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1   **Effects of an extreme weather event on seabird breeding success at a North Sea colony**

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10   **Abstract**

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12   Quantifying the effects of extreme weather is a critical question in population ecology since

13   climate models predict increased climate variability. Effects will vary among and within

14   species due to exposure or susceptibility, yet few studies have considered these sources of

15   variation simultaneously.   We investigated the effects of a summer storm on breeding

16   success of four seabird species at a North Sea colony in relation to aspect, height above sea-

17   level, distance to cliff edge and laying date. The storm lasted 8 hours with gusts of >60 ms^{-1}.

18   In exposed plots, razorbills *Alca torda* had higher failure rates (28.5%) than European shags

19   *Phalacrocorax aristotelis* (15.1%), black-legged kittiwakes *Rissa tridactyla* (15.6%) or

20   common guillemots *Uria aalge* (10.4%). Conversely, failure rates in sheltered plots were

21   negligible (shags 0.0%; kittiwakes 1.9%; no guillemot or razorbill plots in sheltered

22   locations). Guillemots breeding closer to sea-level were more likely to fail, but cliff edge

23   proximity did not affect failure rate. In razorbills, pairs that laid early were more likely to

24   survive the storm. In all species, some failed pairs relaid, and success of relays was lower

25   than pairs that survived. Thus, relaying only provided partial compensation and, overall, the

26   storm caused a net reduction in annual population production of 4.6%, 10.7%, 8.9% and

27   22.8% for shags, kittiwakes, guillemots and razorbills, respectively. Increased storm

28   frequency may therefore have important consequences on seabird populations, but orientation

29   of storms relative to colonies and timing in relation to the breeding season are likely to be

30   critical in determining the overall effect.

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32   **Keywords:** climate change; summer storm; rainfall; IPCC; European shag; black-legged

33   kittiwake; common guillemot; razorbill

34   **Introduction**

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Climate change is having a dramatic effect on the population dynamics of many animal

species, and much research has focussed on the effects of mean temperature, typically at

annual or decadal scales (Walther et al. 2002, Thomas et al. 2004). However, there is

increasing evidence that populations are also affected by climate variability (Parmesan et al.

2000, Moreno & Moller 2011). These effects warrant further investigation since climate

models predict that mean wind speeds and the frequency of severe weather is going to

increase in some regions in the future, in particular at higher latitudes (McInnes et al. 2011,

Young et al. 2011). Such events can take different forms, including extremes of temperature,

high rainfall or strong winds, and usually operate at much shorter time scales than changes in

mean climate, typically hours or days rather than years or decades. The effects of extreme

weather are likely to vary amongst species due to differences in their ecology and life history.

Furthermore, differences are likely among individuals within species due to variation in

exposure or susceptibility. Quantifying variation among and within species is therefore

critical to understanding the impacts of extreme weather events on animal populations.

   A number of studies have shown that the survival and productivity of seabirds can be

affected by extreme weather (Schreiber 2001, Jenouvrier 2013). Extreme weather events are

likely to be important outside the breeding season since this is typically when most adult

mortality occurs, and the population dynamics of seabirds are generally more sensitive to

changes in adult survival rates than changes in breeding success (Weimerskirch 2001).

However, it has proved challenging to attribute variation in adult survival rates to extreme

winter weather because comprehensive data on the timing and location of deaths are not

typically available (but see Frederiksen et al. 2008). Extreme weather may also be important

during the breeding season since individuals are constrained to remain at or close to the

breeding colony.   At this time, adults and chicks can be affected by heat stress (Gaston et al.

60   2002, Oswald et al. 2008, Oswald & Arnold 2012), and high winds and rainfall can result in

61   breeding failure (White et al. 1976, King et al. 1992, Aebischer 1993, Hennicke &

62   Flachsbarth 2009, Mallory et al. 2009, Sherley et al. 2012, Wolfaardt et al. 2012, Boersma &

63   Rebstock 2014, Bonter et al. 2014).

64   While severe weather is widely understood to reduce seabird breeding success, studies

65   that quantify variation amongst and within species are needed to investigate the consequences

66   of extreme weather on seabird communities (Wolfaardt et al. 2012). Such heterogeneity may

67   arise from differences in exposure or susceptibility to wind, waves or rainfall. Thus, species

68   may vary in susceptibility due to physical size or attributes of the nest site. Within species,

69   nests that are oriented in the direction of the storm, closer to sea level and nearer to the cliff

70   edge are likely to be more vulnerable. Intrinsic factors may also be important. For example,

71   pairs that lay early in the season typically have higher average breeding success than those

72   that lay late. Early breeders may therefore have greater ability or willingness to withstand

73   bad weather, may occupy higher quality nest sites that are less exposed and be more likely to

74   relay if they do fail (Potts et al. 1980, Hipfner et al. 1999). On 23rd May 2011, a severe

75   storm was forecast to hit eastern Scotland. This gave us the opportunity to compare the short

76   term impact of prolonged gale force winds and rough seas on the breeding success of four

77   cliff-nesting species, the European Shag *Phalacrocorax aristotelis* (hereafter 'shag'), black-

78   legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake), common guillemot *Uria aalge*

79   (hereafter 'guillemot') and razorbill (*Alca torda*) at a major breeding colony in the region.

80   Within species, we tested whether the effect of the storm had a disproportionate effect on

81   nests located on the exposed (south-westerly) side of the island, closer to sea level and nearer

82   the cliff edge. We also tested whether a pair's laying date was important in determining

83   failure rate in the storm. Finally, we quantified the capacity of species to compensate for

84   losses sustained in the storm by relaying, allowing us to estimate the likely net effect of the

85   storm on annual population production.

