

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

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ABSTRACT: Quantifying the effects of extreme weather is a critical question in population ecology since climate models predict increased climate variability. Effects will vary among and within species due to exposure or susceptibility, yet few studies have considered these sources of variation simultaneously. We investigated the effects of a summer storm on the breeding success of 4 seabird species at a North Sea colony in relation to aspect, height above sea-level, distance to cliff edge and laying date. The storm lasted 8 h with gusts of $>60 \text{ m s}^{-1}$. In exposed plots, razorbills *Alca torda* had higher failure rates (28.5%) than European shags *Phalacrocorax aristotelis* (15.1%), black-legged kittiwakes *Rissa tridactyla* (15.6%) and common guillemots *Uria aalge* (10.4%). Conversely, failure rates in sheltered plots were negligible (shags 0.0%; kittiwakes 1.9%; no guillemot or razorbill plots in sheltered locations). Guillemots breeding closer to sea-level were more likely to fail, but cliff edge proximity did not affect failure rate. In razorbills, pairs that laid early were more likely to survive the storm. In all species, some failed pairs re-laid, and success of re-lays was lower than that of pairs that survived. Thus, re-laying only provided partial compensation, and, overall, the storm caused a net reduction in annual population production of 4.6, 10.7, 8.9 and 22.8% for shags, kittiwakes, guillemots and razorbills, respectively. Increased storm frequency may therefore have important consequences on seabird populations, but orientation of storms relative to colonies and timing in relation to the breeding season are likely to be critical in determining the overall effect.

KEY WORDS: Climate change · Summer storm · Rainfall · European shag · Black-legged kittiwake · Common guillemot · Razorbill

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INTRODUCTION

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 occur 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. 2002, Oswald et al. 2008, Oswald & Arnold 2012), and high winds and rainfall can result in breeding failure (White et al. 1976, King et al. 1992, Aebischer 1993, Hennenke & Flachsbarth 2009, Mallory et al. 2009, Sherley et al. 2012, Wolfaardt et al. 2012, Boersma & Rebstock 2014, Bonter et al. 2014).

While severe weather is widely understood to reduce seabird breeding success, studies that quantify variation amongst and within species are needed to investigate the consequences it has on seabird communities (Wolfaardt et al. 2012). Such heterogeneity may arise from differences in exposure or susceptibility to wind, waves, or rainfall. Thus, species may vary in susceptibility due to physical size or attributes of the nest site. Within species, nests that are oriented in the direction of the storm, closer to sea level and nearer to the cliff edge are likely to be more vulnerable. Intrinsic factors may also be important. For example, pairs that lay early in the season typically have higher average breeding success than those that lay late. Early breeders may therefore have a greater ability or willingness to withstand bad weather, may occupy higher quality nest sites that are less exposed and be more likely to re-lay if they do fail (Potts et al. 1980, Hipfner et al. 1999). On 23 May 2011, a severe storm was forecast to hit eastern Scotland. This gave us the opportunity to compare the short-term impact of prolonged gale force winds and rough seas on the breeding success of 4 cliff-nesting species, the European shag *Phalacrocorax aristotelis* (hereafter 'shag'), black-legged kittiwake *Rissa tridactyla* (hereafter 'kittiwake'), common guillemot *Uria aalge* (hereafter 'guillemot') and razorbill *Alca torda* at a major breeding colony in the region. Within species, we tested whether the effect of the storm had a disproportionate effect on nests located on the exposed (south-westerly) side of the island, closer to sea level and nearer the cliff edge. We also

tested whether a pair's laying date was important in determining failure rate in the storm. Finally, we quantified the capacity of species to compensate for losses sustained in the storm by re-laying, allowing us to estimate the likely net effect of the storm on annual population production.

METHODS

Study site and breeding success measures

Fieldwork took place during the 2011 breeding season on the Isle of May National Nature Reserve, south-east Scotland ($56^{\circ} 11' N$, $02^{\circ} 33' W$). The island is oriented on a north-west/south-east axis with high cliffs facing predominantly to the south-west and gently sloping rocky terrain facing predominantly to the north-east (Fig. 1). Breeding phenology and success of a sample of shag, kittiwake, guillemot and razorbill nest sites was recorded at long-established monitoring plots using standardized methods (Walsh et al. 1995). For shags, 104 nest sites at 11 plots (79 nest sites in 8 plots facing south-west, 25 nest sites in 3 plots facing north-east; Fig. 1) were checked every 7 d from before laying to fledging, and the laying

