

Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds?

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Summary

1. Climate change encompasses changes in both the means and the extremes of climatic variables, but the population consequences of the latter are intrinsically difficult to study.
2. We investigated whether the frequency, magnitude and timing of rare but catastrophic flooding events have changed over time in Europe's largest estuary. Subsequently, we quantified how this has affected the flooding risk of six saltmarsh nesting bird species.
3. We show that maximum high tide has increased twice as fast as mean high tide over the past four decades (0.8 vs. 0.4 cm year⁻¹), resulting in more frequent and more catastrophic flooding of nests, especially around the time when most eggs have just hatched.
4. Using data on species' nest elevations, on their timing of egg-laying and on the duration that their eggs and chicks are at risk from flooding, we show that flooding risks increased for all six studied species (even after accounting for compensatory land accretion) and this is expected to worsen in the near future if they do not adapt. Moreover, our study provides the first evidence that increasing flooding risks have reduced the reproductive output below stable population levels in at least one species, the Eurasian oystercatcher *Haematopus ostralegus*.
5. Sensitivity analyses show that currently birds would benefit most from adapting their nest-site selection to higher areas. However, historically the lower marsh has been favoured for its proximity to the feeding grounds and for its low vegetation aiding predator detection.
6. *Synthesis and applications.* We argue that it is more difficult for birds to infer that habitat quality has decreased from changes in the frequency of rare and unpredictable extreme events than from trends in climatic means. Consequently, at present the lower parts of the saltmarsh may function as an ecological trap. The creation of new (i.e. low) saltmarshes – currently a restoration priority – may thus counteract the goal of increasing the avian biodiversity of an area. Management tools to mitigate the effects of climate change, either by making the higher saltmarsh more attractive (mowing, predator control) or by reducing the flooding risk of the lower marsh (building elevated plots), await to be tested.

Key-words: adaptation, climatic variability, ecological trap, habitat selection, nest elevation, reproductive failure, saltmarsh dynamics, sea-level rise, tidal flooding, timing of reproduction

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Introduction

Climate change not only involves directional changes in the mean values of climatic variables (e.g. global warming), but the frequency and magnitude of various extreme climatic events is also changing (Easterling *et al.* 2001; IPCC 2007). Extreme climatic events – such as flooding, hurricanes and fires – differ from gradual trends by their magnitude (statistical extremeness) combined with their discreteness (short duration, rarity) relative to the lifespan of organisms (Jentsch, Kreyling & Beierkhunlein 2007). Organisms may be specifically vulnerable to changes in extremes, as these may be hard to anticipate and adapt to, and because extreme climatic events can catastrophically reduce population numbers (McLaughlin *et al.* 2002). Consequently, the impact of extreme climatic events on populations and ecosystems is considered by both academics and conservationists as ‘one of the hundred questions of greatest importance to the conservation of global biological diversity’ (Sutherland *et al.* 2009) and currently is the focus of much research (e.g. Chan *et al.* 2005; Jentsch, Kreyling & Beierkhunlein 2007; Thibault & Brown 2008). Many studies have already shown that extreme events can strongly affect demographic rates in a given year (Durant *et al.* 2004; Jentsch, Kreyling & Beierkhunlein 2007). Nevertheless, little is known about how an increasing frequency or magnitude of extreme climatic events will affect species in the long term, primarily because such events are rare and stochastic and thereby intrinsically difficult to study (Tryjanowski, Sparks & Profus 2009).

The shores of estuaries, such as saltmarshes, are subject to strong environmental variability caused by the tidal cycle. Saltmarshes are situated above mean high tide (MHT), but flood occasionally during stormy weather (Fig. 1). In summer, saltmarshes are important breeding areas for many bird species (orders Charadriiformes, Ciconiiformes, Anseriformes, Passeriformes) in all hemispheres of the world (e.g. Bildstein *et al.* 1991; Koffijberg *et al.* 2006). Flooding is rare in any given breeding season; nevertheless their effects can be catastrophic: eggs wash away and chicks die. Thus, more frequent flooding events could impact estuarine ecosystems globally and quantifying and predicting their impact will be crucial to managing

the biodiversity of estuaries (Bildstein *et al.* 1991; Erwin *et al.* 2006). Flooding events also provide a unique opportunity to gain insights into the impact of extreme climatic events on populations, because: (i) the impact of flooding events is directly quantifiable by comparing a storm tide’s height with the elevation of nesting sites; (ii) many tidal gauge stations have long historical records; and (iii) climate change and sea-level rise (SLR) are predicted to alter the frequency and magnitude of flooding events (IPCC 2007).

The Wadden Sea is Europe’s largest wetland (Fig. 2) and the core breeding area in western Europe for dozens of coastal bird species (Koffijberg *et al.* 2006). In this estuary mean sea levels have been rising by 0.1 cm year⁻¹ over the last centuries (Olf *et al.* 1997), but in the second half of the 20th century this rate has increased to 0.3 cm year⁻¹ (Esselink *et al.* 1998) and is expected to increase even further (potentially up to 1.2 cm year⁻¹ in 2100; van Dorland, Dubelaar-Versluis & Jansen 2009). The recent increase in SLR is mainly attributed to global warming causing seawater to expand (IPCC 2007), but some land subsidence due to post-glacial rebound and local gas-extraction also occurs in this estuary (Marquenie & de Vlas 2005).

Saltmarshes naturally compensate for relative SLR, as higher flooding frequencies result in increased sedimentation and thereby land accretion. Notwithstanding, it is not known whether saltmarshes world-wide can keep up with the current high rate of climate change. Some modelling studies have argued that sedimentation can fully compensate for increasing rates of SLR (e.g. Hughes & Paramor 2004; Temmerman *et al.* 2004), while others have argued that marshes will eventually drown (e.g. Erwin *et al.* 2006; Goodman, Wood & Gehrels 2007). The outcome may well vary within and among estuaries due to differences in geomorphology. Using both model and empirical data, van Wijnen & Bakker (2001) suggested that island saltmarshes in the Wadden Sea estuary are already unable to keep up with current rates of SLR and will drown over the next centuries if no action is taken. In addition, lateral erosion of saltmarsh cliffs (Fig. 1) due to wave action has become common, resulting in inland movement of saltmarshes (Wolters *et al.* 2005). New marshes can develop at higher sites,

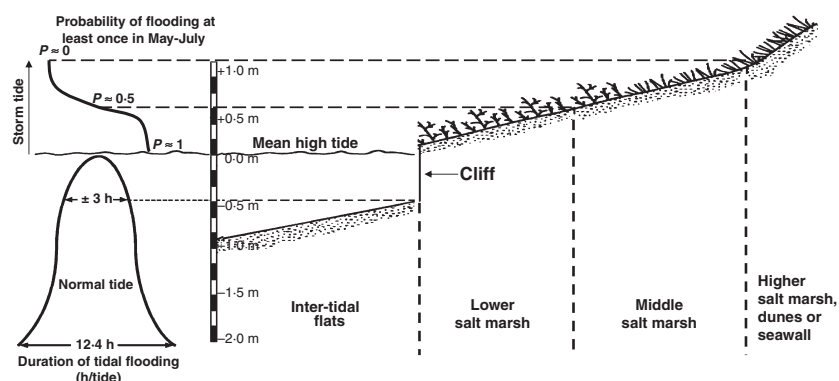


Fig. 1. Zonation of an inter-tidal saltmarsh in relation to the normal tidal dynamics and summer storm tide flooding probabilities. The elevation of a cliff can vary due to the fact that a cliff moves landwards resulting from erosion by waves. When a cliff has not formed, a gradual slope with pioneer vegetation is present instead. Birds typically nest on the saltmarsh and feed on the inter-tidal flats.



