Bolduc and

118 Guillemette 2003, Wilson et al. 2012), and heterogeneity in nesting habitat has been found to cause

119 variable nesting success where avian predation dominates and nests are left exposed (e.g. Götmark

120 and Åhlund 1984, Noel et al. 2005).

121 The common eider has low clutch size for a duck species (mean of 4 eggs) with mean complete nest

122 attendance from the second or third laid egg for females with 4 and 5 egg clutches respectively

123 (Hanssen et al. 2003a). Complete nest attendance results in up to 40 % loss of body mass during

124 incubation and decreased egg predation (Parker and Holm 1990, Swennen et al. 1993, Hanssen et al.

125 2002, Andersson and Waldeck 2006). A wide range of nest loss rates have been documented from

126 less than 10 % to more than 90 % within and between eider colonies (e.g. Mehlum 1991, Noel et al.

127 2005, Coulson 2010, Wilson et al. 2012). Clutch size, egg size, clutch investment, duckling size and

128 duckling survival depend on female condition before the onset of egg laying (Erikstad et al. 1993,

129 Erikstad and Tveraa 1995, Hanssen et al. 2003a). Long-term studies indicate both presence and

130 absence of density-dependent effects acting on different populations (e.g. Desholm et al. 2002, Hario

131 and Rintala 2006, Coulson 2010). Mortality of young due to adverse weather, food availability and

132 food-transmitted infections is particularly prevalent during the first two weeks of duckling stage

133 (Milne 1974, Hario and Rintala 2006) and large-scale mortality of young has been linked to

134 population decline (e.g. Desholm et al. 2002). Furthermore, large-scale variation in climate correlates

135 with adult reproductive success (e.g. D'Alba et al. 2010, Descamps et al. 2010).

136

137 **Study colonies**

138 Grindøya and Håkøya colonies are adjacent low-lying islands approximately 2 km from each other at

139 69˚38 'N, 18˚52 'E and 69˚39 'N, 18˚49 ' E. There were approximately 150 pairs and 50 pairs of

140 common eider in respectively the Grindøya and Håkøya colony in 2006. Habitat and the egg predator

141 communities are described in Stien et al. (2010). Eider is the main ground nesting bird on the islands

142 and their eggs are a main source of terrestrial food for predators in late May on Grindøya. On Håkøya

143 a fluctuating population of tundra voles (*Microtus oeconomus*) exceeds the biomass of eider eggs in

144 most years (Ims unpublished). Grazing of sheep has occurred on Grindøya during the breeding

145 season since 2007.

146 The eider colony on Grindøya has been used for annual long-term monitoring and research since

147 1985 (Erikstad et al. 2009). Individual incubating females have been exposed to varying intensities

148 and frequencies of disturbance for research purposes, including counting and measurement of eggs

149 during laying, capturing of individuals for life history studies and handling of individual females for

150 manipulations of plumage and parasite levels (e.g. Erikstad et al. 1993, Bustnes 1996, Hanssen et al.

151 2005, Hanssen et al. 2006). Disturbance from other human sources is limited due to public access

152 restrictions at the colony. Nest failure is as high as 62 % (Stien et al. 2010). The colony has decreased

153 steeply from over 500 pairs in 1995 to c.150 pairs in 2009 onwards (Erikstad et al. 2010). Adult

154 female survival decreased from > 80 % between 1986 – 2002 to a low of 53% in 2005 with the

155 decrease in 2002 and continued low survival being attributed to mink predation of incubating

156 females (Erikstad et al. 2009, Erikstad et al. 2010). Between 2005 and present, survival has been

157 variable but increasing, with an estimate of 80 % in 2011 (Hanssen unpublished).

158 Håkøya colony has been the focus of low intensity annual nest monitoring since 2006. The colony is a

159 remnant of an active eider down colony with an estimated population of over 600 nesting individuals

160 (Olsen pers. comm.) in the middle of last century. The study area contained at least 49 nesting

161 individuals in 2006, which decreased to 26 in 2011. Individual nest fates are followed but not

162 individual females. Disturbance from other human activity is limited as the colony area was little

163 used during the study period 2006 - 2011. Nest failure is up to 39 % (Stien et al. 2010).