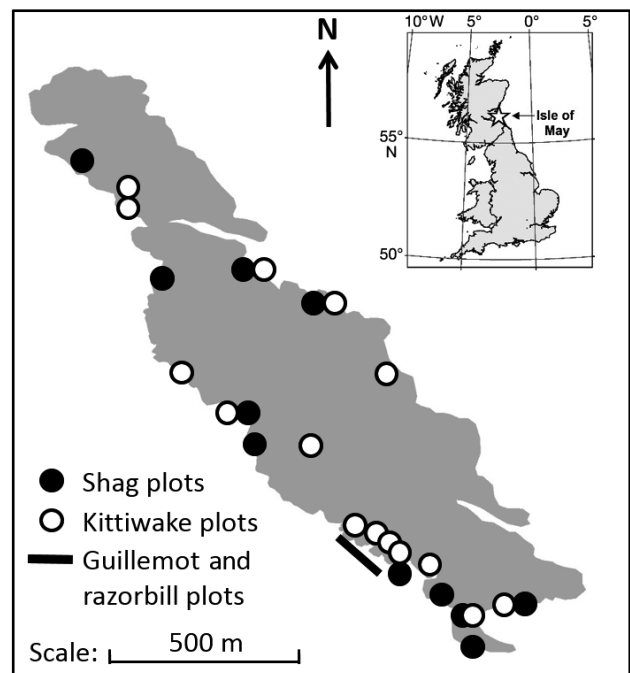


Fig. 1. Location of monitoring plots in the Isle of May National Nature Reserve, Scotland ($56^{\circ} 11' N$, $02^{\circ} 33' W$). Inset shows location of the Isle of May

date (within 7 d, taken to be half-way between the first date incubation is observed and the previous date), number of chicks fledged (range: 0 to 4) and, for unsuccessful pairs, date of failure (minimum accuracy: 7 d) were recorded. For kittiwakes, 166 nests in 6 plots were checked every 5 d from pre-laying to fledging, and as with shags, the laying date (minimum accuracy: 5 d), the number of chicks fledged (range: 0 to 3) and, for unsuccessful pairs, date of failure (minimum accuracy: 5 d) were recorded. At 9 additional kittiwake plots, 283 nests were checked when most pairs had finished laying and again from the day after the first fledged chick was seen in the colony, and the number of chicks fledged was recorded (Harris 1987). Thus, the total sample size for kittiwakes was 449 nest sites in 15 plots of which 397 were in 12 south-west-facing plots and 52 in 3 north-east-facing plots (Fig. 1). For guillemots, 828 nest sites at 6 plots (all on south-west-facing cliffs; Fig. 1) were checked daily from before laying to fledging, and laying date, breeding success (i.e. whether the single chick fledged, since guillemots only lay 1 egg) and, where applicable, date of failure were recorded. The protocol for razorbills, which also lay 1 egg, was similar to that of guillemots ($n = 173$ nest sites at 5 of the 6 plots followed for guillemots; Fig. 1). For guillemot and razorbill nest sites, height above sea level was measured using a marked rope (range: guillemots, 3 to 27 m; razorbills, 4 to 26 m; Harris et al. 1997). Height above sea level was not known for shag or kittiwake nests. In 1 guillemot plot the majority of breeding sites were located on a series of broad flat ledges, and, for these sites, straight line distance from the cliff edge was measured ($n = 250$; horizontal distance range: 0.2 to 3.8 m; height above sea level: 5 m; Harris et al. 1997).

Storm effects

The storm occurred on 23 May 2011. To assess its severity relative to summer weather conditions over the last 40 yr, hourly wind speeds (mean speed and maximum gust speed) were extracted from the weather station at Leuchars ($56^{\circ}23'N$, $02^{\circ}52'W$; 28 km from the Isle of May; source: www.badc.ac.uk) for dates between 1 April and 15 July each year from 1969, when hourly records began. These dates covered the core breeding periods of the 4 study species. The storm was forecast in advance, and its strength was predicted to be of such magnitude that we considered it important to quantify its effects, so a full check of breeding status at each study nest was car-

ried out on the day before and again on the day after the storm. This constituted a departure from standard monitoring frequency for shags and kittiwakes to ensure that any breeding failures over that period could be unequivocally attributed to the storm. Since guillemots and razorbills were being monitored on a daily basis, the effects of the storm could be estimated without the need to depart from standard protocols. Monitored nest sites were categorised as follows: (a) failed before the storm, (b) failed during the storm, (c) survived the storm and (d) eggs laid for the first time after the storm.

Compensation through re-laying

Some pairs that failed before or during the storm (Categories a and b in previous section, respectively) re-laid after the storm. These re-lays were monitored in the same way as other breeding attempts so that final breeding outcome was known for all study pairs. In most cases, we were unable to confirm that the second laid clutch was re-laid by the same pair, as opposed to a different pair occupying the site after the failure of the first pair. However, these species are aggressively territorial, and our long-term studies of these populations has shown that pairs rarely change sites when re-laying. In this study, the same colour-ringed individual was in the pair associated with the second egg in 5/5 cases for guillemots, 1/1 for razorbill and 7/8 for shags. The extent to which re-laying compensated for failure during the storm ('percentage compensation') was estimated as the number of chicks raised as a percentage of the number that could have been raised had all failed nests re-laid and been as successful as those that survived the storm. Thus, full compensation would have a value of 100%.