86

87   **Methods**

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89   Fieldwork took place during the 2011 breeding season on the Isle of May National Nature

90   Reserve, south-east Scotland (56º 11' N, 02º 33' W). The island is oriented on a north-

91   west/south-east axis with high cliffs facing predominantly to the south-west and gently

92   sloping rocky terrain facing predominantly to the north-east (Fig 1). Breeding phenology and

93   success of a sample of shag, kittiwake, guillemot and razorbill nest sites were collected at

94   long established monitoring plots using standardized methods (Walsh et al. 1995). For shags,

95   104 nest sites at 11 plots (79 nest sites in 8 plots facing south-west, 25 nest sites in 3 plots

96   facing north-east; Fig 1) were checked every 7 days from before laying to fledging, and the

97   laying date (within 7 days, taken to be half-way between the first date incubation is observed

98   and the previous date), number of chicks fledged (range 0-4) and, for unsuccessful pairs, date

99   of failure (minimum accuracy 7 days) were recorded. For kittiwakes, 166 nests in 6 plots

100 were checked every 5 days from pre-laying to fledging, and as with shags, the laying date

101 (minimum accuracy 5 days) the number of chicks fledged (range 0-3) and, for unsuccessful

102 pairs, date of failure (minimum accuracy 5 days) were recorded. At 9 additional kittiwake

103 plots, 283 nests were checked when most pairs had finished laying and again from the day

104 after the first fledged chick was seen in the colony, and the number of chicks fledged was

105 recorded (Harris 1987). Thus, the total sample size for kittiwakes was 449 nest sites in 15

106 plots of which 397 were in 12 south-west facing plots and 52 in 3 north-east facing plots (Fig.

107 1). For guillemots, 828 nest sites at 6 plots (all on south-west facing cliffs; Fig 1) were

108 checked daily from before laying to fledging, and laying date, breeding success (i.e whether

109   the single chick fledged, since guillemots only lay one egg) and, where applicable, date of

110   failure was recorded. The protocol for razorbills, which also lay one egg, was similar to that

111   of guillemots (n = 173 nest sites at 5 of the six plots followed for guillemots; Fig 1).   For

112   guillemot and razorbill nest sites, height above sea level was measured using a marked rope

113   (range: guillemots, 3-27m; razorbills, 4-26m; Harris et al. 1997).   Height above sea level was

114   not known for shag or kittiwake nests. In one guillemot plot the majority of breeding sites

115   were located on a series of broad flat ledges and, for these sites, straight line distance from

116   the cliff edge was measured (n = 250; horizontal distance range: 0.2-3.8m; height above sea

117   level: 5m; Harris et al. 1997).

118   The storm occurred on 23rd May 2011. To assess its severity relative to summer weather

119   conditions over the last 40 years, hourly wind speeds (mean speed and maximum gust speed)

120   were extracted from the weather station at Leuchars (56º 23' N, 02º 52' W; 28km from the

121   Isle of May; source: www.badc.ac.uk) for dates between 1st April and 15th July each year

122   from 1969, when hourly records began. These dates covered the core breeding periods of the

123   four study species. The storm was forecast in advance and its strength was predicted to be of

124   such magnitude that we considered it important to quantify its effects, so a full check of

125   breeding status at each study nest was carried out on the day before and again on the day after

126   the storm. This constituted a departure from standard monitoring frequency for shags and

127   kittiwakes to ensure that any breeding failures over that period could be unequivocally

128   attributed to the storm. Since guillemots and razorbills were being monitored on a daily basis,

129   the effects of the storm could be estimated without the need to depart from standard

130   protocols. Monitored nest sites were categorised as follows: a) failed before the storm; b)

131   failed during the storm; c) survived the storm; d) eggs laid for the first time after the storm.

132   Some pairs that failed before or during the storm (categories a) and b), respectively) relaid

133   after the storm. These relays were monitored in the same way as other breeding attempts so

134   that final breeding outcome was known for all study pairs. In most cases, we were unable to

135   confirm that the second laid egg was relayed by the same pair, as opposed to a different pair

136   occupying the site after the failure of the first pair. However, these species are aggressively

137   territorial and our long-term studies of these populations has shown that pairs rarely change

138   sites when relaying. In this study, the same colour-ringed individual was in the pair

139   associated with the second egg in 5/5 cases for guillemots, 1/1 for razorbill and 7/8 for shags.

140   The extent to which relaying compensated for failure during the storm ("percentage

141   compensation") was estimated as the number of chicks raised as a percentage of the number

142   that could have been raised had all failed nests relaid and been as successful as those that

143   survived the storm. Thus, full compensation would have a value of 100%.

144   Our principal variables of interest in analyses of within-species variation in effects of the

145   storm were aspect, height above sea level, distance from cliff edge and laying date. Where

146   possible, we also tested whether the effects of exposure (aspect, height and distance) were

147   dependent on laying date since early breeders may have greater ability or willingness to

148   withstand bad weather, and therefore we might expect any difference between early and late

149   layers to become more marked as exposure increased. We could not test the interaction

150   between aspect and laying date in shags since the former could only be estimated with a

151   randomisation test (see below). We were also not able to test the interaction between aspect

152   and laying date in kittiwakes, since the plots where laying date was recorded were all on the

153   exposed side of the island. For guillemots, we tested the effects of height above sea level,

154   laying date and the interaction between them (correlation between height above sea level and

155   laying date: $r = 0.08$). In a separate analysis, we tested the effects of distance from cliff edge,

156   laying date and the interaction between them (correlation between distance from cliff edge

157   and laying date: $r = 0.11$). The former model was based on a much larger sample size, so was

158   a more comprehensive test of the effect of laying date. However, the effects of laying date in

159   the latter model were qualitatively similar. For razorbills, we tested the effects of height

160   above sea level, laying date and the interaction between them (correlation between height

161   above sea level and laying date: $r = -0.01$).

162   To test whether nests in south-westerly plots were more affected by the storm than those

163   in north-easterly plots for kittiwakes, we carried out a binomial Generalized Linear Mixed

164   Model (GLMM) with logit link function on all breeding attempts active on the day of the

165   storm with failure in the storm (0 or 1) as the response variable, aspect (north-east or south-

166   west) as a fixed effect and plot as a random effect. We could not take this approach with

167   shags since the north-east orientation contained no failed nests, which makes this parameter

168   inestimable in a model-based test. Instead we carried out a randomization test (Fisher Exact

169   Test) on the number of nests active on the day of the storm that failed or survived in south-

170   western and north-eastern plots. To test the effect of height above sea level, laying date and

171   the interaction between them on nest survival from the storm in guillemots and razorbills, we

172   carried out a binomial GLMM on each species on all breeding attempts active on the day of

173   the storm with failure in the storm (0 or 1) as the response variable, height above sea level (in

174   metres), laying date and a height above sea level by laying date interaction as fixed effects

175   and plot as a random effect. To test whether guillemots nesting closer to the cliff edge were

176   more affected, and whether there was an interaction between distance to cliff edge and laying

177   date, we used a binomial GLM on all active nests with failure in the storm (0 or 1) as the

178   response variable and distance from the cliff edge (in metres), laying date and a distance to

179   cliff edge by laying date interaction as fixed effects (nests in this analysis were from a single

180   plot so a GLMM was not required). To test whether early or late breeding birds were more

181   likely to survive the storm in kittiwakes and shags, we carried out a binomial GLMM on all

182   active nests with failure in the storm (0 or 1) as the response variable, laying date as a fixed

183   effect and plot as a random effect. For shags, we repeated the analysis, substituting breeding

184   stage (incubation or chick-rearing) for laying date, to test whether the effect of the storm was

185   dependent on whether pairs were incubating eggs or brooding chicks. This breeding stage

186   test was not undertaken for the other species since all pairs were incubating.