Fig. 2. Map of the Wadden Sea estuary. Island saltmarshes are located on the landward side of the barrier islands, and mainland saltmarshes are located along parts of the mainland's coastline. For each of the 27 tidal measurement stations the annual increase in mean high tide (1st number) and maximum high tide (2nd number) is given in mm year⁻¹ (period 1971–2008; May–July).

but often these higher sites are unavailable due to inland boundaries such as seawalls (i.e. coastal squeeze).

Although faster SLR may cause major habitat loss in the long-term, short-term effects of increased flooding frequencies on birds' nesting success have received little attention. Catastrophic flooding of saltmarsh nesting sites has always occurred (e.g. Becker & Anlauf 1988; Hötter 1998), but recently flooding events have been especially numerous in the Wadden Sea (Willems *et al.* 2005; Koffijberg *et al.* 2006, 2010). Furthermore, climate change may not only cause more frequent but also more catastrophic flooding events, as wind patterns are also changing (IPCC 2007), which can affect the magnitude of storm tides (Oost *et al.* 2005). The critical question therefore is whether climate change has increased the flooding risks of coastal birds (i.e. reduced habitat quality) to such an extent that it substantially reduces their nesting success and thereby population viability. If so, how likely is it that these habitat specialists will adapt their nesting behaviour to rare and unpredictable flooding events?

In this study, we develop a general framework to perform a risk assessment for coastal-nesting bird populations to changes in the frequency, magnitude and timing of extreme climatic events. We first quantify changes in the means and extremes of summer tidal data over the past four decades at 27 stations in the Wadden Sea. Secondly, we evaluate to what extent island saltmarshes compensate for SLR by land accretion, now and in the near future. Thirdly, we combine data on nest elevations, the timing of egg-laying and the duration that eggs and chicks are at risk, to quantify the flooding risk of six saltmarsh nesting bird species: common terns *Sterna hirundo* (L.), pied avocet *Recuvirostra avocetta* (L.), common redshanks *Tringa totanus* (L.), black-headed gulls *Larus ridibundus* (L.), Eurasian oyster-

catchers *Haematopus ostralegus* (L.) and Eurasian spoonbills *Platalea leucorodia* (L.). Fourthly, we combine these previous steps to quantify historical, current and future flooding risks for these species. Fifthly, we assess how flooding events have affected the viability of an oystercatcher population for which 26 years of reproductive data and a population model are available. Finally, we discuss the various mechanisms by which birds can adapt to increased flooding risk and explore the possibility that the lower parts of saltmarshes become an ecological trap (Dwernychuk & Boag 1972).

Materials and methods

TIDAL AND WEATHER DATA

We collated daily high-tide data from 27 stations across the Wadden Sea to estimate flooding risks (Fig. 2; see Fig. S1, Supporting information for location names). We used data from 1971 to 2008, as these 38 years comprise two complete lunar nodal periods of *c.* 19 years each, which cyclically affect tidal patterns (Rossiter 1972). The rate of SLR – with reference to the peak of the breeding season – was defined as the annual increase in MHT as estimated by the linear regression coefficient of MHT in May–July against year (1971–2008). We also estimated the annual increase in maximum high tide (XHT) in May–July using linear regression over the same period.

To investigate how extreme summer tides depend on storminess, data on wind speed and direction from two island and two mainland Wadden Sea weather stations (> 100 km apart) were compared with data from nearby tidal stations (Fig. 2). The height of daily high tides also varies in a roughly fortnightly cycle and the dates of its maximum, known as 'spring tides', were derived from the lunar calendar.

ISLAND SALTMARSHES' RESPONSE TO SEA-LEVEL RISE

To quantify how much saltmarshes compensate for SLR, we used the model of van Wijnen & Bakker (2001), which was specifically developed for island saltmarshes in the Wadden Sea. Their model assumes that the change in saltmarsh elevation (E) from year t to the next year $t + 1$ is the result of the opposing effects of accretion (A) due to clay deposition (a function of elevation-dependent flooding frequency) and shrinkage (S) of the accreted clay-layer:

$$E_{t+1} - E_t = A_t - S_t \quad \text{eqn 1}$$

with

$$A_t = (c \times f) / (1 + \exp^{(g \times (E_t - m - r \times t))}) + h \quad \text{eqn 2}$$

and

$$S_t = C_t \times a + b \quad \text{eqn 3}$$

where C_t is the thickness of the clay layer ($C_t = E_t - E_{t=0}$), r is the annual rate of SLR, m is the MHT at $t = 0$ and other parameters are constants calibrated from field measurements on the relationships between the elevation of a site, flooding frequency, clay deposition and shrinkage ($a = 0.18$, $b = -1.0$, $c = 0.026$, $f = 706$, $g = 0.056$, $h = 0.4$; see van Wijnen & Bakker 2001).

In the Wadden Sea the bulk of sedimentation occurs in winter, as storm tides are much higher and more frequent in winter than in summer (van Wijnen & Bakker 2001).

FLOODING RISK OF NESTS

The risk (q) that a nest will flood at least once during a breeding season is determined by the elevation of a nest (e), the start date of egg laying (s) and the duration a nest is at risk (d):

$$q = 1 - \prod_{j=s}^{j=s+d} (1 - p(e, j)) \quad \text{eqn 4}$$

where $p(e, j)$ is the daily probability of flooding at elevation e and day in season j , as derived from daily recorded water heights at high tide. We assumed that a nest floods if the water height was more than 15 cm higher than the nest elevation, because eggs can survive some water in the nest, but at some point the parents are forced to physically leave the nest and the eggs wash away or become depredated (Ward & Burger 1980). Similarly, when a nest is flooded by $c.$ 15 cm water most chicks will drown, become hypothermic or become separated from their parents (pers. obs. authors). A threshold of 10 or 20 cm resulted in qualitatively similar results (not shown). The sensitivity of q to small changes in $e, s,$ & d can be used to quantify selection gradients on $e, s,$ & d in terms of q and was calculated numerically by means of small perturbations of $e, s,$ or d .