Statistical analysis

Our principal variables of interest in analyses of within-species variation in effects of the storm were aspect, height above sea level, distance from cliff edge and laying date. Where possible, we also tested whether the effects of exposure (aspect, height and distance) were dependent on laying date, since early breeders may have greater ability or willingness to withstand bad weather, and therefore we might expect any difference between early and late layers to become more marked as exposure increased. We could not test the interaction between aspect and lay-

ing date in shags since the former could only be estimated with a randomisation test (see next paragraph). We were not able to test the interaction between aspect and laying date in kittiwakes either, since the plots for which laying date was recorded were all on the exposed side of the island. For guillemots, we tested the effects of height above sea level, laying date and the interaction between them (correlation between height above sea level and laying date: $r = 0.08$). In a separate analysis, we tested the effects of distance from cliff edge, laying date and the interaction between them (correlation between distance from cliff edge and laying date: $r = 0.11$). The former model was based on a much larger sample size, and so was a more comprehensive test of the effect of laying date. However, the effects of laying date in the latter model were qualitatively similar. For razorbills, we tested the effects of height above sea level, laying date and the interaction between them (correlation between height above sea level and laying date: $r = -0.01$).

To test whether kittiwake nests in south-westerly plots were more affected by the storm than those in north-easterly plots, we carried out a binomial generalized linear mixed model (GLMM) with a logit link function on all breeding attempts active on the day of the storm, with failure in the storm (0 or 1) as the response variable, aspect (north-east or south-west) as a fixed effect and plot as a random effect. We could not take this approach with shags since the north-east orientation contained no failed nests, which makes this parameter inestimable in a model-based test. Instead we carried out a randomisation test (Fisher exact test) on the number of nests active on the day of the storm that failed or survived in south-western and north-eastern plots. To test the effect of height above sea level, laying date and the interaction between them on nest survival from the storm, for guillemots and razorbills, we carried out a binomial GLMM on each species on all breeding attempts active on the day of the storm, with failure in the storm (0 or 1) as the response variable, height above sea level (in metres), laying date and a height above sea level by laying date interaction as fixed effects and plot as a random effect. To test whether guillemots nesting closer to the cliff edge were more affected and whether there was an interaction between distance to cliff edge and laying date, we used a binomial GLM on all active nests, with failure in the storm (0 or 1) as the response variable and distance from the cliff edge (in metres), laying date and a distance to cliff edge by laying date interaction as fixed effects (nests in this analysis were from a single plot

so a GLMM was not required). To test whether early or late breeding birds were more likely to survive the storm, for kittiwakes and shags, we carried out a binomial GLMM on all active nests, with failure in the storm (0 or 1) as the response variable, laying date as a fixed effect and plot as a random effect. For shags, we repeated the analysis, substituting breeding stage (incubation or chick-rearing) for laying date, to test whether the effect of the storm was dependent on whether pairs were incubating eggs or brooding chicks. This breeding stage test was not undertaken for the other species since all pairs were incubating.

To test whether early or late breeding birds were more likely to re-lay after loss in the storm, we carried out a binomial GLMM on all nests that failed in the storm, with re-lay incidence (0 or 1) as the response variable, laying date as a fixed effect and plot as a random effect. We substituted laying date for breeding stage in shags to test whether individuals that were incubating eggs at the time of the storm were more likely to re-lay than those that were rearing young. Laying date was not available in a small number of cases, and this is reflected in the slightly smaller sample sizes in these analyses. All statistical analyses were carried out in Genstat 16.

Net effect of storm on production

To quantify the net effect of the storm on the annual population production of each species, we first estimated what the breeding success of nests that failed in the storm would have been had the storm not occurred (predicted breeding success). The simple approach to this estimation assumed that, but for the storm, pairs that failed would have been as successful as those in the same plot that were active at the time of the storm but survived. However, it is possible that the storm affected nests for which breeding success was higher or lower than average, e.g. the latter might occur if young breeders tend to occupy more exposed sites, but also have lower foraging efficiency, thus increasing the probability of chick mortality from starvation (Daunt et al. 2007). To examine this possibility, we compared the past breeding success of nest sites that survived the storm with those that did not in shags (data from 1996 to 2010), guillemots (1981 to 2010) and razorbills (1982 to 2010). In guillemots, long-term breeding success at nest sites that failed during the storm was significantly lower (by 4.7%) than breeding success at nest sites that survived the storm (see the Appendix). We therefore reduced the predicted mean breeding suc-

cess of pairs that failed in the storm by 4.7%. In shags and razorbills, we found no significant difference (see the Appendix), so we used the simple approach outlined above. For kittiwakes, individual nest identity was not retained across years, so we also used the simple approach.

In a second step, we estimated the predicted mean breeding success in exposed monitoring plots (facing south-west) and sheltered monitoring plots (facing north-east) separately. For both groups, predicted mean breeding success was estimated as the average across all nests based on the observed breeding success of pairs unaffected by the storm (i.e. those that failed before the storm, survived the storm, or laid after the storm) and predicted mean breeding success of those pairs that failed in the storm as outlined above. We then extrapolated the predicted mean and observed mean breeding success in exposed monitoring plots to the proportion of the whole population in the south-western part of the island on the assumption that exposure was similar across all nests with this orientation, inside and outside the monitoring plots. We carried out an identical extrapolation from sheltered monitoring plots to the proportion of the population in the north-eastern part of the island. Since there were no guillemot or razorbill monitoring plots in the north-east, we assumed that no nests with this orientation failed in the storm based on failure rates of north-eastern-facing shag and kittiwake monitoring plots (see 'Results'). Relative proportions of the population in the south-western and north-eastern parts of the colony were estimated from whole-island population counts (Pickett & Squire 2011). Equivalent extrapolations from monitoring plots to the population as a whole based on height

above sea level or distance to cliff edge were not feasible since these measures were not available for the majority of nests.