164

165 **Study design**

166 During 6 consecutive breeding seasons (2006 - 2011) we monitored 1003 common eider nests by

167 discrete observational time intervals to estimate nesting success in the two study colonies (Stien et

168 al. 2010). In the 3 last seasons (2009 - 2011) we camera-monitored 203 of the nests (Table 1). Of the

169 camera-monitored nests, 184 yielded data suitable for establishing the causes of individual nest

170 failures, including identity of predator species, while the effects of disturbance on nesting success

171 were estimated from a subset of 103 camera-monitored nests that had complete histories of nest

172 leaving identifiable as due to either disturbance or natural (Table 1). Forty-one matched pairs of

173 camera monitored and non-camera monitored nests were used to estimate effects of cameras on

174 nesting success at both colonies in 2009. Finally, the number of breeding pairs of nesting avian

175 predators at both colonies were recorded by means of transect counts for crows or counts while

176 searching for eider nests for large gulls.

177

178 *Monitoring of colony level nest survival*

179 The outcome of 1003 nests was followed on Grindøya and Håkøya between 2006 and 2011 (Table 1).

180 At both colonies searches for nests were conducted covering the main laying period. Nests were

181 found from the onset of eider breeding between 15 and 22 May (the onset differed slightly between

182 years) and 5 June. Nests were marked by fixing a piece of plastic tape around nearby vegetation. Nest

183 outcomes were monitored until between 28 and 30 June with nest fate being registered as success or

184 failed on each subsequent visit. After laying was complete, nest activity was observed at the same

185 frequency as for camera monitored birds (see below) in order to expose the 2 matched groups of the

186 camera impact assessment to equal researcher visitation. Clutch size upon nest discovery (hereafter

187 referred to as initial clutch size) and maximum clutch size were recorded at both colonies. The

188 recording of maximum clutch size involved disturbing each individual from the nest and was

189 undertaken using different methods at the two colonies in order to have low research related

190 disturbance at Håkøya. On Håkøya, maximum clutch size was recorded by one subsequent visit to

191 nests after discovery, allowing for a full clutch of maximum 6 eggs to be observed. As eiders lay one

192 egg at approximately 1-day intervals (Watson et al. 1993, Hanssen et al. 2002), the interval depended

193 on the initial clutch size. On Grindøya, nests for the current study were also part of the parallel long-

194 term studies carried out over the same period as the current project and so monitoring followed the

195 procedures of the parallel long-term project. These involved disturbing females from nests every

196 second or third day to count and measure subsequently laid eggs until no new eggs were laid on 2

197 successive visits to record maximum clutch size (Erikstad et al. 1993), catching females of still active

198 nests during incubation and disturbing females from nests in late incubation to check for hatching

199 success. Catching of females occurred on day 5 and 20 of incubation for nests with known onset of

200 incubation (i.e. for nests with subsequent laid eggs observed during egg laying monitoring), and once

201 for females of unknown onset of incubation in order to read leg rings or apply leg rings to non-ringed

202 individuals. Where initial capture of females was unsuccessful, several attempts were made on

203 subsequent days to catch targeted females. From day 20 of incubation until females and chicks left

204 the nest, nests were revisited in order to check for hatching success. Nest monitoring was co-

205 ordinated between the present study and the long-term monitoring project in order to limit extra

206 disturbance. All nests disturbed due to research and monitoring were covered with down or

207 vegetation where nests were not lined with down after researcher visits.

208

209 *Camera monitoring of individual nest*

210 RECONYX cameras were deployed at time of nest discovery at 158 nests on Grindøya and 45 nests

211 on Håkøya between 17 May and 5 June between 2009 and 2011 (Table 1). On Grindøya, an

212 additional 34 (10 in 2009 and 12 in both 2011 and 2012) cameras were laid out on nests in the first

213 week of June that had been found during the parallel long-term monitoring project between 7 and

214 13 days previously. We aimed to set out 10 cameras on each nest-finding day in order to take

215 account of seasonal effects on nesting success (Stien et al. 2010). We covered open, wooded and

216 thicket habitat within searches in order to take account of possible habitat effects on nesting success.