SPECIES' CHARACTERISTICS

For each of the six birds species considered in our study we collected data on the distribution of nest elevations, the distribution of start dates of egg laying and the duration that a nest is at risk. Nest elevations of common terns were measured at Ameland (2006–2007; $n = 73$), of pied avocet at Holwerd (1990s; $n = 30$; van de Kam *et al.* 2004), of common redshanks at Jadebusen (2007–2008; $n = 60$), of black-headed gulls both at Schiermonnikoog (2008; $n = 51$) and Holwerd (1990s; $n = 15$; van de Kam *et al.* 2004), of Eurasian oystercatchers both at Schiermonnikoog (1995, 1996, 2008; $n = 539$) and Ameland (2009; $n = 41$) and of Eurasian spoonbills at Ameland (2006–2007 & 2009; $n = 418$), see Fig. 2. For oystercatchers and for black-headed gulls data were available from two sites and these were pooled in the analyses, as we found no evidence that nest elevations (in cm above MHT) differed between sites (t -test both $P > 0.2$). All nest elevations were measured *in situ* using electronic theodolites, except for nest elevations of common redshanks which were determined by combining nest locations recorded by differential GPS with a 1×1 m resolution elevation map (NLWK 2004).

Start dates of egg laying were obtained from the same nests of which elevation was measured (common redshank and Eurasian oystercatcher) or from nests at other Wadden Sea saltmarshes (common tern at Jadebusen, $n = 396$ (Becker & Anlauf 1988); pied avocet at Hamburger Hallig, $n = 238$ (Hötter 1998, 2002); black-headed gull at Pieterburen, $n = 113$; Eurasian spoonbills at Schiermonnikoog, $n = 874$; Fig. 2).

The duration that a nest is at risk is determined by a species egg-incubation period plus the duration that chicks are at risk from drowning, becoming hypothermic, or getting separated from their parents. Incubation period varied relatively little within species (S.D. of 1–2 days; Hötter 1998; own unpublished data, authors), therefore the duration a nest is at risk was assumed to be (approximately) constant within each species. Altricial Eurasian spoonbill chicks younger than 21 days and precocial pied avocet and Eurasian oystercatcher chicks younger than 14 days typically do not survive a flooding (de Vries & Krottje 2004; T. Lok & M. van de Pol, unpublished data). Based on our own experiences, we assumed that precocial common tern, common redshank and black-headed gull chicks were also at risk for 14 days.

HISTORICAL, CURRENT AND FUTURE IMPACT ON SPECIES

Except for redshanks and oystercatchers, nest elevations e and start dates of egg-laying s were not measured on the same nests. To quantify the mean flooding risk of nests for all six species, we generated 10 000 virtual nests with combinations of e and s values by independent random sampling from each species distribution (with replacement). For each species we assumed independence of nest elevation and start date of egg-laying, as e and s of the same nests were not tightly correlated in oystercatchers nor in redshanks (both $r < 0.1$).

Daily flooding probabilities ($p(e, j)$, eqn 4) were based on tidal data from the 10 stations closest to where nest elevations were measured (Fig. 2), as changes in tidal patterns varied geographically (see Results). Current risks were calculated using tidal gauge data from the last 19 years (1990–2008). Historical (1971–1989) flooding risks were calculated using tidal gauge data from the years 1971–1989, while accounting for changes in saltmarsh elevation over time due to compensatory land accretion (using accretion rates of a 50-year old island saltmarsh; van Wijnen & Bakker 2001). Similarly, future (2009–2027) flooding risks were projected using tidal gauge data from the years 1990–2008 adjusted for future mean SLR of $0.41 \text{ cm year}^{-1}$ (see Results), while accounting for land accretion. For both historical and future projections we assumed that birds used the same nesting locations as in the current period and did not change their timing of egg-laying (see Discussion). Using a null model of no change in e and s allows us to calculate changing flooding risks under a scenario of no adaptation or alternatively to predict how much birds need to adapt their timing and nest site selection to climate change to experience a constant, stable flooding risk over time.

FLOODING RISK, NESTING SUCCESS AND POPULATION VIABILITY: A CASE STUDY

For one species, the Eurasian oystercatcher, long-term reproductive data and a population viability model were available. Data were collected as part of a study on a saltmarsh breeding population on the island of Schiermonnikoog (1984–2009; for details see Ens *et al.* 1992; van de Pol *et al.* 2007). Since birds can have multiple clutches within a breeding season and other factors besides flooding also affect nesting success, we first assessed the shape of the relationship between the annual mean flooding risk \bar{q} and the annual fledgling production. Subsequently, we identified what values of \bar{q} allowed for a productivity sufficient to ensure a stable viable oystercatcher population, as determined by a stochastic stage-structured population matrix model (van de Pol *et al.* 2010).

Results

CHANGES IN FREQUENCY, MAGNITUDE AND TIMING OF FLOODING EVENTS

Flooding events have increased both in frequency and in magnitude. The MHT in May–July has increased at an average rate of $0.41 \text{ cm year}^{-1}$ over the last four decades at 27 Wadden Sea sites. The rates of SLR varied strongly among sites (0.21 – $0.77 \text{ cm year}^{-1}$), with the smallest increases in the western (Dutch) and largest increases in the northern (Danish) Wadden Sea (Fig. 2). Over the same period, XHT increased twice as much ($0.83 \text{ cm year}^{-1}$) compared to MHT averaged across

sites. Rates of change in XHT also varied strongly among sites (0.39–1.59 cm year⁻¹), again with smallest increases in western and the largest increases in northern parts (Fig. 2).

The daily probability of an extreme high tide (> 50 cm above MHT; which floods at least the entire lower saltmarsh) changes dramatically during the breeding season: it is high at the beginning of April, decreases fourfold to a low in May, after which it increases gradually over the course of June, July and August (Fig. 3; see Fig. S2, Supporting information for patterns at individual sites). The timing of flooding events also changed when comparing the periods 1971–1989 and 1990–2008: averaged across all stations extreme tides have become more common over most of the breeding season and especially in the second half of June and first half of July (Fig. 3), when the eggs of most species have just hatched.

Extreme summer tides generally coincided with spring tides and/or strong westerly winds. Higher than normal tides (30–50 cm above MHT) and extreme tides (> 50 cm above MHT) were respectively 50% and 20% more likely to occur around a spring tide (± 2 day period) than during other days in May–July. Furthermore, higher than normal and extreme tides were associated with stronger winds (6.8 ± 1.0 and 8.5 ± 1.2 m s⁻¹, respectively) than during the rest of May–July (5.1 ± 0.6 m s⁻¹) and were always associated with a specific range of south-western to north-western winds (mean 270°, 90%-percentiles 224°–315°), atypical for that time of the year. This pattern did not differ between island and mainland sites (Fig. S3, Supporting information), suggesting that their opposite landward and seaward saltmarsh orientation does not further influence flooding risks (i.e. western winds cause summer flooding events by pushing water from the North Sea into the Wadden Sea, not by blowing water from the Wadden Sea onto saltmarshes). Due to the geographical bend in the Wadden Sea (Fig. 2), marshes north of the German Bight typically flood during south-western winds, while marshes west of the

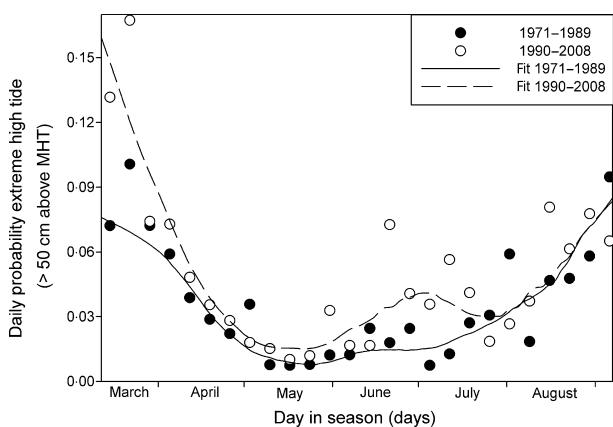


Fig. 3. Seasonal changes in the daily probability that the lower saltmarsh (0–50 cm above mean high tide) floods, averaged over all 27 stations in the Wadden Sea for the periods 1971–1989 and 1990–2008. Dots represent averages per week; lines are fitted on raw daily data using a negative exponential smoothing function. The *x*-axis runs from the first date (March 11th) to the last date (September 7th) that any nest was at risk from flooding.