For each species, we combined the results for the 2 parts of the colony into estimates of predicted mean and observed mean breeding success for the whole population as follows:

$$\text{Predicted population breeding success} = (\text{predicted mean breeding success in SW plots} \times \text{proportion of population in SW}) + (\text{predicted mean breeding success in NE plots} \times \text{proportion of population in NE}) \quad (1)$$

$$\text{Observed population breeding success} = (\text{observed mean breeding success in SW plots} \times \text{proportion of population in SW}) + (\text{observed mean breeding success in NE plots} \times \text{proportion of population in NE}) \quad (2)$$

Finally, we combined these 2 estimates to calculate the net effect of the storm on annual population production as follows:

$$\text{Net effect (\%)} = (\text{predicted population breeding success} - \text{observed population breeding success}) / \text{predicted population breeding success} \quad (3)$$

RESULTS

Storm effects

The storm lasted approximately 8 h, with mean wind speeds of 36.3 m s^{-1} and maximum hourly gust speeds $>50 \text{ m s}^{-1}$ recorded throughout the period from 12:00 to 20:00 h. The storm came from a westerly direction and coincided with high tide. A comparison with historical weather data showed that it was the most severe severe summer storm since hourly records began in 1969, such that the 4 highest, and 8 of the 10 highest hourly maximum gust speeds from April to mid-July, 1969 to 2011, occurred on this day (Fig. 2).

Since the storm came from a westerly direction, the majority of monitoring plots were exposed since they were positioned on the south-west side of the island (shags: 8 of 11 plots; kittiwakes: 12 of 15 plots; guillemots: 6 of 6 plots; razorbills: 5 of 5 plots). The storm occurred during early to mid-incubation for kittiwakes, late incubation for guillemots and razorbills and late incubation to early chick-rearing for shags (median lay dates—shags: 11 April; kittiwakes: 10 May; guillemots: 23 April; razorbills: 26 April), with laying almost complete in

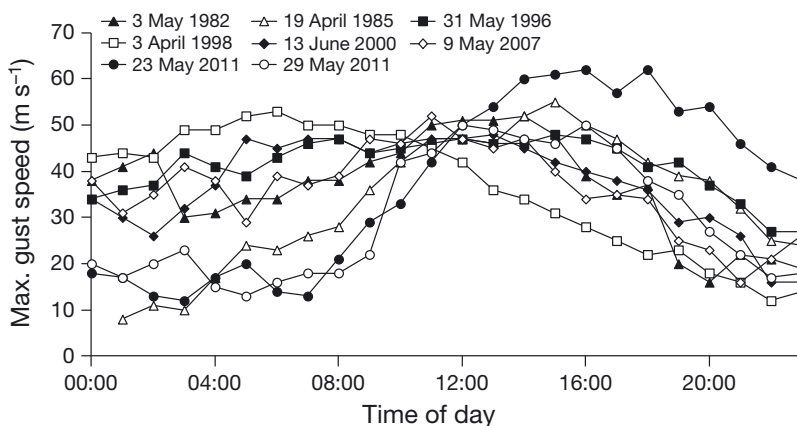


Fig. 2. Mean hourly wind speed on 23 May 2011 and the 7 other storms between April and mid-July, 1969 to 2011, in which maximum gust speed exceeded 45 m s^{-1} in 5 h or more. Seven of these storms were in a westerly direction, and one in an easterly direction (3 April 1998)

Table 1. Immediate effects of the storm on 23 May, percentage that re-laid and mean breeding success (mean chicks fledged per pair) of each nest category and of all study nests of 4 species (shag *Phalacrocorax aristotelis*, kittiwake *Rissa tridactyla*, guillemot *Uria aalge*, razorbill *Alca torda*) on the Isle of May, Scotland, in 2011

	Shag	Kittiwake	Guillemot	Razorbill
No. of monitored nests	104	449	828	173
No. failed before storm	5	5	26	7
No. active when storm occurred	95	437	798	158
No. laid after storm	4	7	4	8
Percent active in storm and failed	11.6	14.0	10.4	28.5
Percent re-laid 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
Survived storm	1.86	1.01	0.84	0.74
Failed in storm and re-laid	0.80	0.42	0.05	0.00
Failed in storm, all nests	0.36	0.16	0.01	0.00
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

all species (percentage pairs that laid before the storm—shags 96.2%; kittiwakes 98.4%; guillemots 99.5%; razorbills 95.4%; Table 1). A small proportion of nests failed before the storm, so the percentages of nests that were active when the storm occurred for shags, kittiwakes, guillemots and razorbills were 91.3, 97.3, 96.4 and 91.3% respectively.