217 In 2010 and 2011, cameras were laid out at the first 10 nests we found due to variation in the daily

218 frequencies of nest initiation. In 2009, cameras were laid out on alternately found nests to enable

219   the effects of cameras to be estimated. Cameras were deployed at nests with both known and

220   unknown incubation date as lay date could not always be determined on the first visit.

221   *Nest habitat* was initially categorised into the three broad categories open, wood and thicket but

222   these were not considered further as a measurement of cover at the nest captured well the

223   difference between these categories. This *nest cover* variable was scored at an ordinal scale between

224   0 and 5 at time of nest discovery and time of failure. As cover did not vary substantially between time

225   of nest initiation and time of failure, we used cover at nest discovery in the analysis. We estimated a

226   30 cm^2 cube cage over each nest and using the photos taken by the automatic camera scored the

227   nest cover as 1 if more than ≥ 50 % of the cube was covered by vegetation or man-made structures

228   and 0 if < 50 % of the face was covered. Thus the minimum score, zero would occur if there was < 50

229   % cover on all 5 faces and the maximum score, 5 would occur if there was > 50 % cover on all 5 sides.

230   *Nearest neighbour distance* (between nests) was calculated from GPS nest co-ordinate positions in

231   order to check for density-dependent predation. *Distance to the sea* was measured in Map Source

232   (Garmin) as the shortest distance in metres from each nest to the high water line.

233   Camera settings were set to motion sensor, where the change in focal point temperature in relation

234   to background temperature triggers the shutter. Cameras were placed 2 – 3 m from nests and

235   positioned between 30 and 50 cm above the ground to allow a clear view of the nest contents. They

236   were secured to tree trunks or to a weathered stake hammered in to the ground where suitable

237   trees were not available. In 2009, 2 GB memory cards were used, while in 2010 and 2011 larger

238   capacity cards of 4GB were used to reduce the number of visits to nests. In 2009, cards were changed

239   once a week, whereas in 2010 and 2011 cards were changed once every 10 days to reduce

240   disturbance. This overlapped visitation due to catching of incubating females on Grindøya, but did

241   not necessarily result in the incubating bird leaving the nest.

242   Nest leaving recorded from camera monitoring was identified as either *natural* (hereafter referred to

243   as natural) or *disturbed* (hereafter referred to as disturbance). The category natural was recorded

244   when individuals covered their eggs with vegetation or down before leaving the nest and the

245   category disturbance was recorded when individuals left their eggs uncovered and moved quickly off

246   their nest. One hundred and four of the 184 nests with environmental variables had both

247   uninterrupted camera monitoring from initial deployment of cameras at nest finding and all nest

248   leaving events identifiable as disturbance or natural. These nests with complete nest-leaving histories

249   were used to account for possible effects of previous nest leaving on nesting outcome. The remaining

250   82 nests had either periods of non-monitoring due to memory cards being filled and / or

251   unidentifiable nest leaving cause.

252 Of the original 203 deployed cameras, data was not used from 17. Eight cameras malfunctioned at

253 deployment and GPS location and / or nest cover was not recorded 9 nests. The reduction is unlikely

254 to bias the results as these omissions were spread over all years of the study period and at both

255 colonies (Table 2).

256

257 *Effect of nest cameras on eider nesting success*

258 Previous studies have shown that nesting success can be influenced positively or negatively by the

259 presence of a camera at bird nests (e.g. Richardson et al. 2009). We tested whether cameras

260 affected nesting success in this study by following the fate of 32 and 10 nest pairs with and without

261 nest cameras on Grindøya and Håkøya respectively between 19 May and 4 June in 2009. Each pair

262 consisted of chronologically found odd numbered nests being deployed with a camera and

263 chronologically found even number nests receiving no camera. To control for the previously

264 demonstrated season effect on nesting success at both colonies (Stien et al. 2010), paired nests were

265 found on the same day. Camera deployed nests were visited on the same day as their non-camera

266 monitored pairs, thus ensuring comparison of effects even in cases of camera malfunction. No

267 females left their nests during these visits.