German Bight typically flood during north-western winds (Fig. S3).

RESPONSE OF ISLAND SALTmarshES TO SEA-LEVEL RISE

Under current rates of SLR, land rise can only keep up at the lowest parts of newly formed island saltmarshes (< 30 cm above MHT, 0-year old; Fig. 4). Saltmarshes of 50–100 year old –most common in the Wadden Sea– are much less resilient than new saltmarshes (Fig. 4). Old saltmarshes have built up thick clay layers and therefore shrink more (van Wijnen & Bakker 2001). When modelling how a new saltmarsh develops over time, it can be seen that eventually all parts develop an elevation deficit as they age, causing them to drown (Fig. 4).

CURRENT FLOODING RISKS OF NESTS

Plotting flooding risk *q* as a function of *e*, *s* & *d*, shows that low-nesting species have a window of opportunity during a period of low flooding risks from mid April until mid May (Fig. 5a). This time window narrows with an increasing duration that nests are at risk (Fig. 5a–f); birds with a long duration of risk also need to nest at higher elevations than birds with a shorter breeding cycle to experience the same flooding risk during their breeding attempt. The six species under study experienced widely different mean annual flooding risk, varying from 0.09 in common redshanks (i.e. nests lost once every 11 years) to 0.84 in common terns (nests lost virtually every year) over the period 1990–2008 (Fig. 5g–l). In each species, nests were situated so low that they probably flooded in any given breeding season (*q* > 0.95), ranging from 2% of nests in redshanks up to 28% in common terns (Fig. 5a–f).

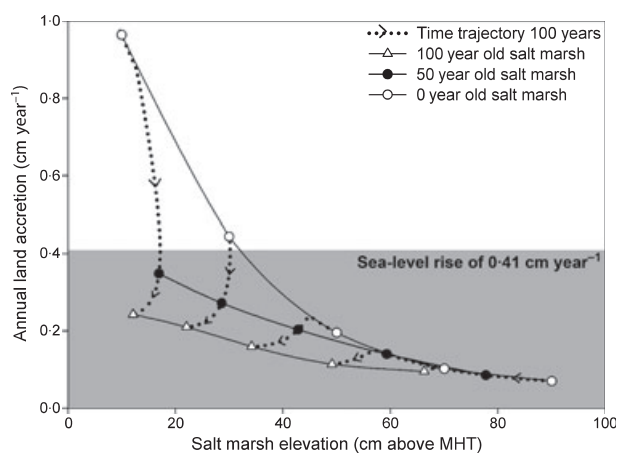


Fig. 4. Predicted annual rate of vertical land accretion of island saltmarshes according to the model of van Wijnen & Bakker (2001). At current rates of sea-level rise (SLR), new saltmarshes (0-year old) have accretion surpluses (accretion > SLR) at low elevations, but as they age (see time-trajectories) saltmarshes rapidly develop deficits at all elevations. Note that when following time-trajectories the elevation of a site is relative to the mean high tide in a given year.

