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ORIGINAL ARTICLE

Storm-induced shifts in optimal nesting sites: a potential effect of climate change

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Abstract Extreme storm events encountered during any stage of the annual cycle can result in increased mortality and influence population dynamics. Storms during the reproductive season, when birds are tied to fixed nesting locations, can be particularly problematic. Given predicted changes in the frequency and intensity of storms in a changing climate, studies examining the impacts of storms on reproductive success in model systems are important. Island-nesting seabirds may be particularly vulnerable to changes in storm frequency and intensity. Here, we report on the effects of an extreme storm in June 2012 on Herring Gull (*Larus argentatus*) reproduction on an island in the Gulf of Maine, USA. More than 22 % of monitored nests were lost in this single event leading to a seasonal shift in the optimal nesting locations for birds in our population. Nests closer to water and nests located at low elevations were disproportionately affected by the unusual weather, reversing trends in optimal nesting sites recorded in previous seasons. Spatiotemporal shifts in optimal nesting locations, therefore, may be one result of climate-induced changes in storm frequency and intensity. Although some birds with nests destroyed in the storm attempted to renest, these attempts experienced low success, and overall reproductive success in the storm-affected season was lower than in the previous three nesting seasons.

Keywords Gull reproduction · Nest site selection · Weather · Seabird colony

Zusammenfassung

Veränderungen der optimalen Neststandorte durch Stürme: Ein möglicher Effekt des Klimawandels

Extreme Stürme, die irgendwann im Jahreszyklus auftreten, können zu erhöhter Mortalität führen und die Dynamik von Populationen beeinflussen. Stürme während der Brutsaison, wenn Vögel an feste Nistplätze gebunden sind, können besonders problematisch sein. In Anbetracht der vorhergesagten Veränderungen der Häufigkeit und Intensität von Stürmen im Rahmen des Klimawandels sind Studien, welche die Auswirkungen von Stürmen auf den Fortpflanzungserfolg in Modellsystemen untersuchen, besonders wichtig. Auf Inseln brütende Seevögel dürften gegenüber Veränderungen der Sturmhäufigkeit und -intensität besonders empfindlich sein. Hier berichten wir über die Effekte eines extremen Nordoststurms im Juni 2012 auf die Fortpflanzung von Silbermöwen (*Larus argentatus*) auf einer Insel im Golf von Maine, USA. Über 22 % der überwachten Nester wurden bei diesem Einzelereignis zerstört, wodurch es zu einer saisonalen Veränderung der optimalen Neststandorte für die Vögel in unserer Population kam. Nester, die näher am Wasser und in niedrigerer Höhe lagen, wurden vom ungewöhnlichen Wetter unverhältnismäßig stark beeinflusst, was die in vorherigen

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Jahren beobachteten Trends in Bezug auf optimale Neststandorte umkehrte. Raumzeitliche Verschiebungen in den optimalen Neststandorten können daher ein Ergebnis von klimainduzierten Veränderungen der Sturmhäufigkeit und -intensität sein. Einige Vögel, deren Nester durch den Sturm zerstört worden waren, versuchten, erneut zu nisten, doch diese Brutversuche waren von geringem Erfolg, und insgesamt war der Fortpflanzungserfolg in der vom Sturm betroffenen Saison niedriger als in den vorherigen drei Brutzeiten.

Introduction

Studies demonstrating the impacts of extreme events on wildlife populations are limited in part due to the rarity of such events (Wilson and Peach 2006), and the need to gather data both before and after the event in order to quantify effects. Increases in the frequency and intensity of storm events, however, are a predicted result of climate change (Easterling et al. 2000), and additional research into the ecological effects of extreme events is required. Increases in weather extremes, with ecological effects that are out of proportion to the short duration of weather events, are predicted under current climate change scenarios (Jentsch et al. 2007).