268

269 *Monitoring of nest predator density*

270 The number of territorial crows (*Corvus cornix*) present at both colonies was counted from transect

271 lines covering the study areas 100 m apart, 65 ha on Grindøya and 64 ha on Håkøya. The location of

272 nests and territorial behaviour were recorded between 12 and 19 May each year. The approximate

273 number of large gull (greater black-backed (*Larus marinus*) and herring gull (*L. argentatus*)) breeding

274 pairs were recorded each year during the searches for eider nests.

275

276 **Statistical analysis**

277 *Colony level differences*

278 We used 4492 nest visitation intervals to estimated nest survival for all 1003 monitored nests using a

279 logistic exposure model (see Stien et al. 2010). This type of model gives reliable estimates of daily

280 nesting success when nest visitation intervals vary between nests (Shaffer 2004). Predictor variables

281 used were, colony, year, Julian day and clutch size. Preliminary exploration of models comparing AIC

282 values revealed that Julian day was best fitted as a 3rd order polynomial whilst clutch size was best

283 fitted as a linear variable. The most complicated model considered contained the interactions

284 between area and year fitted as a categorical predictors and area and clutch size at nest discovery.

285 These models were included to evaluate the possibility that differences in survival were due to

286 differences between colony clutch size at nest discovery rather than differences in disturbance, and

287 to see whether differences in nest survival were significantly different between colonies within the

288 same year.

289

290 *Effect of nest disturbance on individual nests*

291 We used Cox proportional hazards models to estimate the effect of disturbance on the success of the

292 103 nests for which complete nest leaving histories were available. The proportional hazard model

293 estimates the instantaneous risk of failure at time *t* for an individual nest given its success (i.e.

294 survival) up to that time and allows the inclusion of covariates to correct for biases. It also takes

295 account of incomplete event histories in the sampled population at the end of sampling time (i.e.

296 right censoring in case of incomplete covering of nest outcomes due to malfunctioning cameras).

297 The frequencies of disturbance and natural were calculated as the average daily number of

298 disturbance or natural nest leaving events over the period the nest was monitored (i.e. number of

299 events per nest day). In addition to the focal disturbance effects, the most complicated statistical

300 model considered included the following covariates: frequency of natural nest leaving, colony, year

301 (categorical), Julian day, initial clutch size, cover, distance to the sea and nearest neighbour distance.

302 The initial clutch size was used as a proxy for the amount of investment females had used at time of

303 nest finding and is referred to as clutch size hereafter. Maximum clutch size was not used as it was

304 not possible to determine all egg laying events at camera-monitored nests. Preliminary investigation

305 indicated that Julian day, clutch size and cover could be added as continuous untransformed

306 variables. Distance to the sea and nearest neighbour distance were square root transformed to

307 centralise their distributions as this improved the fit of the models. The simplest model included the

308 effect of disturbance.

309

310 *Effect of photo boxes on eider nesting success*

311 We estimated nest survival for camera-monitored and control paired non-camera-monitored nests

312 using a logistic exposure model (see above). Three hundred and fifty-five nest visitation intervals

313 were used to estimate the effects of camera deployment on daily nesting success. A model with an

314 additive effect of camera presence, area (Grindøya and Håkøya) and the covariates day and clutch

315 size were used to evaluate the effects of cameras on nesting success.

316

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

349   year effects on nest survival and none of the habitat variables entered the proportional hazard rate

350   model. This result even applied to a model applied to all nests (n=184) with functioning cameras.