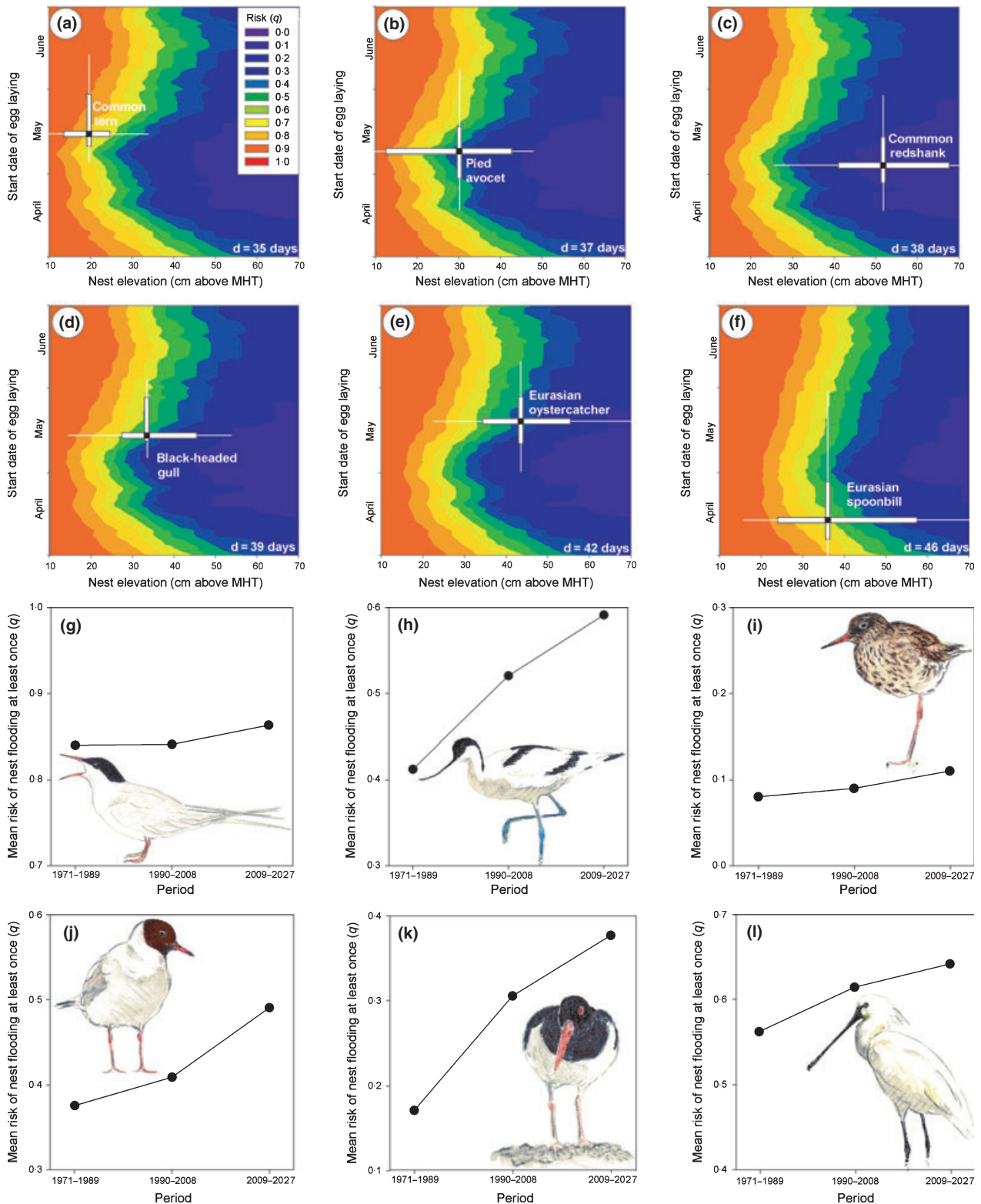


Fig. 5. (a–f) The three characteristics that determine a nest’s flooding risk for each of the bird species: the elevation of a nest site (e ; x-axes), the start date of egg-laying (s ; y-axes) and the duration a nest is at risk (d ; different panels). Bi-directional box-plots cross at the medians, with boxes representing quartiles and error bars representing 5%/95% percentiles of each species distribution of e and s . Also shown is each species risk of a nest flooding at least once (q) as a function of e , s and d , with different colours representing different degrees of risk (data 1990–2008). (g–l) Historical (1971–1989), current (1990–2008) and future (2009–2027) flooding risks averaged over the entire distribution of e , s & d for each bird species (assuming birds use the same nesting locations in all periods). Note that y-axes (in g–l) differ in range.

CHANGES IN FLOODING RISKS

When comparing historical, current and future flooding risks, all six species are predicted to have experienced increased risks and this is expected to worsen in the near future, if birds do not adapt their nest-site selection (Fig. 5g–l). In absolute terms, the increase in risk over time was smallest in common terns, a species with already high overall flooding risks. Common redshanks were also predicted to experience only slight increases in absolute flooding risk ($\bar{q}_{1971-1989} = 0.08$, $\bar{q}_{2009-2027} = 0.11$), but this does imply that the expected flooding frequency increased from once every 13 years in 1971–1989 to once every 9 years in 2009–2027.

SELECTION FOR ADAPTATIONS TO FLOODING RISKS

Sensitivity analyses of flooding risk showed that all species would benefit most from selecting higher nest sites, as q was typically more sensitive to a 1 cm change in nest elevation than to a 1 day change in the timing of egg-laying (i.e. delay or advancement towards a period with lower flooding risks) or to a 1 day reduction of the duration a nest is at risk (Table 1). This conclusion is reinforced if we assume that it is less costly or easier to increase the nest elevation by 1 cm than changing the start of egg laying or reducing the period nests are at risk by 1 day. In addition, when looking at sensitivities of q to changes of e , s & d in units of standard deviations, this also suggests that birds would benefit most from adjusting their nest elevation (Table 1).

The benefit of selecting higher sites is huge, as a 10 cm higher nest site than is currently typical for a species would reduce the flooding risk by 0.07 in common redshanks and up to 0.28 in common terns. Eurasian spoonbills would typically benefit from delaying egg laying, while common terns, black-headed gulls and Eurasian oystercatchers would gain from laying earlier. On average pied avocets and common redshanks would gain little by adjusting their timing of egg-laying, since sensitivities were close to zero (Table 1; Fig. 5b,c). The common redshank, the species with the lowest flooding risk (Fig. 5i), is likely to gain least from reducing the duration that their nests are at risk (Table 1).

FLOODING RISK, NESTING SUCCESS AND POPULATION VIABILITY: THE EURASIAN OYSTERCATCHER

As expected, annual mean flooding risk \bar{q} was not a simple linear predictor of annual fledgling production. Flooding risk primarily appears to impose a ceiling to productivity of Eurasian oystercatchers (Fig. 6a). When in a given year the mean flooding risk was high, then reproduction was low. However, when the flooding risk was low, then fledgling production could be either high or low (probably depending on other determinants of nesting success such as predation and food abundance; Ens *et al.* 1992; van de Pol *et al.* 2010). Most importantly, Fig. 6a shows that the predicted increases in flooding risk \bar{q} for oystercatchers (Fig. 5k) are expected to severely limit this population's potential to reach an annual fledgling production high enough to sustain a stable and viable population.

The response of annual productivity to flooding risk is further shaped by the fact that oystercatchers' nests with the highest flooding risk also have the highest potential value. In a year without extreme flooding events, low nests closest to the inter-tidal flats (with direct access to food; Ens *et al.* 1992) produce much more offspring than high nests further inland (Fig. 6b; but a threshold nest elevation above the normal range of spring tides is required for success). Thus, even a small increase in flooding risk at 30–50 cm above MHT is expected to disproportionately reduce mean productivity and thereby oystercatchers' population viability.

Discussion

CLIMATE CHANGE AND FLOODING RISKS

We have shown that a rare extreme climatic event – summer flooding – has become less rare and more extreme, especially during the period when the eggs of most species have just hatched (Figs. 2 and 3). Land rise of island saltmarshes is insufficient to keep pace (Fig. 4), and consequently the changes in the frequency, magnitude and timing of catastrophic flooding events are likely to reduce the nesting habitat quality of six bird species (Fig. 5). Our study also shows for the first time

Table 1. Predicted changes in nest flooding risk (q) to adaptations (i.e. small changes) in nest elevation (e), start date of egg-laying (s) and the duration nests are at risk (d) evaluated for a typical nest for each species (i.e. at each species median values e^* , s^* , d^* , see Fig. 5a–f) using tidal data from 1990–2008. Sensitivity values reflect how much q is expected to change in response to a 1 cm increase in nest elevation, a 1 day later start of egg-laying or a 1 day longer duration nests are at risk. Note that a change in the opposite direction only changes the sign of the sensitivity-values (e.g. spoonbills would reduce q by delaying the start of egg laying s , while common terns would reduce q by laying earlier). Values between parentheses reflect how much q is expected to change in response to an increase in e , s , or d of one standard deviation of the population distribution

| Species | $\frac{\partial q}{\partial e} _{e^*, s^*, d^*}$ | $\frac{\partial q}{\partial s} _{e^*, s^*, d^*}$ | $\frac{\partial q}{\partial d} _{e^*, s^*, d^*}$ |
|------------------------|--|--|--|
| Common tern | –0.028 (–0.36) | +0.015 (+0.20) | +0.017 (+0.03) |
| Pied avocet | –0.027 (–0.38) | –0.005 (–0.08) | +0.028 (+0.04) |
| Common redshank | –0.007 (–0.12) | +0.000 (+0.00) | +0.002 (+0.00) |
| Black-headed gull | –0.025 (–0.33) | +0.014 (+0.12) | +0.016 (+0.02) |
| Eurasian oystercatcher | –0.019 (–0.49) | +0.010 (+0.13) | +0.014 (+0.02) |
| Eurasian spoonbill | –0.020 (–0.54) | –0.016 (–0.31) | +0.015 (+0.02) |