The storm had a similar impact on shags, kittiwakes and guillemots, with 11.5, 14.0 and 10.4% of active nests failing, respectively. However, a higher percentage of razorbill nests was affected (28.5%; Table 1). There was a tendency for south-westerly facing shag nests to be more vulnerable to the storm

than north-easterly nests, with 11/73 (15.1%) and 0/22 (0.0%) failing in the storm, respectively (Fisher exact test: $p = 0.06$). South-westerly facing kittiwake nests were significantly more vulnerable to the storm than north-easterly nests, with 60/385 (15.6%) nests in south-westerly plots failing in the storm and 1/52 (1.9%) nests failing in north-easterly facing plots (GLMM: Wald statistic, $W = 4.05$, $p < 0.05$). In guillemots, a lower failure rate was apparent with increasing height above sea level, but there was no effect of laying date or interaction between height above sea level and laying date ($n = 768$; GLMM, height above sea level: $W = 10.63$, $p < 0.01$ [Fig. 3] laying date: $W = 0.70$, $p = 0.40$ [Fig. 4c] interaction term: $W = 0.00$,

$p = 0.97$). In contrast, there was no effect of height above sea level on failure rate in razorbills, but those nests with an earlier laying date were more likely to survive; the interaction term was not significant ($n = 153$; GLMM, height above sea level: $W = 0.48$, $p = 0.49$ [Fig. 3] laying date: $W = 5.40$, $p < 0.05$ [Fig. 4d] interaction term: $W = 0.00$, $p = 0.96$). Failure rate was not related to distance from the cliff edge in guillemots, and there was no effect of laying date in this subset of nests (in line with findings from the larger sample), nor was there a significant interaction between these 2 variables ($n = 250$; GLM, distance from cliff edge: $W = 1.71$, $p = 0.19$; laying date: $W = 1.31$, $p = 0.25$; interaction term: $W = 3.08$, $p = 0.08$). There was no effect of laying date on failure rate in shags ($n = 95$, $W = 0.09$, $p = 0.76$; Fig. 4a) or kittiwakes ($n = 148$, $W = 0.33$, $p = 0.57$; Fig. 4b), nor was breeding stage related to failure rate in shags ($n = 95$, $W = 0.06$, $p = 0.80$).

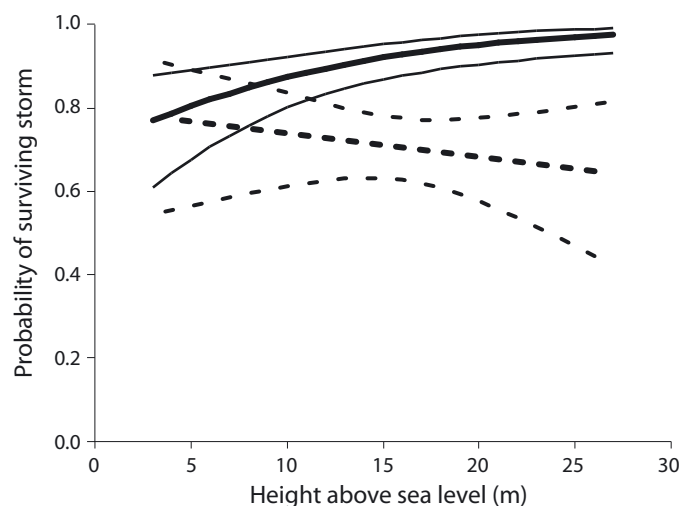


Fig. 3. Fitted lines ($\pm 95\%$ CI, thin lines) for nest survival from the storm in relation to height above sea level from the GLMMs for guillemots (*Uria aalge*; solid lines; $n = 768$ active nests when the storm occurred) and razorbills (*Alca torda*; dashed lines; $n = 153$)

Compensation through re-laying

Not all pairs that failed during the storm re-laid (pairs re-laying: shags: 45.5%; kittiwakes: 39.3%; guillemots: 25.3%; razorbills: 17.8%), and such pairs were ultimately less successful than those that survived the storm (Table 1). Thus, failure during the storm was only partially compensated for through re-laying (percentage compensation for shags: 19.6%; kittiwakes: 16.3%; guillemots: 1.4%; razorbills: 0.0%). There was a tendency for early laying pairs to be more likely to re-lay among ra-