Island-nesting seabirds may be particularly vulnerable to increased storm activity because seabirds usually demonstrate high fidelity to natal colonies, and nesting areas are often near sea-level where storms can have devastating impacts. The increase in storm activity that is predicted to accompany global climate change may put many nesting colonies at risk (van de Pol et al. 2010; Hatfield et al. 2012). In addition to the increase in storm frequency, sea-level rise due to the thermal expansion of water and the melting of polar ice and glaciers is projected at 1–2 m by the end of the twenty-first century (Vermeer and Rahmstorf 2009; Rahmstorf 2010). Even sea-level rises at the lower end of the predicted range could severely limit the amount of available nesting habitat on low-lying rookery islands (Hatfield et al. 2012), and could have profound effects when combined with an increase in storm severity or frequency.

Nesting in dense colonies on islands is thought to confer advantages due to limited or absent mammalian predators, the benefits of group anti-predator defense, and the improvement of foraging success due to information sharing (Ward and Zahavi 1973; Götmark and Andersson 1984). Colonial nesting, however, can also expose large numbers of birds to the same environmental perturbation, such as a storm. Not all members of the colony may be similarly affected within nesting colonies because various nest site contexts may confer advantages or disadvantages, depending upon the year. In one colony, for instance, birds nesting in large aggregations close to the shore experienced greater reproductive success than birds nesting in more isolated, upland contexts in an average year (Savoca et al. 2011). The advantages of one nesting context over another within a colony may be ephemeral or vary from season to season, yet little research has focused on year-to-year variability in optimal nesting contexts.

Here, we examine the ecological effects of a protracted storm that battered the New England coast of North America from June 2–5, 2012, with heavy rain, wind gusts in excess of 78 km/h, and high-tide cycles that submerged many low-lying areas on offshore islands (US National Oceanographic and Atmospheric Administration 2012). This storm affected Appledore Island, Maine, the site of a multi-year study on nesting gulls, as most of the eggs were approaching hatch day. Our first objective was to quantify the impact of the storm on the reproductive success of Herring Gulls (*Larus argentatus*) nesting on the island at different elevations and distances from the shoreline. Because the periphery of the island suffered the brunt of the storm's effects, we predicted that the spatial arrangement of optimal nesting habitat would shift in favor of interior nesting during the storm-affected season.

Second, we examine the renesting behaviour of birds that lost nests in the storm and compare the relative success of renesting attempts versus attempts initiated early in the season. Larids are known to lay replacement clutches if the entire nest is lost prior to hatching, but later nesting pairs typically experience lower reproductive success than earlier nesting pairs (Parsons 1975; Brown and Morris 1996). Lower success can be related to a seasonal decline in food availability (Safina and Burger 1985; Gasparini et al. 2006), to lower investment in replacement clutches due to decreased female condition (Brown and Morris 1996), or to increased predation pressure on the chicks later in the season (Davis and Dunn 2008). If these factors influenced reproductive success in our population, we predicted that egg and clutch sizes would be smaller for renesting attempts than for first nesting attempts due to the additional energetic stress of laying a replacement clutch.

Methods

Research was conducted on Appledore Island, Maine (42°59′21″N, 70°36′52″W), a 38-ha island located in the Isles of Shoals approximately 10 km east of Portsmouth, New Hampshire, USA, in the Gulf of Maine. This island hosts approximately 750 nesting pairs of Herring Gulls which nest in dense subcolonies distributed around the rocky periphery of the island as well as in more isolated situations in vegetated areas along paths and around buildings occupied by the Shoals Marine Lab research station. Each nesting season from 2009 to 2012, nests from multiple subcolonies around Appledore Island were selected during the nest construction and incubation stage in late May for subsequent monitoring (range 52–153 nests/year). We measured the length, width, and weight of each egg, and labeled nests with a unique identifier. Nests were then checked on a daily basis through mid-July and nest contents recorded. Chicks were weighed on days 1, 3, 5, 7, and 9 after hatching for growth rate calculations. Most adult gulls were not individually marked, so presumed renesting attempts following the storm in 2012 are based on nests constructed at the exact same locations as lost nests. Although not all individual birds in our population were identifiable, banded birds tend to nest in the exact same location from year to year. The high nest site fidelity in this species is a strong indication that nests initiated after the storm were renesting attempts by the same pair that lost their first clutch. We measured eggs and monitored reproductive success from presumed renesting attempts where egg measurements from the initial nest attempts were recorded ($n = 15$ nests) as well as from an additional 15 nests built at locations where nests were known to be destroyed during the storm but for which pre-storm nesting data were lacking.