187   To test whether early or late breeding birds were more likely to relay after loss in the

188   storm, we carried out a binomial GLMM on all nests that failed in the storm with relay

189   incidence (0 or 1) as the response variable, laying date as a fixed effect and plot as a random

190   effect. We substituted laying date for breeding stage in shags to test whether individuals that

191   were incubating eggs at the time of the storm were more likely to relay than those that were

192   rearing young. Laying date was not available in a small number of cases which is reflected in

193   the slightly smaller sample sizes in these analyses. All statistical analyses were carried out in

194   Genstat 16.

195   To quantify the net effect of the storm on the annul population production of each species,

196   we first estimated the predicted breeding success of nests that failed in the storm had the

197   storm not occurred. The simple approach to this estimation assumed that, but for the storm,

198   pairs that failed would have been as successful as those in the same plot that were active at

199   the time of the storm but survived. However, it is possible that the storm affected nests

200   whose breeding success was higher or lower than average e.g. the latter might occur if young

201   breeders tend to occupy more exposed sites, but also have lower foraging efficiency thus

202   increasing the probability of chick mortality from starvation (Daunt et al. 2007). To examine

203   this possibility, we compared the past breeding success of nest sites that survived the storm

204   with those that did not in shags (data from 1996-2010), guillemots (1981-2010) and razorbills

205   (1982-2010). In guillemots, long-term breeding success of nest sites that failed during the

206   storm was significantly lower (by 4.7%) than breeding success of nest sites that survived the

207   storm (Appendix A). We therefore reduced the predicted breeding success of pairs that failed

208   in the storm by 4.7%. In shags and guillemots, we found no significant difference (Appendix

209   A), so we used the simple approach outlined above. For kittiwakes, individual nest identity

210   was not retained across years, so we used the simple approach.

211   In a second step, we estimated the predicted mean breeding success in exposed

212   monitoring plots (facing south-west) and sheltered monitoring plots (facing north-east)

213   separately. For both groups, predicted mean breeding success was estimated as the average

214   across all nests based on the observed breeding success of pairs unaffected by the storm (i.e.

215   those that failed before the storm, survived the storm or laid after the storm) and predicted

216   breeding success of those pairs that failed in the storm as outlined above. We then

217   extrapolated the mean predicted and observed breeding success in exposed monitoring plots

218   to the proportion of the whole population in the south-western part of the island on the

219   assumption that exposure was similar across all nests with this orientation, inside and outside

220   the monitoring plots. We carried out an identical extrapolation from sheltered monitoring

221   plots to the proportion of the population in the north-eastern part of the island. Since there

222   were no guillemot or razorbill monitoring plots in the north-east, we assumed that no nests

223   with this orientation failed in the storm based on failure rates of north-eastern facing shag and

224   kittiwake monitoring plots (see results). Relative proportions of the population in south-

225   western and north-eastern parts of the colony were estimated from whole-island population

226   counts (Pickett & Squire 2011). Equivalent extrapolations from monitoring plots to the

227   population as a whole based on height above sea level or distance to cliff edge were not

228   feasible since these measures were not available for the majority of nests.

229   For each species, we combined the results for the two parts of the colony into estimates of

230   predicted and observed breeding success for the whole population as follows:

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232   Predicted breeding success = (predicted breeding success in SW plots * propn. of population

233   in SW) + (predicted breeding success in NE plots * propn. of population in NE)

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235   Observed breeding success = (observed breeding success in SW plots * propn. of population

236   in SW) + (observed breeding success in NE plots * propn. of population in NE)

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238   Finally, we combined these two estimates to calculate the net effect of the storm on

239   annual population production as follows:

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241   Net effect = (predicted breeding success − observed breeding success) / predicted breeding

242   success %

243

244   **Results**

245

246   The storm lasted approximately eight hours, with mean wind speeds of 36.3ms^{-1} and

247   maximum hourly gust speeds >50ms^{-1} recorded throughout the period from 12.00h to 20.00h.

248   The storm came from a westerly direction and coincided with high tide. A comparison with

249   historical weather data showed that it was the most severe summer storm since hourly records

250   began in 1969, such that the four highest, and seven of the 10 highest hourly maximum gust

251   speeds during April-mid July 1969-2011 occurred on this day (Fig. 2).

252   Since the storm came from a westerly direction, the majority of monitoring plots were

253   exposed since they were positioned on the south-west side of the island (shag: 8 out of 11

254   plots; kittiwake: 12 out of 15 plots; guillemot: 6 out of 6 plots; razorbill: 5 out of 5 plots).

255   The storm occurred during early to mid-incubation for kittiwake, late incubation for

256   guillemot and razorbill, and late incubation to early chick-rearing for shag (median lay dates:

257   shag: 11th April; kittiwake: 10th May; guillemot: 23rd April; razorbill: 26th April), with laying

258   almost complete in all species (percentage pairs that laid before the storm: shag 96.2%;

259 kittiwake 98.4%; guillemot 99.5%; razorbill 95.4%; Table 1). A small proportion of nests

260 failed before the storm, so the percentages of nests that were active when the storm occurred

261 for shag, kittiwake, guillemot and razorbill were 91.3%, 97.3%, 96.4% and 91.3%

262 respectively.