351   On average disturbance frequencies were 2.26 times higher on Grindøya than Håkøya (F $_{(1,24.97)}$=

352   16.04, P < 0.001, Table 2) and natural frequencies were 3.15 times higher on Håkøya than Grindøya

353   (F $_{(1,24.91)}$ = 13.39, P = 0.001). Disturbance accounted for 61 % of recorded nest leaving on Grindøya

354   and 30 % on Håkøya. There was a weak negative correlation between the frequency of disturbance

355   and natural (r = - 0.19, P = 0.09). The photographic evidence showed that the majority of females

356   returned to the nest after disturbance or natural events. On the 12 occasions females did not return,

357   disturbance accounted for 11 of the 12 nest leavings and all 12 nests were predated.   Absences

358   varied from one minute to 1.79 days with 75% of absences less than 63 minutes and median absence

359   of 28 minutes (mean = 2.43 hours). There were no significant colony differences between length of

360   absence for disturbed or natural events (F $_{(1, 35.79)}$ = 0.35, P = 0.55). Mean absence length for nest

361   leaving due to disturbance was 2.87 (se ± 0.72) hours and was significantly longer than the mean

362   value of 1.81 (se ± 0.45) hours due to natural leaving (F $_{(1,527.44)}$ = 4.56, P = 0.03). When absence was

363   split into early laying (associated with low attendance and referred to as pre-incubation) and

364   incubation (associated with almost 100 % attendance) periods, mean absence for pre-incubation was

365   7.62 ± 0.98 to 12.61 ± 1.93 hours for incubation defined as attendance from the second egg and third

366   egg respectively. Mean absence time during incubation was 1.52 ± 0.13 to 1.72 ± 0.13 hours for

367   incubation from the second and third egg. Pre-incubation absences were significantly longer than

368   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

369   and third egg incubation respectively). There was no effect of change in natural nest leaving time

370   during incubation phase (4 eggs or more) for birds with clutches between 4 and 6 eggs (F $_{(2, 158.12)}$) =

371   0.20, P = 0.81).

372   Time to predation varied between 1 minute and 48 hours with a median of 1.9 hours and was not

373   statistically different between nest leaving due to disturbance and natural causes (F $_{(1, 19.57)}$ = 2.60, P =

374   0.12). Analysis of the 41 paired camera-monitored and control nests (without cameras) in 2009

375   indicated that there was no effect of cameras on nesting success (Figure 2). The best logistic

376   exposure model included effects of day, area and clutch size (Appendix C).

377

378   *Abundance and identity of nest predators*

379   On both Grindøya and Håkøya the number of crow territories remained constant during the study

380   period with 4 and 1 territory respectively between 2009 and 2011 (Table 3). The number of nesting

381   large gulls (mostly herring gull) increased between 2009/2010 and 2011 at Grindøya from

382 approximately 30 to over 80 pairs. On Håkøya, the number of greater blacked back gull and herring

383 gull territories remained low (4 – 6 pairs). Among the 184 nests that had functioning cameras there

384 were 85 events of camera-monitored predation (Table 3). On Grindøya crows were clearly the most

385 important predators followed by greater blacked-backed gulls, while mammalian predation was

386 negligible. The few predation events on Håkøya were quite evenly distributed among the predator

387 species identified from camera-monitored nests. The majority of predation resulted in loss of the

388 entire clutch (nest loss) (Table 3). All predation events occurred in the absence of the females and

389 81% of these events when the nest had been disturbed. Of these disturbed nests, 37 were due to

390 researcher disturbance (i.e. eggs were covered after visiting), while the causes of nest leaving of the

391 remaining 29 disturbance events could not be determined.

392

393 **Discussion**

394 The results from this study are consistent with the hypothesis that the lower nesting success at

395 Grindøya is due to a constantly higher rate of disturbance of nests at this colony. That is, the

396 frequency of nest disturbance was much higher at Grindøya than Håkøya and this led to a steeply

397 increased risk of nest failure due to predation. There was no evidence of any additional colony effect

398 in the hazard model when the disturbance effect was included, implying that the overall difference in

399 nesting success between the two colonies could be accounted for by the contrasting disturbance

400 rates. This also implies that we did not find evidence for the alternative hypothesis that the general

401 predation pressure differed between the two colonies, which should have amounted to an

402 independent colony effect. For the hooded crow, the predator species that inflicted most of the

403 predation events, there were more crow territories on Grindøya than on Håkøya. However, the ratios

404 of crow territories to eider nests were very similar for the two colonies, 0.03 and 0.04 at Grindøya

405 and Håkøya respectively. Erikstad et al. (2009, 2010) suggested that predation by American mink

406 (*Neovison neovison*) on incubating birds was important for the recent decline in the population.