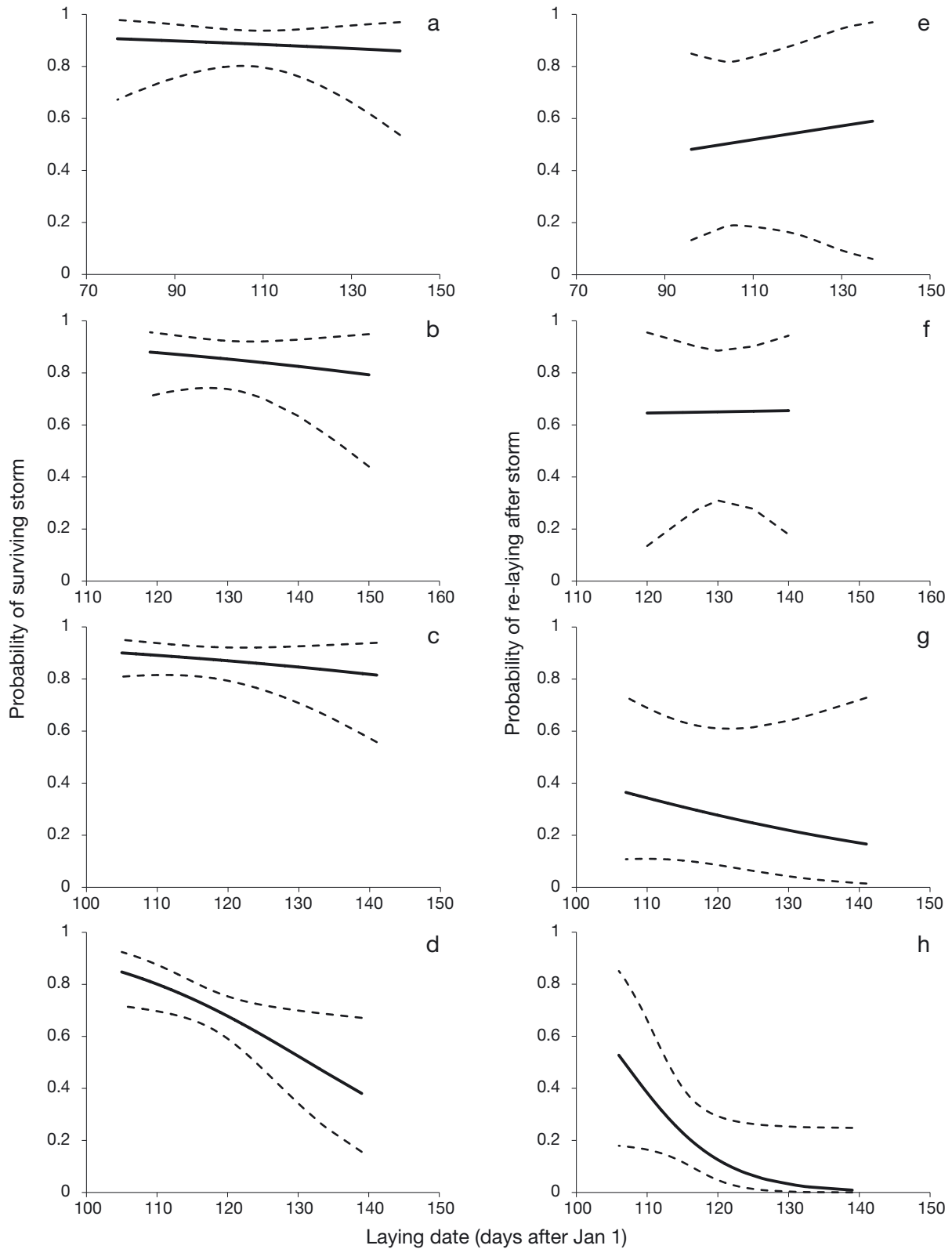


Fig. 4. (a–d) Fitted lines ($\pm 95\%$ CI, dashed lines) for survival from the storm in relation to laying date for the GLMMs for (a) shags (*Phalacrocorax aristotelis*; n = 95), (b) kittiwakes (*Rissa tridactyla*; n = 148), (c) guillemots (*Uria aalge*; n = 768) and (d) razorbills (*Alca torda*; n = 153). (e–h) Fitted lines ($\pm 95\%$ CI, dashed lines) from the GLMMs of post-storm re-laying in relation to laying date for (e) shags (n = 11), (f) kittiwakes (n = 20), (g) guillemots (n = 82) and (h) razorbills (n = 44)

Table 2. Input values for the estimate of net effect of the storm on annual population production (observed mean breeding success and predicted mean breeding success in exposed, sheltered and all sites, and proportion of the population in exposed and sheltered sites) and net effect as a percentage reduction of predicted population breeding success. The observed breeding success for guillemots *Uria aalge* and razorbills *Alca torda* in sheltered sites was estimated based on failure rates during the storm for shags *Phalacrocorax aristotelis* and kittiwakes *Rissa tridactyla*. Breeding success is mean chicks fledged per pair

Species	Exposed			Sheltered			Whole population		
	Observed	Predicted	Proportion of population	Observed	Predicted	Proportion of population	Observed	Predicted	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

zorbill (n = 44, $W = 3.68$, $p = 0.06$; Fig. 4h). However, there was no such relationship in shags (n = 11, $W = 0.05$, $p = 0.82$; Fig. 4e), kittiwakes (n = 20, $W = 0.00$, $p = 0.98$; Fig. 4f), or guillemots (n = 82, $W = 0.48$; $p = 0.49$; Fig. 4g), nor was breeding stage related to re-lay probability in shags (n = 11, $W = 0.13$, $p = 0.71$).

Net effect of storm on production

The observed mean and predicted mean breeding successes had the storm not occurred of pairs in exposed and sheltered parts of the island are given in Table 2. The majority of kittiwakes, guillemots and razorbills were located in exposed areas (85 to 93%), whilst the bulk of the shag population was breeding in the sheltered part of the island (69%; Table 2). Combining predicted mean and observed mean breeding success in exposed and sheltered nests with these proportions, we estimated that the net reduction in annual population production of shags was 4.6%, reflecting the high proportion of the population located in sheltered areas. In contrast, estimates of net reduction in annual population production for the other 3 species matched those in the monitoring plots closely, demonstrating that the high impact of the storm on razorbills was apparent in the population as a whole (kittiwakes: -10.7%; guillemots: -8.9%; razorbills: -22.8%; Table 2). The greater impact of the storm on razorbills can be seen when comparing the overall breeding success in 2011 with the long-term mean (\pm SD) for each species (shags: 1.54 in 2011 vs. 1.01 ± 0.57 chicks per pair, 1985–2010; kittiwakes: 0.87 vs. 0.55 ± 0.38 , 1985–2010; guillemots: 0.73 vs. 0.73 ± 0.13 , 1981–2010; razorbills: 0.50 vs. 0.66 ± 0.08 , 1982–2010). Razorbill breeding success in 2011 was the worst on record (previous range: 0.52–0.86 chicks per pair).