Nest locations were identified via hand-held GPS units (Garmin) and plotted in Arc GIS v.10.0 (ESRI 2010). Nest elevation was extracted in ARC GIS from a 1.9 arc sec LIDAR raster provided by the USGS National Elevation Dataset (USGS 2013). The high tide line was hand-digitized from a 2012 infrared orthophoto, and the distance of each nest from the high tide line was determined using the NEAR tool in Arc GIS.

Statistical methods

Differences in elevation and distance to the nearest high tide line between failed and surviving nests in 2012 were calculated using Wilcoxon rank sum tests for non-normal distributions (PROC NPAR1WAY in SAS v.9.2, SAS Institute 2003). Differences in clutch size and the number of eggs hatched between initial nesting attempts and renesting attempts were calculated using Poisson-distributed models for count data (PROC GENMOD). Differences in average egg volume between initial nest attempts and renesting attempts were calculated using a generalized linear model (PROC GLM) where egg volume = (length) × (width)^2 × 0.476 (Harris 1964). We tested for differences in chick weight between initial nesting attempts and renesting attempts on hatch day and on day 5 after hatching (few chicks from renesting attempts survived past day 5). Because gulls hatch asynchronously and chick growth is strongly influenced by position in the hatch order, position (A, B, or C chick) was included in the model testing for differential chick weight between initial and renesting attempts. Because multiple chicks were repeatedly sampled in each nest, nest label was used as a random variable in a mixed linear model testing for differential chick weight between initial and renesting attempts (PROC MIXED). SAS was used for all statistical analyses and means ± 1SE are reported.

Nest survival curves were constructed for each season by combining daily observations into nine 7-day intervals beginning on May 19 and ending on July 20. A nest was considered active if it contained at least 1 egg or chick at any point during each 7-day interval.

Results

Of 146 nests monitored beginning in late May 2012, all 33 (22.6 %) lost during the storm event were located around the periphery of the island (Fig. 1a, b). These nests were generally completely washed away by high wave action, with failed nests located at lower elevations (4.51 ± 0.40 m asl) than nests that survived the storm (8.17 ± 0.44 m, $W = 1{,}323$, $P < 0.001$). Failed nests were also closer to the typical high tide line (15.39 ± 1.09 m) than nests that survived the storm event (45.23 ± 4.38 m, $W = 1{,}284$, $P < 0.001$; Fig. 1c).

Analysis of clutch and egg parameters for 15 pairs which lost nests in the storm and later renested found larger average clutch and egg sizes during the original nesting attempt than during the renesting attempt, with a significant decline recorded in egg volume (Table 1). When comparing all initial ($n = 146$) and renesting ($n = 30$) attempts, renesting attempts were generally less successful than initial nests. More chicks hatched per nest in initial nests that survived the storm than from renesting attempts and hatch weights were greater for chicks from initial nests than from renesting attempts (Table 1). By day 5 after hatch, however, the weight of chicks was comparable between the initial nesting attempts and renesting attempts after controlling for hatch order (Table 1; Fig. 2). Chicks from both initial and renesting attempts grew over time (age effect, $F_{1,474} = 1{,}189.51$, $P < 0.001$) and hatch order influenced chick weight ($F_{2,474} = 12.61$, $P < 0.001$) with the first and second chicks weighing more than the third chick within a nest.