407 However, here we have shown that mink predation was not at all important over the 3 breeding

408 seasons of camera monitoring between 2009 and 2011.

409 As far as we are aware, this is the first study that has been able to relate complete nest leaving

410 histories that included both natural causes and disturbance to nest losses in order to investigate the

411 role of disturbance on the nesting success of common eider. This allowed us to show that in contrast

412 to absences from nests due to disturbance, a high frequency of natural nest leaving was not

413 associated with increased nest losses. Moreover, we found that disturbance leads to breeding failure

414 through nest predation rather than nest abandonment as the majority of females returned to nests

415 after disturbance events. The camera monitoring also allowed us to establish which predators were

416 most important. Both crows and large gulls are known to be common nest predators in eider

417 colonies (e.g. Gerell 1985, Götmark 1989, Mehlum 1991, Swennen et al. 1993). However, although

418 large gulls were much more abundant than crows at Grindøya, crow had a disproportionately higher

419 nest predation rate. The consistent high rate of nest predation by crows supports earlier studies

420 indicating that this visual predator is particularly good at homing in on, and remembering novel cues

421 and human activity (Milne 1974, Picozzi 1975, Sonerud and Fjeld 1987, Marzluff and Neatherlin

422 2006), especially if they are within crow territories (Erikstad et al. 1982). Indication of homing in on

423 human cues in the present study comes from the rapidity of predation and domination of predation

424 of nests that have been visited by researchers. Since the contents of disturbed nest were covered by

425 the researchers in the same manner as birds themselves do in connection with natural nest leaving,

426 crows may have been observing the disturbance events. The use of cues may well be a reason for the

427 lack of strong positive effect of clutch size on nesting success and the lack of effect of clutch size on

428 absence length, which would have supported the clutch investment hypothesis (Coleman et al. 1985,

429 Andersson and Waldeck 2006). Disturbed, vacated nests are made apparent to predators and

430 available to predation, thus maintaining a high risk of nest loss regardless of the stage of the nesting

431 attempt.

432 Nest-loss rates due to disturbance do not necessarily translate into lower life time reproductive

433 success as the reproductive rate of this long-lived sea duck is low (acting through high nesting failure)

434 and as such we cannot attribute the human related disturbance of eiders at Grindøya to an ongoing

435 population decline of this colony. An unknown proportion of disturbance mediated predated nests

436 may have failed later in the breeding period due to poor female body condition (Hanssen et al.

437 2003a). However, an experimental study undertaken between 1997 and 2001 at the same colony

438 (Hanssen and Erikstad 2012) found long-term negative effects of nest failure due to nest predation

439 on future reproductive output . They found that fifty percent of females that failed during egg laying

440 did not relay during the same season and furthermore, females that lost their first clutch due to

441 predation regardless of whether they re-nested or not, had a lower number of breeding attempts

442 during the following 4 seasons than females that successfully hatched young (Hanssen and Erikstad

443 2012). Also, Hario and Rintala (2006) indicated that repeated reproductive failure (fledging rate) can

444 be enough to cause a decline in an eider population in Southern Finland. For populations

445 experiencing sharp declines such as is apparent at Grindøya and Håkøya (possibly mainly owing to

446 high female mortality [Erikstad et al. 2009]), the human induced breeding failures over multiple years

447 may suppress fledging rates, thereby adding to the decline.

448 To what extent any given population is resilient to disturbance will depend on the extent of density-

449 dependent population regulation (Sinclair 1989). Long-term studies of eider suggest both presence,

450 and absence of density dependence in eider populations (Hario and Rintala 2006, Coulson 2010). To

451 what extent density-dependent factors were acting on any demographic factor in the two study

452 colonies in Northern Norway is unknown. We did not find however, any evidence for density-

453 dependent predation as nearest-neighbour distance did not predict predation rates.