DISCUSSION

Variation among and within species

Few studies have investigated among- and within-species variation in the effects of extreme weather on seabird breeding success. We quantified these effects in 4 species of cliff-nesting seabirds during the most severe summer storm recorded in the region in 40 yr. We demonstrated important, and in some cases unexpected, effects of the extreme weather event on the breeding success of this seabird community. Our results supported our prediction that nests on the exposed side of the island and low down the cliff would be more severely affected. However, we did not foresee that razorbills would be much more vulnerable than the other species. Razorbills typically breed on more sheltered sites than the closely related guillemot (Olsthoorn & Nelson 1990). However, on the Isle of May, the 2 species breed in close proximity, and exposure to wind, waves and spray seemed likely to have been similar. Due to the ferocity of the wind, it was not possible to directly observe losses in the storm. However, razorbills may have been more susceptible to being physically lifted off their sites, since they are 30% lighter than guillemots. This effect may have been particularly important higher up the cliff, where wind speeds are typically highest. If both species are susceptible to spray, whilst guillemots are more able to withstand high wind speeds, this may explain why we detected an effect of height above sea level on nest survival from the storm in guillemots but not in razorbills. Further, it may explain why vulnerability to the storm was unrelated to horizontal distance in guillemots, since level of spray is likely to be determined more by height than distance to the cliff edge. Whatever the mechanisms driving the variation among the 2 species in overall loss and the effect of height, the high impact of the storm on razorbills resulted in

the lowest breeding success at this colony since records began in 1982. In contrast, breeding success for the other 3 species was at or above the long-term average, despite losses in the storm.

The disproportionate effect of the storm on exposed compared to sheltered locations had a strong influence on the population-level effects for each species in line with their breeding distribution on the island. Although shag nests in exposed plots were affected by the storm to a similar extent as those of kittiwakes and guillemots, the majority of shag nests are located on the north-east side of the island, so the overall impact on the population was comparatively small. In contrast, the other 3 species are concentrated on the south-west side of the island, so they were more exposed to the storm. The majority of severe summer storms recorded on the Isle of May over the last 40 yr have been from a westerly direction (Fig. 2). This would suggest that these interspecific differences have occurred repeatedly in recent decades. However, in contrast to the other species, the distribution of shag nests on the island has changed substantially over this period. Thus, a westerly storm in May 1982 had a dramatic effect on shag breeding success because, at that time, the bulk of the population bred on the south-west side of the island (Aebischer 1993). Our results therefore suggest that the effects of summer storms on breeding seabirds are likely to be strongly dependent on the direction of the storm relative to breeding sites. However, predicting future effects of extreme weather is challenging since both storm direction and changes in breeding distribution, such as we have observed in the shag population on the Isle of May over the last 3 decades, would have to be considered. The percentage of shag nests in exposed locations that failed was much lower in 2011 than 1982 (15 vs. 49%). One possibility for this difference is that nests were on average closer to sea level when densities were higher in the south-west. Storm duration may also have been a contributory factor since the 1982 storm was longer, with gale force winds experienced for most of the day (Aebischer 1993; our Fig. 2).

Compensation through re-laying

A proportion of breeding pairs that failed in the storm re-laid, and the success of these pairs was significantly lower than that of the pairs that survived the storm. In combination, these 2 effects resulted in only partial compensation for the storm, ranging from 0.0 to 19.6% across the 4 species. We do not know how

typical this level of compensation is, but breeding success of those pairs unaffected by the storm was at or above the long-term average in all species, suggesting that, aside from the storm, environmental conditions were favourable. Thus, it is possible that compensation would be lower in years when overall conditions are poorer, since breeding individuals would likely be in poorer condition and therefore less likely to re-lay. These estimates only relate to breeding success, yet compensation may have been even lower in terms of longer term fitness, since there is a decline in post-fledging survival with fledging date in shags and guillemots at this colony (Harris et al. 1994, Lahoz-Monfort et al. 2014). Post-fledging survival may also be related to the nutritional quality of the egg, which is likely to be lower on average in re-laid eggs (Nager et al. 2000, Krist 2011). However, these potential effects require formal testing since a study of Brünnich's guillemots *Uria lomvia* in the Canadian Arctic found no difference in recruitment rates of individuals from first-laid and replacement eggs (Hipfner 2001). Long-term fitness effects of re-laying may not be limited to impacts on chicks. The costs associated with re-laying may also have reduced the survival probability of adults (Nager et al. 2001), which could have consequences for population size.