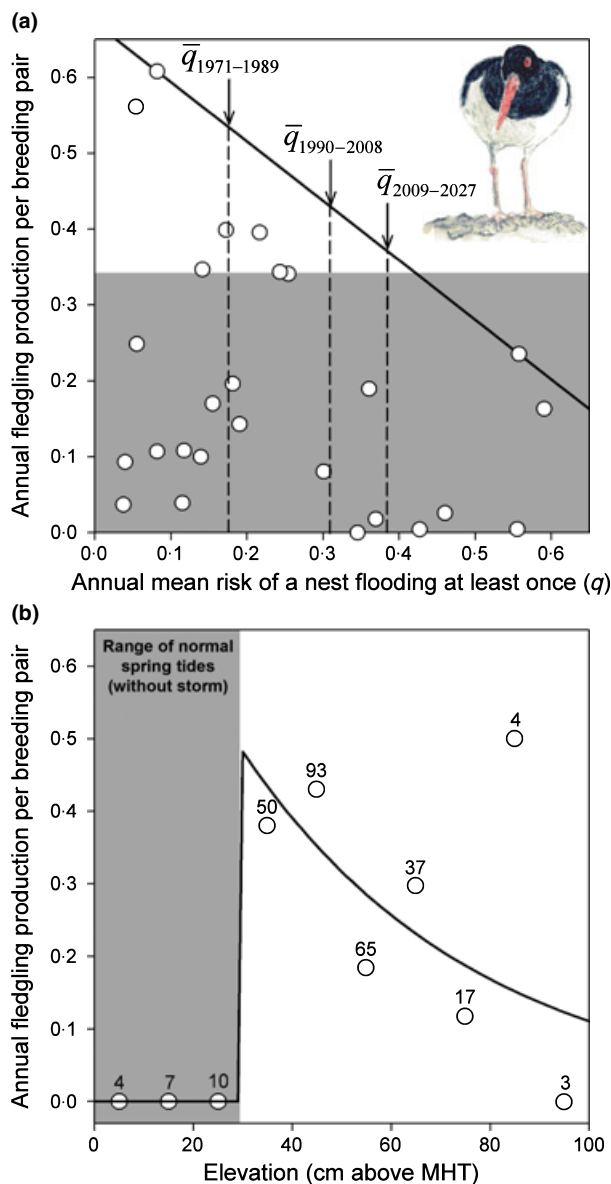


Fig. 6. (a) The relationship between the annual mean risk of nests flooding and the annual fledgling production per Eurasian oystercatcher pair on the island of Schiermonnikoog (1984–2009). The solid line depicts the quantile regression of the 95th percentile ($t_1 = 3.1$, $P = 0.005$, $n = 26$ years), suggesting that flooding events impose an upper limit on fledgling production. The grey area indicates values of fledgling production too low for a stable population size (van de Pol *et al.* 2010). The dashed lines depict estimated historical, current and future flooding risks (Fig. 5k). (b) The relationship between nest elevation and oystercatcher's fledgling production in a year with no catastrophic flooding event ($\bar{q}_{1996} = 0.14$). The line is a spline function fitted by Poisson regression ($P < 0.001$); numbers above dots refer to sample sizes (no. of pairs). Note that nests below 30 cm above mean high tide (grey area) never produce any fledglings because their nests flood during normal spring tides (~fortnightly) even when these spring tides do not coincide with stormy weather.

that changing flooding risks decreased the population viability locally for at least one species (Fig. 6).

In the Wadden Sea area 45% of Eurasian spoonbills, 72% of pied avocets, 81% of Eurasian oystercatchers, 83% of com-

mon redshanks, 83% of black-headed gulls, and 96% of common terns nest in areas that are potentially at risk from tidal flooding (Koffijberg *et al.* 2006), suggesting that their entire meta-populations could be heavily impacted. Moreover, changing tidal patterns probably affect various other saltmarsh nesting species (wader-, gull-, duck- and songbird-species) and potentially beach-nesting species too (tern- and plover-species). Alarming many bird species have declined over the last two decades in the Wadden Sea estuary (including four, possibly five of our six study species; Koffijberg *et al.* 2010). Although we do not claim that increased flooding risks have been the main driver behind these declines, flooding events can severely limit productivity in some years. We therefore think that changes in extreme flooding events form a dangerous cocktail in combination with other threats (agriculture, fisheries, recreation, eutrophication, predation; Koffijberg *et al.* 2006) and future research should specifically consider their combined interactive effects.

Substantial geographical differences nonetheless exist. We focussed on the dynamics of island saltmarshes; while mainland saltmarshes in the Wadden Sea estuary can have much higher accretion rates and thus might be more resilient (Esse-link *et al.* 1998). Also, flooding of northern sites was caused by different winds than flooding of western sites (Fig. S3, Supporting information), suggesting sites might respond differentially to changing wind patterns (changes in maximum high tides were in fact strongest in Denmark; Fig. 2). Finally, birds may nest higher on the marsh in some areas than in others, potentially depending on predators and vegetation characteristics (grazing or mowing management). A better knowledge of what causes geographical differences will be crucial for accurately predicting the future impact of changes in flooding events on a larger scale and for different types of saltmarshes.

Although it is well established that mean SLR is mainly caused by climate change (IPCC 2007), current climate models are still insufficiently detailed to predict future changes in the magnitude and timing of flooding events in summer. Climate models predict that winter storminess and thereby tidal variability will increase in the Wadden Sea (Oost *et al.* 2005), but to our knowledge no studies have investigated summer storms. Irrespective of whether the magnitude of summer storm tides will continue to increase and thereby further decrease habitat quality in the near future, in the long-term major habitat loss seems unavoidable as island saltmarshes are already unable to keep up with the current rates of SLR (van Wijnen & Bakker 2001), and this will only worsen as saltmarshes age (Fig. 4) and SLR continues to accelerate (van Dorland, Dubelaar-Versluis & Jansen 2009).

Sea level rise is mainly caused by global warming (IPCC 2007), therefore saltmarshes around the world are likely to face similar problems (Bildstein *et al.* 1991). Regrettably, little is known about southern or Arctic breeding sites. However, at various sites along the Atlantic coast of North America sea levels are also rising faster than land accretion can keep up with, causing summer flooding to become more frequent. It is feared that many North American coastal-nesting species will suffer as a consequence (Erwin *et al.* 2006). Global warming could

even affect nesting areas which until now have not been subject to flooding.

MECHANISMS OF ADAPTATION

Coastal-nesting birds are generally strict habitat specialists and thus face no other option than to locally adapt to their uncertain future. We showed that all bird species studied here would typically benefit most from choosing higher nest sites, and to a much lesser extent from adjusting their timing of egg laying or reducing the duration nests are at risk. Nest elevation can be increased by building taller nests or by selecting higher sites. However, various factors might constrain birds to adapt their nest's elevation. Building taller nests is only an option for species using extensive nesting materials and may increase conspicuousness to predators (Storey *et al.* 1988). Notwithstanding, the Eurasian spoonbills considered in our study build nests varying between 5 and 36 cm tall, suggesting there is potential for adaptation.