263   The storm had a similar impact on shag, kittiwake and guillemot, with 11.5%, 14.0% and

264 10.4% of active nests failing, respectively. However, a higher percentage of razorbill nests

265 was affected (28.5%; Table 1). There was a tendency for south-westerly facing shag nests to

266 be more vulnerable to the storm than north-easterly nests, with 11/73 (15.1%) and 0/22

267 (0.0%) failing in the storm, respectively (Fisher Exact Test: $p = 0.06$). South-westerly facing

268 kittiwake nests were significantly more vulnerable to the storm than north-easterly nests, with

269 60/385 (15.6%) nests in south-westerly plots failing in the storm and 1/52 (1.9%) nests failing

270 in north-easterly facing plots (GLMM: $W = 4.05$: $p < 0.05$). In guillemots, a lower failure

271 rate was apparent with increasing height above sea level, but there was no effect of laying

272 date and no interaction between height above sea level and laying date (n=768; GLMM:

273 height above sea level: $W = 10.63$, $p < 0.01$, Fig 3; laying date: $W = 0.70$, $p = 0.40$, Fig 4c;

274 interaction term: $W = 0.00$, $p = 0.97$) . In contrast, there was no effect of height above sea

275 level on failure rate in razorbills, but those nests with an earlier laying date were more likely

276 to survive; the interaction term was not significant (n=153; GLMM: height above sea level:

277 $W = 0.48$, $p = 0.49$, Fig 3; laying date: $W = 5.40$, $p < 0.05$, Fig 4d; interaction term: $W = 0.00$,

278 $p = 0.96$). Failure rate was not related to distance from the cliff edge in guillemots, and there

279 was no effect of laying date in this subset of nests (in line with findings from the larger

280 sample), nor was there a significant interaction between these two variables (n = 250; GLM:

281 distance from cliff edge: $W = 1.71$, $p = 0.19$; laying date: $W = 1.31$, $p = 0.25$; interaction

282 term: $W = 3.08$; $p = 0.08$). There was no effect of laying date on failure rate in shags (n = 95;

283   W = 0.09, p = 0.76; Fig 4a) or kittiwakes (n = 148; W = 0.33, p = 0.57; Fig 4b), nor was

284   breeding stage related to failure rate in shags (n = 95; W = 0.06; p = 0.80).

285   Not all pairs that failed during the storm relaid (pairs relaying: shag: 45.5%; kittiwake:

286   39.3%; guillemot: 25.3%; razorbill: 17.8%), and such pairs were ultimately less successful

287   than those that survived the storm (Table 1). Thus, failure during the storm was only partially

288   compensated for through re-laying (percentage compensation: shags: 19.6%; kittiwakes:

289   16.3%; guillemots: 1.4%; razorbills: 0.0%). There was a tendency for early laying pairs to be

290   more likely to relay among razorbills (n = 44; W = 3.68, p = 0.06; Fig 4h). However, there

291   was no relationship in shags (n = 11; W = 0.05, p = 0.82; Fig 4e), kittiwakes (n=20, W =

292   0.00, p = 0.98; Fig 4f) or guillemots (n = 82; W = 0.48; p = 0.49; Fig 4g), nor was breeding

293   stage related to relay probability in shags (n = 11; W = 0.13; p = 0.71).

294   The observed mean and predicted mean breeding successes had the storm not occurred of

295   pairs in exposed and sheltered parts of the island are given in Table 2. The majority of

296   kittiwakes, guillemots and razorbills were located in exposed areas (85-93%) whilst the

297   majority of the shag population was breeding in the sheltered part of the island (69%, Table

298   2). Combining mean predicted and observed breeding success in exposed and sheltered nests

299   with these proportions, we estimated that the net reduction in annual population production of

300   shags was 4.6%, reflecting the high proportion of the population located in sheltered areas. In

301   contrast, estimates of net reduction in annual population production for the other three species

302   matched closely those in the monitoring plots, demonstrating that the high impact of the

303   storm on razorbills was apparent in the population as a whole (kittiwake: 10.7%; guillemot:

304   8.9%; razorbill: 22.8%; Table 2). The greater impact of the storm on razorbills can be seen

305   when comparing the overall breeding success in 2011 with the long-term mean for each

306   species (shag: 1.54 in 2011 vs 1.01 ± 0.57 mean ± sd chicks/pair, 1985-2010; kittiwake 0.87

307   vs 0.55 ± 0.38, 1985-2010; guillemot: 0.73 vs 0.73 ± 0.13, 1981-2010; razorbill 0.50 vs 0.66

308 ± 0.08, 1982-2010). Razorbill breeding success in 2011 was the worst on record (previous

309 range 0.52 – 0.86 chicks/pair).

310

311 **Discussion**

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313 Few studies have investigated among and within-species variation in the effects of extreme

314 weather on seabird breeding success. We quantified these effects in four species of cliff

315 nesting seabirds during the most severe summer storm recorded in the region in 40 years. We

316 demonstrated important, and in some cases unexpected, effects of the extreme weather event

317 on the breeding success of this seabird community. Our results supported our prediction that

318 nests on the exposed side of the island and low down the cliff would be more severely

319 affected. However, we did not foresee that razorbills would be much more vulnerable than

320 the other species. Razorbills typically breed on more sheltered sites than the closely related

321 guillemot (Olsthoorn & Nelson 1990). However, on the Isle of May the two species breed in

322 close proximity and exposure to wind, waves and spray seemed likely to have been similar.

323 Due to the ferocity of the wind it was not possible to directly observe losses in the storm.

324 However, razorbills may have been more susceptible to being physically lifted off their sites,

325 since they are 30% lighter than guillemots. This effect may have been particularly important

326 higher up the cliff, where wind speeds are typically highest. If both species are susceptible to

327 spray, whilst guillemots are more able to withstand high wind speeds, this may explain why

328 we detected an effect of height above sea level on nest survival from the storm in guillemots

329 but not in razorbills. Further, it may explain why vulnerability to the storm was unrelated to

330 horizontal distance in guillemots, since level of spray is likely to be determined more by

331 height than distance to the cliff edge. Whatever the mechanisms driving the variation among

332 the two species in overall loss and the effect of height, the high impact of the storm on

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333 razorbills resulted in the lowest breeding success at this colony since records began in 1982.

334 In contrast, breeding success for the other three species was at or above the long term

335 average, despite losses in the storm.