Relative nesting success varied between years, with the storm event in 2012 contributing to the greatest weekly nest losses during the 4-year study (week 3; Fig. 3). Isolated nests at the core of the island were less likely to survive to near-fledging than nests in the dense colony settings around the periphery of the island in 2009 and

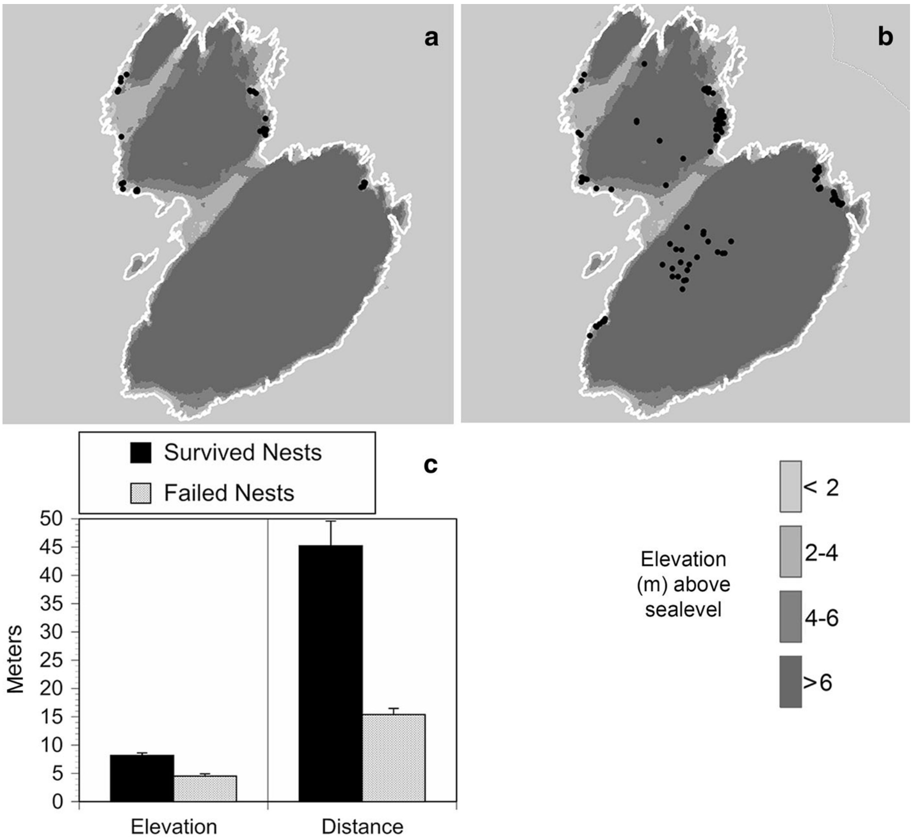

Fig. 1 Appledore Island, Maine, USA, showing locations of nests of Herring Gulls (*Larus argentatus*) (*black dots*) lost during the June 2–5, 2012 storm event (**a**), and locations of all Herring Gull nests monitored during the 2012 breeding season (**b**). Failed nests were at lower elevations and closer to the high tide line, on average, than nests that survived the storm (**c**)

Table 1 Comparison of reproduction parameters between initial (pre-storm) nesting attempts and renesting attempts by Herring Gulls (*Larus argentatus*) (sample sizes in parentheses)

Parameter	Initial nest attempt	Renest attempt	Significance
Clutch size	2.47 ± 1.18 (15)	2.07 ± 1.20 (15)	$\chi^2_{1,28} = 0.53$, $P = 0.467$
Egg volume[a]	81,948 ± 1,807 (37)	78,471 ± 2,451 (31)	$t_{1,13} = 1.78$, $P = 0.049$
Chicks per nest	1.61 ± 1.07 (146)	0.97 ± 1.20 (30)	$\chi^2_{1,173} = 7.47$, $P = 0.006$
Hatch day weight[b]	64.70 ± 0.59 g (212)	59.94 ± 1.52 g (27)	$F_{2,117} = 20.80$, $P < 0.001$
Day 5 weight[b]	105.43 ± 2.29 (142)	102.38 ± 6.88 (12)	$F_{2,62} = 2.75$, $P = 0.669$

[a] $n = 15$ paired initial versus renesting attempts

[b] Mixed model controlling for position in the hatch order with nest as a random variable. Model estimates are reported

2010, but the pattern was reversed in 2011 and 2012 (Fig. 4).