454 Long-term research is important to increase knowledge of ecological functioning, behaviour and

455 evolution of species (Clutton-Brock and Sheldon 2010).   However, potential negative effects of

456 research activity should regularly be quantified and evaluated, especially as many common species

457 (including eider) are in decline (e.g. Inger et al. 2015). In addition, the study shows the potential

458 negative effects on nesting success from general human disturbance in areas that are newly exposed

459 to increasing frequencies of human recreation. Using camera monitoring of individual nests, we have

460 shown that the intensity of activities undertaken during the study period at Grindøya clearly inflicted

461 high nest losses. We suggest that nest loss should be reduced at the Grindøya and Håkøya colonies,

462 by reducing nest predation. Stien et al. (2010) demonstrated that removal of territorial crows on

463 Grindøya alone had no effect on nest predation rates, possibly due to crows on nearby islands

464 compensating for predation carried out by removed crows (Stien unpublished). Thus, disturbance

465 leading to nest leaving could be reduced by the use of less invasive study protocols or disturbed nests

466 could be subjected to some kind of nest guarding until females return.   In association with the

467 reduced nest predation, a longitudinal study should be implemented in order to investigate whether

468 high nesting success can lead to increased recruitment and halt the decline in the population of

469 breeding common eiders.

470 **Acknowledgements**

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671

672 **Appendix**

673 **Appendix A**

674 Table 1A. The five logistic exposure models of daily nesting survival of 1003 nests on Grindøya and

675 Håkøya between 15 May and 30 June, 2006 – 2011 ranked according to Akaike's Information Criteria

676 (AICc and ΔAIC) and Akaike's weights (w_i) The ΔAIC values are expressed in relation to the best fitting

677 model. K is the number of parameters in the models. Clutch is the initial clutch size at nest discovery

678 and day is Julian day.

679

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

680

681 **Appendix B**

682 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

683 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.

684 K is the number of parameters in the models. Clutch is the initial clutch size at nest discovery and day is Julian day.

685

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

686

687 **Appendix C**

688 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

689 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

690 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.

691

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

692

693 Table 1. Number of nests followed for monitoring of nesting success on Grindøya and Håkøya

694 colonies between 17 May and 30 June 2006 – 2011. Observational monitoring refers to nests

695 followed to estimate nesting success of the two colonies during the entire monitoring period.

696 Camera monitoring refers to the subset of nests equipped with cameras and for which the success of

697 individual nest level could be related to nest covariates and nest leaving histories. Sample size for

698 estimation of effects of cameras on nesting success is shown in parenthesis, which is a subset of the

699 total number of camera-monitored nests in 2009.

700

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

721   Table 3. Predator species responsible for full (nest loss) and partial predation of camera monitored

722   nests on Grindøya and Håkøya between 17 May and 30 June 2009 – 2011.

723

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

724

725 Figure 1. Predicted common eider nesting success at Grindøya and Håkøya from a logistic exposure

726 model. The predictions are obtained from back-transformed coefficient estimates and 95% C.I. for

727 the area*year effect with nesting success expressed as an average for the eider nesting period of 28

728 days (assumes average clutch size of four and average incubation period of 24 days; adapted from

729 Erikstad et al. 1993).

730

731 Figure 2.a) Predictions (solid lines with 95 % C.I. shown by broken lines) of nest survival rate as a

732 function of number of days since nest detection obtained from the best Cox proportional hazard

733 model for 103 camera monitored nests on Grindøya and Håkøya. a) Mean effects of all covariates

734 included in the model while b - d) gives predictions for contrasting levels of covariates. b) disturbance

735 (P = < 0.001), where lower solid line is a maximum rate of disturbances per nest life day (2

736 disturbances) and upper solid line is a rate of 0.5 disturbances per nest day life; c) Julian day (P =

737 0.02), where lower solid line is 17 May and upper solid line is 27 May; d) clutch size (P = 0.05), where

738 lower solid line is 1 egg and upper solid line is 6 eggs.

739

740 Figure 3. Effect of cameras from best exposure model on the nesting success of 42 pairs of eider on

741 Grindøya and Håkøya monitored between 19 May and 30 June 2009. Daily interval estimates from

742 the model have been raised to the power of 7 and clutch is set to mean clutch size (3) to estimate

743 average weekly nesting success. Estimates are shown with 95 % C.I.

744

Days Since Nest Discovery

745