336   The disproportionate effect of the storm on exposed compared to sheltered locations had a

337 strong influence on the population-level effects for each species in line with their breeding

338 distribution on the island. Although shag nests in exposed plots were affected by the storm to

339 a similar extent as kittiwakes and guillemots, the majority of nests of this species are located

340 on the north-east side of the island, so the overall impact on the population was

341 comparatively small. In contrast, the other three species are concentrated on the south-west

342 side of the island, so were more exposed to the storm. The majority of severe summer storms

343 recorded on the Isle of May over the last 40 years have been from a westerly direction (Fig

344 2). This would suggest that these interspecific differences have occurred repeatedly in recent

345 decades. However, in contrast to the other species, the distribution of shag nests on the island

346 has changed substantially over this period. Thus, a westerly storm in May 1982 had a

347 dramatic effect on shag breeding success because, at that time, the majority of the population

348 bred on the south-west side of the island (Aebischer 1993). Our results therefore suggest that

349 the effects of summer storms on breeding seabirds are likely to be strongly dependent on the

350 direction of the storm relative to breeding sites. However, predicting future effects of

351 extreme weather is challenging since both storm direction and changes in breeding

352 distribution, such as we have observed in the shag population on the Isle of May over the last

353 three decades, would have to be considered. The percentage of shag nests in exposed

354 locations that failed was much lower in 2011 than 1982 (15% vs 49%). One possibility for

355 this difference is that nests were on average closer to sea level when densities were higher in

356 the south-west. Storm duration may also have been a contributory factor since the 1982

357 storm was longer, with gale force winds experienced for most of the day (Aebischer 1993;

358 Fig 2).

359   A proportion of breeding pairs that failed in the storm relaid, and success of these pairs

360 was significantly lower than those that survived the storm. In combination, these two effects

361 resulted in only partial compensation for the storm, ranging from 0.0-19.6% across the four

362 species. We do not know how typical this level of compensation is, but breeding success of

363 those pairs unaffected by the storm was at or above the long-term average in all species,

364 suggesting that, aside from the storm, environmental conditions were favourable. Thus, it is

365 possible that compensation would be lower in years when overall conditions are poorer, since

366 breeding individuals would likely be in poorer condition and therefore less likely to relay.

367 These estimates only relate to breeding success, yet compensation may have been even lower

368 in terms of longer term fitness since there is a decline in post-fledging survival with fledging

369 date in shags and guillemots at this colony (Harris et al. 1994, Lahoz-Monfort et al. 2014).

370 Post-fledging survival may also be related to the nutritional quality of the egg, which is likely

371 to be lower on average in relaid eggs (Nager et al. 2000, Krist 2011). However, these

372 potential effects require formal testing since a study of Brünnich's guillemots *Uria lomvia* in

373 the Canadian Arctic found no difference in recruitment rates of individuals from first laid and

374 replacement eggs (Hipfner 2001). Long term fitness effects of relaying may not be limited to

375 impacts on chicks. The costs associated with relaying may also have reduced the survival

376 probability of adults (Nager et al. 2001), which could have consequences for population size.

377   Our prediction that early laying pairs would be more likely to survive the storm was

378 upheld in razorbills. Late breeders may be less able to withstand bad weather, or show

379 reproductive restraint which may increase likelihood of abandonment in poor conditions

380 (Williams 1966). Alternatively, they may occupy lower quality nest sites that are more

381 exposed to wind and spray. It is not clear why laying date was not an important determinant

382   of nest survival from the storm in the other species, but one possibility is that the losses

383   resulted from catastrophic events (e.g. a nest or clutch being washed away or dislodged by

384   gusting wind) where intrinsic effects are less likely to play a role. We found a tendency that

385   early laying pairs that failed in the storm were more likely to relay than late laying pairs in

386   razorbills. As with the effect of laying date on nest survival probability, this may reflect

387   intrinsic differences in ability or effort.

388   The relative timing of an extreme weather event is likely to be critical to the overall effect

389   on breeding success. Losses to extreme weather may be higher during chick-rearing than

390   incubation since chicks are sensitive to exposure to extreme rain, wind and temperature

391   (White et al. 1976, Demongin et al. 2010, Boersma & Rebstock 2014). Furthermore, chick

392   mortality during extreme weather may occur indirectly through a reduction in adult foraging

393   success. A study of guillemots at this colony showed that during stormy weather, chick-

394   rearing adults increased their foraging effort, caught smaller fish and showed reduced nest

395   attendance (Finney et al. 1999). A recent study on southern rockhopper penguins (*Eudyptes*

396   *chrysocome*) provides further evidence that wind affects foraging success (Dehnhard et al.

397   2013). Such indirect effects of weather on breeding performance are likely to be more

398   profound during chick-rearing than incubation, where there is greater capacity for the non-

399   attending bird to extend the time away from the nest since no provisioning is required.

400   However, it is possible that the storm was not of sufficient duration for these indirect effects

401   to occur, since shags did not do worse than the other species, despite breeding being more

402   advanced with some pairs rearing chicks at the time of the storm. The extent to which

403   individuals compensate through replacing lost eggs may also be linked to the timing of

404   extreme weather relative to the breeding season. Studies of shags, kittiwakes and guillemots

405   (both common and Brünnich's) have shown that the proportion relaying and success of relays

406   declines with date (Gaston & Nettleship 1981, Harris & Birkhead 1985, Aebischer 1993,

407 Wanless & Harris 1997, Daunt 2000, Coulson 2011). As shown in razorbills in this study,

408 breeders that lay earlier in the season are more likely to relay than later breeders (Hipfner et

409 al. 1999). Furthermore, at the individual level, relaying is more likely if failure occurs sooner

410 after laying, perhaps linked to body condition which is on average higher at that time than

411 later in the breeding season (unpublished data on guillemots on the Isle of May from 1982-

412 present: correlation between days incubated prior to loss and probability of relaying: $r = -$

413 0.95). Thus, if the 2011 storm had occurred earlier in the breeding season, relaying might

414 have compensated more fully for clutches that were lost. Conversely, reduced compensation

415 from relaying is likely had the storm occurred later in the season. However, species

416 differences are clearly apparent since shags had a comparatively high relay rate despite their

417 breeding season being more advanced.