Selecting higher sites is problematic when other factors constrain habitat choice, such as territorial exclusion by con- or hetero-specifics (Burger & Shisler 1980). Potentially, birds have more options to select higher sites when competition decreases, which could cause the impact of flooding events to weaken with declining population size. Furthermore, birds are thought to favour lower nesting sites for other reasons, as lower sites are closer to the inter-tidal feeding grounds (Ens *et al.* 1992) and have less dense and lower vegetation which makes ground predators easier to detect (Nguyen, Nol & Abraham 2003). Preferences even vary among species: although five of our study species favour low vegetation, redshanks favour high vegetation to nest in (Thyen & Exo 2003).

Investigating whether birds select the highest sites within their territories (Lauro & Burger 1989) and if not, what factors constrain them from doing so, may provide important insights into management actions that could mitigate the effects of climate change. Intensified grazing or mowing regimes together with predator removal could make the higher marsh more attractive for nesting. Increasing heterogeneity in elevation at the lower marsh by building artificially elevated plots has proven to be unsuccessful so far (Rounds, Erwin & Porter 2004), but this may depend on the scale of elevated plots and could differ between species. Experiments that test these ideas in the field are a crucial next step.

ADAPTIVE RESPONSE OR ECOLOGICAL TRAP?

Instead of soliciting an adaptive response, rapid environmental change can also cause the formation of ecological traps (Dwernychuk & Boag 1972). If either the habitat quality or the cue used in habitat selection changes so that one does not reliably indicate the other, organisms may be lured into, or remain in poor habitat. Our study shows that climate change decreases the habitat quality of low areas due to increased flooding risks, but the corresponding environmental cues are probably hard to track for most animal species, because flooding is a rare and unpredictable event. For a bird nesting at a specific elevation it

will be extremely difficult and require many years to learn that the annual flooding risk has increased from 0.2 to 0.4 (a change in flooding frequency from once to twice in every 5 years), while this could mean the difference between a viable and non-viable population, as shown for Eurasian oystercatchers. Furthermore, other cues (e.g. proximity to food) might still suggest that low areas should be preferred over high areas. In theory, long-term fledgling productivity of conspecifics might be the most reliable and integrative cue to use; however in practice this cue is time-consuming to assess and constrained by sampling effort (Doligez, Danchin & Clobert 2002).

Birds even seem to be surprisingly poor at assessing flooding risks. In each of the six species investigated 2%–28% of all individuals repeatedly nested so low that their nests virtually always flooded (risk > 0.95 in Fig. 5). The common terns in our study even selected nest sites with a mean flooding risk of 0.84, and no young were seen to fledge from these nests (J.K. pers. obs.). Other studies have also shown that some species readily re-use nesting sites even though their nests are washed away (Burger & Shisler 1980; Nol 1989; Erwin *et al.* 1998). Re-use even occurs when other factors that reduce reproductive output, such as high predation risk, lead them to alter their nest site choice (Burger 1982).

The apparent lack of an adaptive response is worrying, especially since a major restoration aim for the Wadden Sea estuary is to vastly increase the area of saltmarshes in the coming decades (Trilateral Wadden Sea Plan 1997). Creating new (i.e. low) saltmarshes is thought of as a way to expand the area of nesting habitat for birds as well as to simultaneously buffer the impact of climate change (i.e. reduce the destructive impact of increased wave action on more inland human coastal defences). However, restored saltmarshes may function as ecological traps for some species instead and therefore may actually counteract the restoration goal of increasing the bird numbers in an area. Newly restored as well as existing marshes may thus require novel management strategies to maximize their contribution to the avian biodiversity (e.g. grazing regimes that make the high marsh more suitable for nesting).

Finally, the literature on adaptation to climate change primarily involves research into adaptation to climate trends (e.g. global warming; Visser 2008), and not to extreme climatic events (Jentsch, Kreyling & Beierkhunlein 2007). This is unfortunate, because extreme events may strongly impact populations, as our study illustrates. Adapting to climate trends might be 'difficult' in itself, but may nonetheless still be relatively 'easy' as typically corresponding cues are available before the breeding season (e.g. temperature-dependent timing of egg-laying; though mismatches can develop; Visser 2008). We think that more research focussing on adaptation to various types of less predictable extreme events will be important to obtain a more balanced view about the adaptive potential of species to all aspects of climate change.