Discussion

Effects of weather on bird populations

Our study documented the spatially nonrandom consequences of an extreme storm event on the reproductive success of gulls nesting on an island in the Gulf of Maine. As climate change contributes to the increased frequency of extreme events (Easterling et al. 2000), birds may become more vulnerable to departures from normal weather patterns at all stages of the annual cycle. This study demonstrates the vulnerability of birds to severe storm events during the breeding season, particularly for birds nesting at low elevations near the water. Previous research shows that our results are not isolated. For multiple marsh-nesting species along the Wadden Sea, van de Pol et al. (2010) demonstrated an increased risk of nest loss due to flooding attributable to sea level rise and the influence of a changing climate on extreme high tides. Increased winds and wave action can be particularly problematic as, for instance, a study of Eared Grebes (*Podiceps nigricollis*) discovered that waves generated by

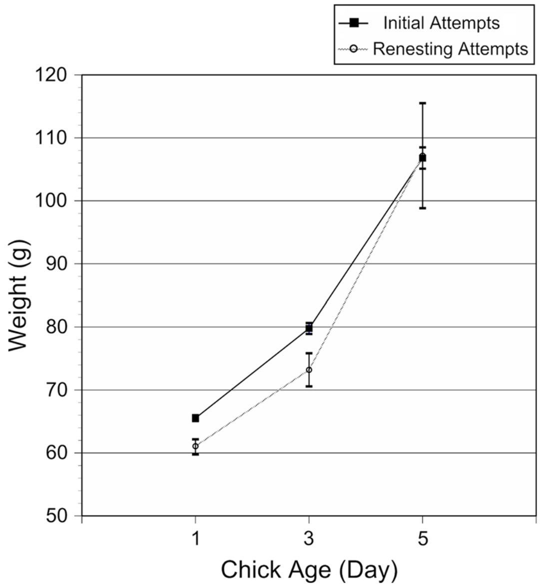

Fig. 2 Growth rates (through day 5) of Herring Gull chicks in 2012 comparing chicks in initial nest attempts with renesting attempts. Raw means are reported

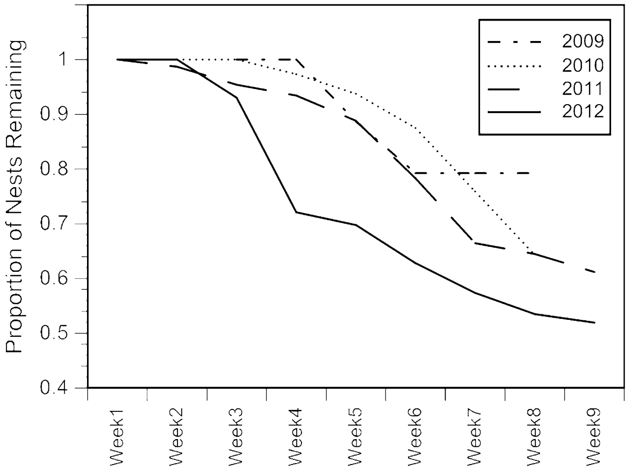

Fig. 3 Seasonal decay in the proportion of active monitored nests beginning in late May in 2009 ($n = 53$), 2010 ($n = 109$), 2011 ($n = 152$), and 2012 ($n = 129$). Note that the monitoring window was reduced in some years