Phenological effects

Our prediction that early laying pairs would be more likely to survive the storm was upheld in razor-bills. Late breeders may be less able to withstand bad weather, or show reproductive restraint, which may increase likelihood of abandonment in poor conditions (Williams 1966). Alternatively, they may occupy lower quality nest sites that are more exposed to wind and spray. It is not clear why laying date was not an important determinant of nest survival from the storm in the other species, but one possibility is that the losses resulted from catastrophic events (e.g. a nest or clutch being washed away or dislodged by gusting wind) where intrinsic effects are less likely to play a role. We found a tendency in razorbills that early laying pairs that failed in the storm were more likely to re-lay than late laying pairs. As with the effect of laying date on nest survival probability, this may reflect intrinsic differences in ability or effort.

The relative timing of an extreme weather event is likely to be critical to the overall effect on breeding success. Losses to extreme weather may be higher during chick-rearing than incubation since chicks are sensitive to exposure to extreme rain, wind and tem-

perature (White et al. 1976, Demongin et al. 2010, Boersma & Rebstock 2014). Furthermore, chick mortality during extreme weather may occur indirectly through a reduction in adult foraging success. A study of guillemots at this colony showed that during stormy weather, chick-rearing adults increased their foraging effort, caught smaller fish and showed reduced nest attendance (Finney et al. 1999). A recent study on southern rockhopper penguins *Eudyptes chrysocome* provides further evidence that wind affects foraging success (Dehnhard et al. 2013). Such indirect effects of weather on breeding performance are likely to be more profound during chick-rearing than incubation, where there is greater capacity for the non-attending bird to extend the time away from the nest since no provisioning is required. However, it is possible that the storm was not of sufficient duration for these indirect effects to occur, since shags did not do worse than the other species, despite breeding being more advanced, with some pairs rearing chicks at the time of the storm. The extent to which individuals compensate by replacing lost eggs may also be linked to the timing of extreme weather relative to the breeding season. Studies of shags, kittiwakes and guillemots (both common and Brünnich's) have shown that the proportion re-laying and success of re-lays declines with date (Gaston & Nettleship 1981, Harris & Birkhead 1985, Aebischer 1993, Wanless & Harris 1997, Daunt 2000, Coulson 2011). As shown in razorbills in the present study, breeders that lay earlier in the season are more likely to re-lay than later breeders (Hipfner et al. 1999). Furthermore, at the individual level, re-laying is more likely if failure occurs sooner after laying, perhaps linked to body condition which is on average higher at that time than later in the breeding season (M. P. Harris et al. unpubl. data on guillemots on the Isle of May from 1982 to the present: correlation between days incubated prior to loss and probability of re-laying: $r = -0.95$). Thus, if the 2011 storm had occurred earlier in the breeding season, re-laying might have compensated more fully for clutches that were lost. Conversely, reduced compensation from re-laying would have been likely had the storm occurred later in the season. However, species differences are clearly apparent, since shags had a comparatively high re-lay rate despite their breeding season being more advanced.

Conclusions

Extreme weather events are an understudied but potentially important driver of seabird breeding suc-

cess (Schreiber 2001, Jenouvrier 2013). A number of studies have shown that extremes in temperature, high rainfall, strong wind and rough seas can all result in major offspring mortality (e.g. Aebischer 1993, Gaston et al. 2002, Bonter et al. 2014). Here, we have shown that the overall effect of extreme weather varies both among and within species, likely due to variation in exposure and susceptibility. Our study highlights the value of recording immediate impacts and compensation from re-laying to enable estimation of the net effects on annual breeding output of such events. Quantifying the impacts of extreme weather on breeding success is likely to become increasingly important, since many models predict that the frequency of extreme events is going to increase in some regions, in particular at higher latitudes (McInnes et al. 2011, Young et al. 2011). An isolated event such as this is unlikely to have a dramatic effect on population size, especially in seasons such as the study year where (razorbills excepting) the breeding season was moderately good, despite the storm. However, a greater frequency of summer storms of this severity could result in discernible impacts on population size (Descamps et al. 2015), although the orientation of storms relative to breeding sites, storm duration and timing in relation to the breeding season are likely to be critical in determining the overall effect.

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Appendix. Analysis of historical breeding data

Methods

To examine whether the storm affected nests where failure rate is higher or lower than 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 ($n = 1497$ 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 ($n = 3800$ 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 1 egg, we carried out a GLMM of number of chicks fledged (0 or 1) with year, plot and nest site (with nest site nested in plot) as random effects, and storm effect (survived vs. not survived) as a fixed effect, with binomial errors and a logit link function.

Results

There was no difference in past breeding success of nest sites that survived the storm and those that did not for shag (LMM, storm survival: $W = 0.44$, $p = 0.51$) or razorbill (GLMM, storm survival: $W = 2.52$, $p = 0.12$). However, there was a significant relationship between past breeding success of nest sites and survival in the storm in guillemots (GLMM, storm survival: $W = 6.95$, $p < 0.01$), with nest sites that failed in the storm fledging 4.7% fewer chicks on average over the period 1981–2010 than those that survived the storm. Therefore, for guillemots we reduced the predicted mean breeding success of pairs that failed in the storm by 4.7%.