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References

- Becker, P.H. & Anlauf, A. (1988) Nest site choice and breeding success of marsh nesting common terns (*Sterna hirundo*) II: floodings. *Ecology of Birds*, **10**, 45–58.
- Bildstein, K.L., Bancroft, G.T., Dugan, P.J., Gordon, D.H., Erwin, R.M., Nol, E., Payne, L.X. & Senner, S.E. (1991) Approaches to the conservation of coastal wetlands in the western hemisphere. *Wilson Bulletin*, **103**, 218–254.
- Burger, J. (1982) The role of reproductive success in colony-site selection and abandonment in black skimmers (*Rynchops niger*). *The Auk*, **99**, 109–115.
- Burger, J. & Shisler, J. (1980) Colony and nest site selection in laughing gulls in response to tidal flooding. *Condor*, **82**, 251–258.
- Chan, K.S., Mysterud, A., Øritsland, N.A., Severinsen, T. & Stenseth, N.C. (2005) Continuous and discrete extreme climatic events affecting the dynamics of a high-arctic reindeer population. *Oecologia*, **145**, 556–563.
- Doligez, B., Danchin, E. & Clobert, J. (2002) Public information and breeding habitat selection in a wild bird population. *Science*, **297**, 1168–1170.
- van Dorland, R., Dubelaar-Versluis, W. & Jansen, B. (2009) *The state of the climate 2008*. Panel for Communication on Climate Change, De Bilt.
- Durant, J.M., Stenseth, N.C., Anker-Nilssen, T., Harris, M.P., Thompson, P.M. & Wanless, S. (2004) Marine birds and climate fluctuation in the North Atlantic. *Marine Ecosystems and Climate Variation* (eds N.C. Stenseth, G. Ottersen, J.W. Hurrell & A. Belgrano), pp. 95–105. Oxford University Press, Oxford.
- Dwernychuk, L.W. & Boag, D.A. (1972) Ducks nesting in association with gulls – an ecological trap? *Canadian Journal of Zoology*, **50**, 559–563.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2001) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.
- Ens, B.J., Kersten, M., Brenninkmeijer, A. & Hulscher, J.B. (1992) Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **61**, 703–715.
- Erwin, R.M., Nichols, J.D., Eyler, T.B., Stotts, D.B. & Truitt, B.T. (1998) Modeling colony-site dynamics: a case study of gull-billed terns (*Sterna nilotica*) in coastal Virginia. *The Auk*, **115**, 970–978.
- Erwin, R.M., Sanders, G.M., Prosser, D.J. & Cahoon, D.R. (2006) High tides and rising seas: potential effects on estuarine waterbirds. *Studies in Avian Biology*, **32**, 214–228.
- Esselink, P.E., Dijkema, K.S., Reents, S. & Hageman, G. (1998) Vertical accretion and profile changes in abandoned man-made tidal marshes in the Dollard estuary, the Netherlands. *Journal of Coastal Research*, **14**, 570–582.
- Goodman, J.E., Wood, M.E. & Gehrels, W.R. (2007) A 17-yr record of sediment accretion in the salt marshes of Maine (USA). *Marine Geology*, **242**, 109–121.
- Hötter, H. (1998) Intraspecific variation in length of incubation period in avocets *Recurvirostra avoseta*. *Ardea*, **86**, 33–41.
- Hötter, H. (2002) Arrival of pied avocets *Recurvirostra avoseta* at the breeding site: effects of winter quarters and consequences for reproductive success. *Ardea*, **90**, 379–387.
- Hughes, R.G. & Paramor, O.A.L. (2004) On the loss of salt marshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, **41**, 440–448.
- IPCC (2007) Climate change 2007: synthesis report. *Report of the Intergovernmental Panel on Climate Change*, **4**, 1–104.
- Jentsch, A., Kreyling, J. & Beierkhunlein, C. (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and Environment*, **5**, 365–374.
- van de Kam, J., Ens, B.J., Piersma, T. & Zwarts, L. (2004) *Shorebirds - An Illustrated Behavioural Ecology*. KNNV publishers, Utrecht.
- Koffijberg, K., Dijkens, L., Hälterlein, B., Laursen, K., Potel, K. & Südbeck, P. (2006) Breeding Birds in the Wadden Sea in 2001 – Results of the total survey in 2001 and trends in numbers between 1991–2001. *Wadden Sea Ecosystem*, **22**, 136.
- Koffijberg, K., Dijkens, L., Hälterlein, B., Laursen, K. & Potel, K. (2010) Breeding birds in the Wadden Sea in 2006 – Results of the total survey in 2006 and trends in numbers between 1991 and 2006. *Wadden Sea Ecosystem*, in press.
- Lauro, B. & Burger, J. (1989) Nest-site selection of American Oystercatchers (*Haematopus palliatus*) in salt marshes. *The Auk*, **106**, 185–192.
- Marquenie, J. & de Vlas, J. (2005) The impact of subsidence and sea-level rise in the Wadden Sea: prediction and field verification. *Managing European Coasts: Past, Present, and Future* (eds J.E. Vermaat, L. Bouwer, K. Turner & W. Salomons), pp. 355–363. Springer Verlag, Berlin.
- McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002) Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences USA*, **99**, 6070–6074.
- Nguyen, L.P., Nol, E. & Abraham, K.F. (2003) Nest success and habitat selection of the semipalmated plover on Akimiski island, Nunavut. *Wilson Bulletin*, **115**, 285–291.
- NLWK (2004) *Niedersächsischer Landesbetrieb für Wasserwirtschaft und Küstenschutz, Laserscan-Befliegung Jadebusen, Bereich II*. Oldenburgischer Deichband, Norden.
- Nol, E. (1989) Food supply and reproductive performance of the American Oystercatcher in Virginia. *Condor*, **91**, 429–435.
- Olf, H., de Leeuw, J., Bakker, J.P., Platerink, R.J., van Wijnen, H.J. & de Munck, W. (1997) Vegetation succession and herbivory in a salt marsh: changes induced by sea-level rise and silt deposition along an elevational gradient. *Journal of Ecology*, **85**, 799–814.
- Oost, A., Becker, G., Fenger, J., Hofstede, J. & Weisse, R. (2005) Climate. *Wadden Sea Ecosystem*, **19**, 75–82.
- van de Pol, M., Pen, I., Heg, D. & Weissing, F.J. (2007) Variation in habitat choice and delayed reproduction: adaptive queuing strategies or individual quality differences? *The American Naturalist*, **170**, 530–541.
- van de Pol, M., Vindenes, Y., Sæther, B.-E., Engen, S., Ens, B.J., Oosterbeek, K. & Tinbergen, J.M. (2010) Effects of climate change and variability on population dynamics in a long-lived shorebird. *Ecology*, **91**, 1192–1204.
- Rossiter, J.R. (1972) Sea-level observations and their secular variation. *Philosophical Transactions of the Royal Society of London Series A*, **272**, 131–139.
- Rounds, R.A., Erwin, R.M. & Porter, J.H. (2004) Nest-site selection and hatching success of waterbirds in coastal Virginia: some results of habitat manipulation. *Journal of Field Ornithology*, **75**, 317–329.
- Storey, A.E., Montevicchi, W.A., Andrews, H.F. & Sims, N. (1988) Constraints on nest site selection: a comparison of predator and flood avoidance in four species of marsh-nesting birds. *Journal of Comparative Psychology*, **102**, 14–20.
- Sutherland, W.J., Adams, W.M., Aronson, R.B., Aveling, R., Blackburn, T.M., Broad, S. *et al.* (2009) One hundred questions of importance to the conservation of global biological diversity. *Conservation Biology*, **23**, 557–567.
- Temmerman, S., Govers, G., Wartel, S. & Meire, P. (2004) Modelling estuarine variations in tidal marsh sedimentation: response to changing sea level and suspended sediment concentrations. *Marine Geology*, **212**, 1–19.
- Thibault, K.M. & Brown, J.H. (2008) Impact of an extreme climatic event on community assembly. *Proceedings of the National Academy of Sciences USA*, **105**, 3410–3415.
- Thyen, S. & Exo, K.-M. (2003) Wadden Sea salt marshes: ecological trap or hideaway for breeding Redshanks *Tringa totanus*? *Wader Study Group Bulletin*, **100**, 43–46.
- Trilateral Wadden Sea Plan (1997) *Ministerial Declaration of the 8th Trilateral Governmental Conference on the Protection of the Wadden Sea*. Stade, Germany.
- Tryjanowski, P., Sparks, T.H. & Profus, P. (2009) Severe flooding causes a crash in production of white stork (*Ciconia ciconia*) chicks across Central and Eastern Europe. *Basic and Applied Ecology*, **10**, 387–392.
- Visser, M.E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London B*, **275**, 649–659.
- de Vries, A. & Krottje, G. (2004) Research on Avocet Chicks at Ferwerd. Report 2003. URL: <http://home.hetnet.nl/~vrsmenork/map15/kluut2003.htm> (accessed 28 January 2010).
- Ward, L.D. & Burger, J. (1980) Survival of herring gulls and domestic chicken embryos after simulated flooding. *Condor*, **82**, 142–148.
- van Wijnen, H.J. & Bakker, J.P. (2001) Long-term surface elevation change in salt marshes: a prediction of marsh response to future sea-level rise. *Estuarine, Coastal and Shelf Sciences*, **52**, 381–390.

Willems, F., Oosterhuis, R., Dijkse, L., Kats, R. & Ens, B.J. (2005) Breeding success of shorebirds in the Wadden Sea 2005. SOVON report 2005/07, pp. 1–100

Wolters, M., Bakker, J.P., Bertness, M.D., Jefferies, R.L. & Moller, I. (2005) Salt marsh erosion and restoration in south-east England: squeezing the evidence requires realignment. *Journal of Applied Ecology*, **42**, 844–851.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Map with location and names of measurement stations.

Fig. S2. Plots of time-series of mean high tide and maximum high tide over the period 1971–2008 during the months May–July for each of the 27 stations.

Fig. S3. Wind roses of two mainland and two island weather stations for days with normal and days with higher than normal tides (data 1971–2008).

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