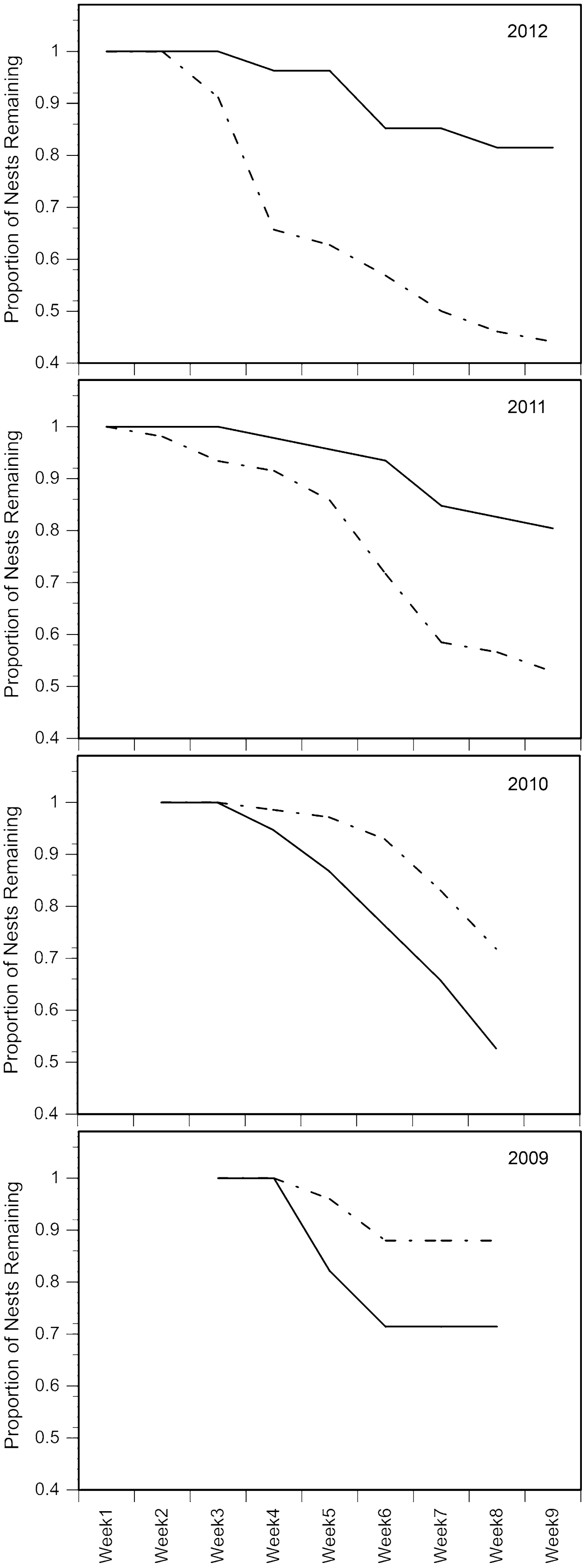

Fig. 4 Spatio-temporal shifts in optimal nesting contexts within the ▶ larger colony. The periphery nests (*dashed lines*) were generally at low elevations, near water, and in more dense subcolonies on exposed rocky substrates. The interior nests (*solid lines*) were generally at high elevation, separated from nearest neighbors by >10 m, and were often located in dense vegetation

high winds were responsible for 44 % of total nest losses (Boe 1994). Likewise, in Western Grebes (*Aechmophorus occidentalis*), nests located near the colony edge were prone to wave action with storm losses in a high-wave year reaching 38 % (Allen et al. 2008). Wave action and major storm events have also contributed to reproductive failure in the Bank Cormorant (*Phalacrocorax neglectus*) in southern Africa (Sherley et al. 2011), and in Forster's Terns (*Sterna forsteri*) and Black Terns (*Chlidonias niger*) in central North America (Bergman et al. 1970; Cuthbert and Louis 1993).

In the current study, the storm event coincided with a high-tide cycle resulting in extremely high water levels. Similar combinations of storms and tides contributed to nest losses in saltmarsh breeding Pied Avocets (*Recurvirostra avosetta*) in Germany (Hötker and Segebade 2000) and in Laughing Gulls (*Leucophaeus atricilla*) in New Jersey. As in the current study, research in the New Jersey system shows that birds nesting around the periphery of the marsh (closer to the water) were more likely to be adversely affected when tides and weather conspired to raise water levels (Montevecchi 1978).

Adverse weather can also decrease chick growth and survival by interfering with foraging success or the food supply (Becker and Specht 1991). Low temperatures and strong winds depressed growth rates of South Polar Skuas (*Catharacta maccormicki*) in Antarctica, with the negative influence of high wind speeds lasting for multiple days (Ritz et al. 2005). In the current study, most nests were still at the egg stage during the 2012 storm which certainly interfered with the foraging ability of the adults. If the storm had occurred during the chick stage, the impacts could have been more widespread due to starvation and exposure.