418 Extreme weather events are an understudied but potentially important driver of seabird

419 breeding success (Schreiber 2001, Jenouvrier 2013). A number of studies have shown that

420 extremes of temperature, high rainfall, strong wind and rough seas can all result in major

421 offspring mortality (King et al. 1992, Aebischer 1993, Gaston et al. 2002, Oswald et al. 2008,

422 Hennicke & Flachsbarth 2009, Mallory et al. 2009, Oswald & Arnold 2012, Sherley et al.

423 2012, Wolfaardt et al. 2012, Boersma & Rebstock 2014, Bonter et al. 2014). Here, we have

424 shown that the overall effect of extreme weather varies both among and within species, likely

425 due to variation in exposure and susceptibility. Our study highlights the value in recording

426 immediate impacts and compensation from relaying to enable estimation of the net effects on

427 annual breeding output of such events. Quantifying the impacts of extreme weather on

428 breeding success is likely to become increasingly important, since many models predict that

429 their frequency is going to increase in some regions, in particular at higher latitudes (McInnes

430 et al. 2011, Young et al. 2011). An isolated event such as this is unlikely to have a dramatic

431 effect on population size, especially in seasons such as the study year where (razorbills

432	excepting) the breeding season was moderately good, despite the storm. However, a greater

433	frequency of summer storms of this severity could result in discernible impacts on population

434	size (Descamps et al. 2015), although orientation of storms relative to breeding sites, storm

435	duration and timing in relation to the breeding season are likely to be critical in determining

436	the overall effect.

437

438	**Acknowledgements**

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447	**References**

448

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567 Table 1: Immediate effects of the storm on 23rd May, percentage that relaid and final breeding

568 success (mean chicks fledged per pair) of four species on the Isle of May in 2011.

569

	Shag	Kittiwake	Guillemot	Razorbill
Number of monitored nests	104	449	828	173
Number failed before storm	5	5	26	7
Number active when storm occurred	95	437	798	158
Number laid after storm	4	7	4	8
% active in storm and failed	11.6	14.0	10.4	28.5
% relaid after failing in storm	45.5	39.3	25.3	17.8
Breeding success, failed before storm	0.00	0.00	0.00	0.00
Breeding success, survived storm	1.86	1.01	0.84	0.74
Breeding success, failed in storm and relaid	0.80	0.42	0.05	0.00
Breeding success, failed in storm, all nests	0.36	0.16	0.01	0.00
Breeding success, laid after storm	0.00	0.00	0.75	0.38
Mean breeding success of study nests	1.54	0.87	0.73	0.50

570

571

572   Table 2: Input values for the estimate of net effect of the storm on annual population

573   production (observed mean breeding success and predicted mean breeding success in

574   exposed, sheltered and all sites, and proportion of the population in exposed and sheltered

575   sites) and net effect as a percentage reduction of predicted breeding success. The observed

576   breeding success for guillemots and razorbills in sheltered sites was estimated based on

577   failure rates during the storm for shags and kittiwakes. Breeding success is mean chicks

578   fledged per pair.

579

580

Species	Exposed			Sheltered			Whole population		
	Observed breeding success	Predicted breeding success	Propn. of population	Observed breeding success	Predicted breeding success	Propn. of population	Observed breeding success	Predicted breeding success	Net effect (%)
Shag	1.58	1.81	0.31	1.40	1.40	0.69	1.46	1.53	-4.6
Kittiwake	0.92	1.04	0.85	0.50	0.49	0.15	0.86	0.96	-10.7
Guillemot	0.73	0.81	0.93	0.81	0.81	0.07	0.73	0.81	-8.9
Razorbill	0.51	0.69	0.85	0.69	0.69	0.15	0.54	0.69	-22.8

581

Figure legends

Fig 1: Location of monitoring plots on the Isle of May National Nature Reserve.

Fig 2: Mean hourly wind speed on 23rd May 2011 and the seven other storms between April and mid-July 1969-2011 where maximum gust speed exceeded 45 ms^{-1} in five hours or more. Seven of these storms were in a westerly direction and one in an easterly direction (3rd April 1998).

Fig 3: Fitted lines (± 95% C.I.) for nest survival from the storm in relation to height above sea level from the GLMMs for guillemots (solid lines; $n = 768$ active nests when the storm occurred) and razorbills (dashed lines; $n = 153$).

Fig 4: Fitted lines (± 95% C.I.) for survival from the storm in relation to laying date for the GLMMs for a) shags (n=95); b) kittiwakes (n=148); c) guillemots (n=768) and d) razorbills (n=153); fitted lines (± 95% C.I.) from the GLMMs of post-storm relaying in relation to laying date for e) shags (n=11); f) kittiwakes (n=20); g) guillemots (n=82) and h) razorbills (n=44).
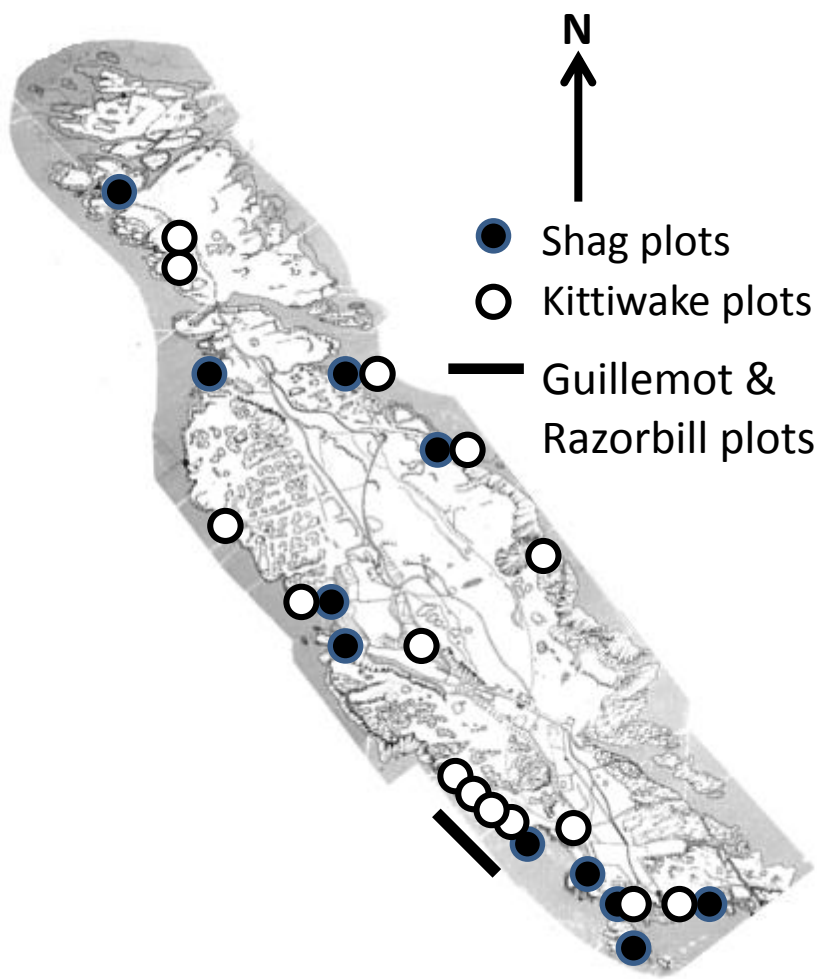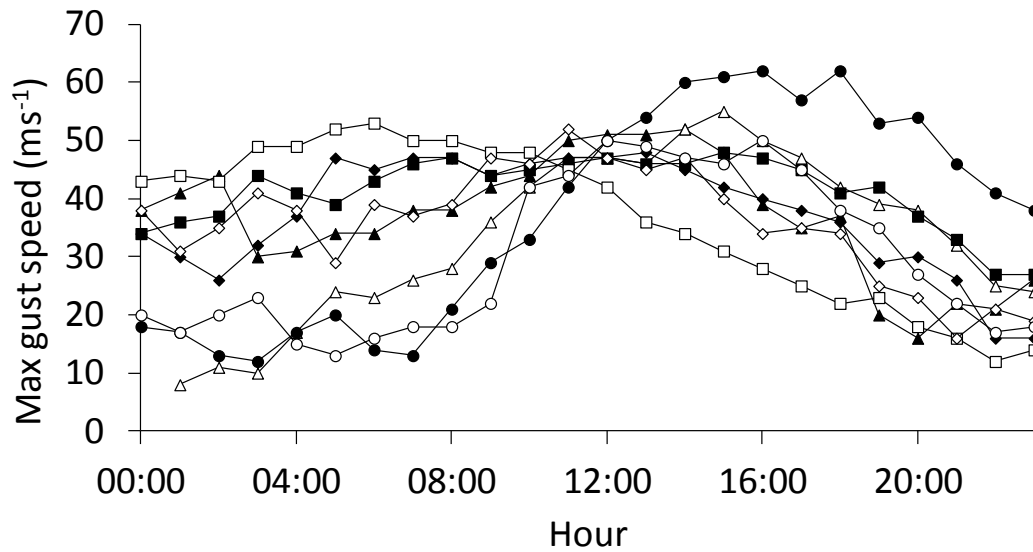
602   Fig 1