Renesting behaviour

Despite the destruction of nearly 23 % of monitored nests during the storm, many affected pairs attempted to renest. Renesting occurred approximately 2 weeks following the storm (14.6 ± 1.4 days), a timeline that is comparable to another study of Herring Gulls which lost first clutches (14.7 ± 0.4; Parsons 1976), and in other Larids including the Black-legged Kittiwake *Rissa tridactyla*, (12.4 ± 1.4; Wooller 1980) and Ring-billed Gull *Larus delawarensis*, (11.6 ± 1.9; Brown and Morris 1996). Whether or not clutches are replaced is likely related to the seasonal timing of loss, with a larger percentage of clutches being replaced if the first clutch was lost early in the incubation stage (Parsons 1975). In the current study, nearly all birds that lost nests were nearing the end of the incubation stage, yet many pairs still attempted to renest.

Of the 15 storm-affected pairs with egg measurement data from original and renesting attempts, we detected a decline in egg volume of 4.3 % between the initial and second attempts. Likewise, experimental removal of Little Auk (*Alle alle*) eggs to instigate relaying resulted in a decreased volume of the second clutch (Jakubas and Wojczulanis-Jakubas 2012). We are unaware of experimental tests of egg volume changes in Herring Gulls, but previous research indicates a progressive decline in mean clutch size with lay date (Parsons 1975), and a study of Ring-billed Gulls found that clutches were smaller in renesting attempts than in first attempts (Brown and Morris 1996).

Spatiotemporal shift in optimal nesting locations

We previously demonstrated in our study system that birds nesting in dense colonies located on the rocky periphery of the island had greater reproductive success than birds nesting in more isolated, higher-elevation sites, at least in some years (Savoca et al. 2011). If peripheral colonies provide superior nesting sites, then birds should only nest in relative isolation in more vegetated areas of the colony if (1) space is limited in the periphery colonies, or (2) some factor makes nesting in the vegetated interior of the island the superior approach in some years. If one nesting context always provides a reproductive advantage, then selection should eventually lead all individuals in the population to colonize these superior areas assuming that space is available. The spatio-temporal shift in optimal nesting locations between the storm year of 2012 and the 2009 and 2010 nesting seasons demonstrates that the relative quality of various nesting habitats or locations is not static. Indeed, the large-scale storm losses in the dense colonies (located around the perimeter of the island) likely flipped the advantage towards birds nesting in relative isolation at higher elevations during the summer of 2012. The 2012 storm was directly responsible for the losses of 33 monitored nests in the periphery colonies and no nests in the interior colonies. Although the storm had a demonstrable impact on the 2012 nesting season, the relative lack of success in the peripheral colonies during the 2011 season remains unexplained.

Increased storm severity or frequency may increase the relative quality of inland nesting sites, but not all nesting colonies provide opportunities for birds to move to higher elevations. Birds nesting on low-lying islands will be particularly vulnerable if storm severity and frequency increase during the nesting season. Renesting attempts at the exact locations of flooded nests suggest that birds are not changing their nest site preferences within a season (Erwin et al. 1998). Multi-year reproductive failures in the low-lying, peripheral colonies are likely required before significant shifts in the spatial distribution of subcolonies would be evident. Although re-use of territories and nest sites may be adaptive in a time-limited breeding season, increased frequency of storm events would place even greater selective pressure on choices of nesting locations and select for birds choosing higher-elevation sites. The ability of species to adapt quickly to a changing environment is critical for understanding potential population-level effects of climate change (Visser 2008), yet plasticity in nest site selection in gulls and other island-nesting species remains poorly understood.

A species' vulnerability to extreme events needs to be considered when attempting to predict responses to a changing climate (Frederiksen et al. 2008). Because severe storm events can dramatically impact the reproductive success of endangered species, including Laysan Finch *Telespiza cantans* (Morin 1992) and the Bermuda Petrel *Pterodroma cahow* (Madeiros et al. 2012), further examination of the influence of weather extremes on reproduction in model systems is warranted. Although gulls are fairly long-lived birds that often engage in multiple nesting attempts, our study population is experiencing an ongoing decline (estimated 5.1 % annual decline, 1966–2011; Sauer et al. 2013), and poor reproductive success will further contribute to these declines.

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