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N

● Shag plots

○ Kittiwake plots

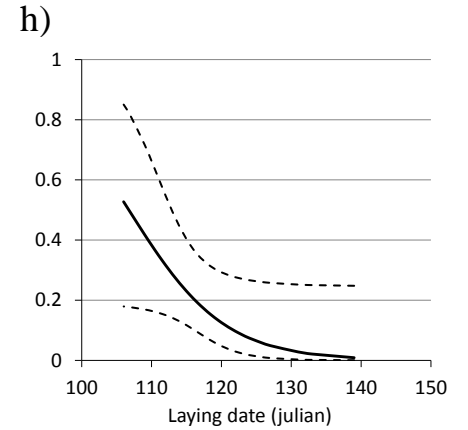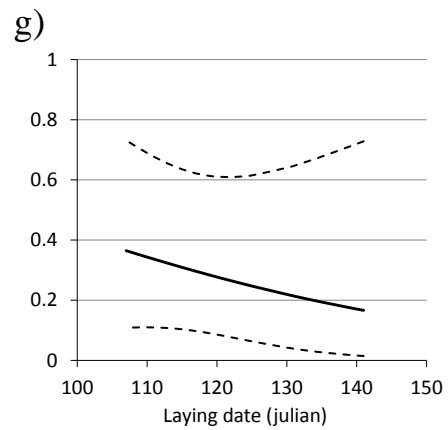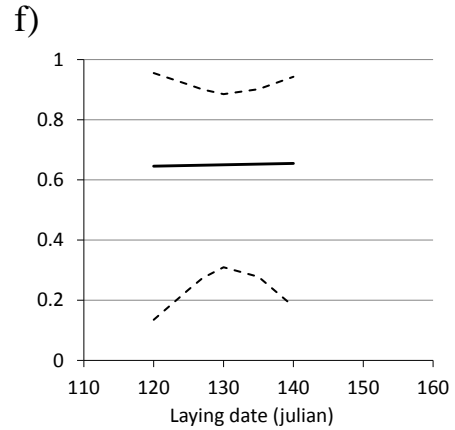▬ Guillemot &
   Razorbill plots

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607 Fig 2
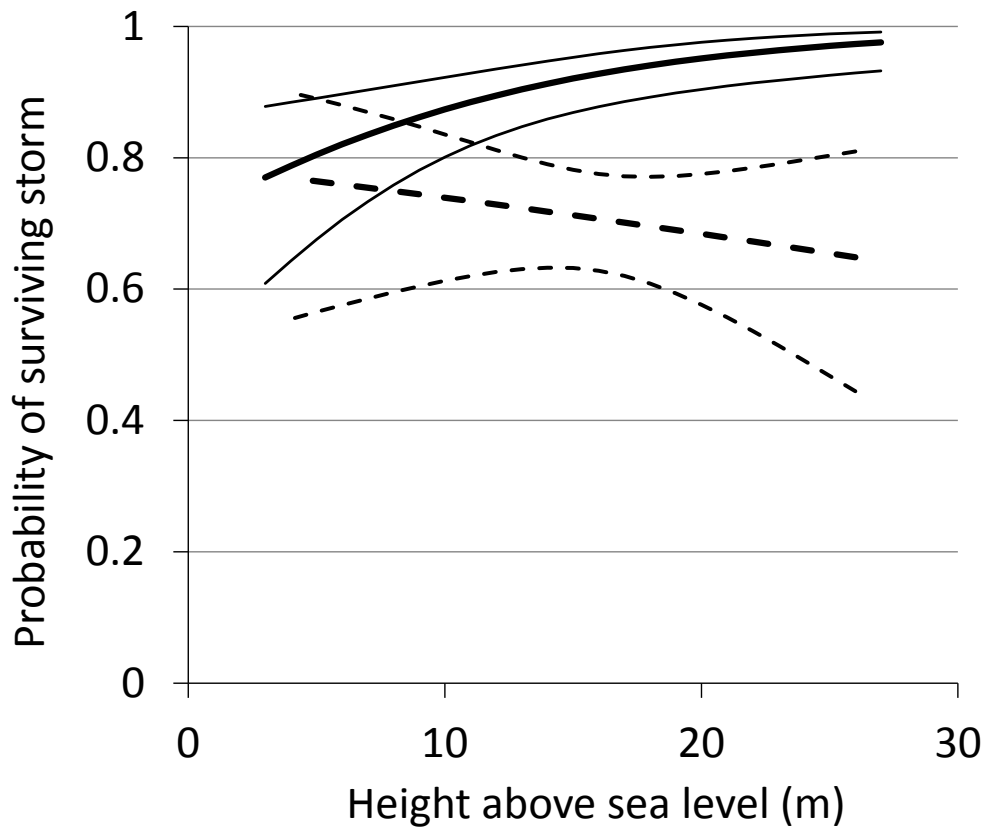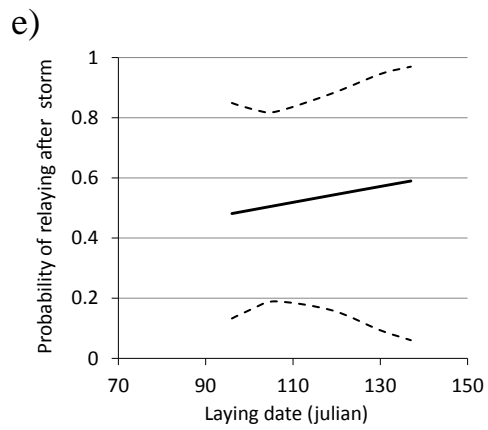
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609   Fig 3

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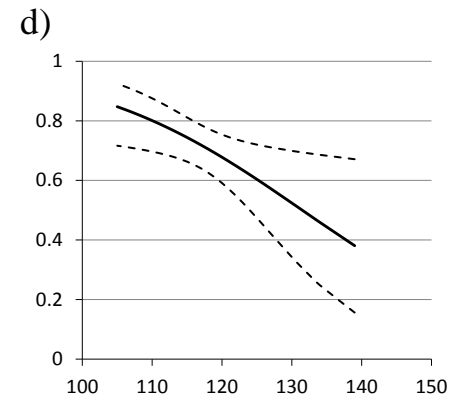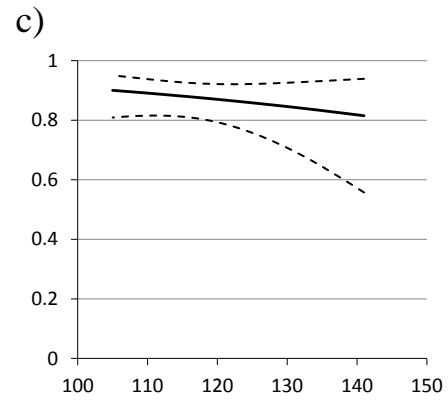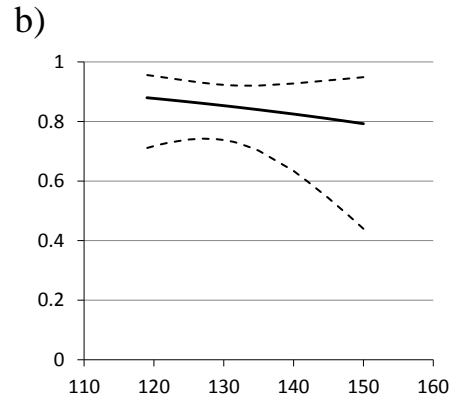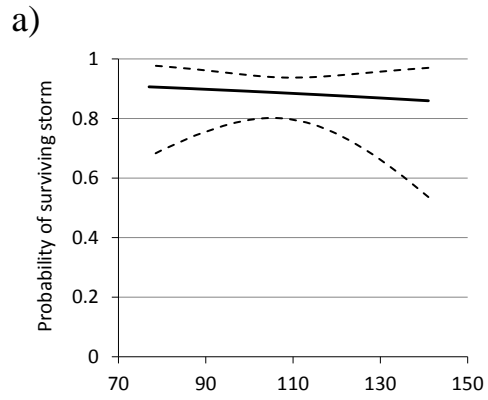
613   Fig 4

Appendix A: Analysis of historical breeding data

Methods

To examine whether the storm affected nests where failure rate is higher or lower on average, we compared the past breeding success of nest sites that survived the storm with those that did not. Data on past breeding success of study nests in monitoring plots where individual nest identity was retained across years were available from 1996 for shags (n = 1,497 breeding records; breeding success was first recorded in 1985 but individual nest identity was only retained across years from 1996 onwards), 1981 for guillemots (n = 16,773 breeding records) and 1982 for razorbills (n = 3,800 breeding records). The analysis was not possible for kittiwakes, since individual nest identity is not retained across years in this species. For shags, a linear mixed model (LMM) was fitted to historical breeding success by Restricted Maximum Likelihood estimation (REML), with number of chicks fledged per pair as the response variable (range 0-4), year, plot id and nest site (with nest site nested in plot) as random effects and storm effect (survived vs not survived) as a fixed effect. Shag breeding success could be treated as a Poisson variable, given it can only take on integer values. However, we found that model residuals were approximately normally distributed. To ensure that model outcomes did not arise from the choice of error structure, we repeated the analysis in a GLMM with Poisson errors and fixed effects inferences were very similar (following Daunt et al. (2014)). We therefore only present results based on the LMM. For guillemots and razorbills, where number of chicks fledged is binomial since they only lay one egg, we carried out a GLMM of number of chicks

637   fledged (0 or 1) with year, plot and nest site (with nest site nested in plot) as random

638   effects and storm effect (survived vs not survived) as a fixed effect, with binomial

639   errors and a logit link function.

640

641   **Results**

642   There was no difference in past breeding success of nest sites that survived the storm

643   and those that did not for shag (LMM: storm survival: $W = 0.44$, $p = 0.51$) or razorbill

644   (GLMM: storm survival: $W = 2.52$, $p = 0.12$). However, there was a significant

645   relationship between past breeding success of nest sites and survival in the storm in

646   guillemots (GLMM: storm survival: $W = 6.95$, $p < 0.01$), with nest sites that failed in

647   the storm fledging 4.7% fewer chicks on average over the period 1981-2010 than

648   those that survived the storm. Therefore, for guillemots we reduced the predicted

649   breeding success of pairs that failed in the storm by 4.7%.