

**Between the devil and the deep blue
sea: Consequences of extreme
climatic events in the Eurasian
oystercatcher (*Haematopus
ostralegus*)**



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DECLARATION

The research presented in this thesis is my own original work. I am the senior and author and principal contributor for all chapters. No part of this thesis has been submitted for any previous degree.

Liam Daniel Bailey

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The fact that a Ph.D. is awarded to a single person belies the amazing effort of friends, family and colleagues across the years. In reality, a Ph.D. is a product built from the love, support, care, compassion and tolerance of a multitude of invaluable behind the scenes staff. These are the unsung heroes of any academic endeavour and in this section I seek to provide them with the spotlight they deserve, however briefly.

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A Ph.D. is a funny thing. You live in constant fear that one day somebody might notice that you actually have no idea what you're doing here and you're just stumbling along trying to keep from drowning under a pile of papers, R-scripts, manuscript revisions and field permits. And then, suddenly, it's over. You look back on a pile of work that seems much larger than you remembered. Honestly, you're not really sure how it all got done or how you maintained the motivation. Motivation: an intangible and fleeting feeling throughout the whole ordeal. You had it sometimes, but you never really knew where it came from. But at this point, looking back over the mountains you climbed and the valleys you crossed, you realise your motivation came from the people around you. That is why we have an acknowledgements section.

ABSTRACT

Anthropogenic climate change will not only change mean climatic conditions but is also predicted to alter the patterns of extreme climatic events (ECEs). Changes in the frequency and magnitude of ECEs can have broad impacts; however, empirical work on the topic has been limited. This thesis focuses on ECEs, with chapters one and two discussing the theory behind ecological research on ECEs and chapters 3 to 5 documenting the impacts of ECEs in a 32 year individual based dataset of the Eurasian oystercatcher (*Haematopus ostralegus*).

1. Research on ECEs has been limited by a lack of cohesiveness and structure. I will discuss the current challenges in ECE research, considering the way in which we define ECEs and design studies on the topic. I specifically highlight the need to conduct research that encompasses multiple ECE occurrences, as opposed to more common single event studies.

2. To understand the impacts of ECEs on biological systems it is necessary to identify the time period over which organisms are most sensitive to climatic changes. This is often done in an arbitrary way, limiting our biological understanding. To overcome this issue, I present a statistical toolbox in R to conduct climate sensitivity analyses using a variety of statistical methods.

3. Despite the growing interest in ECEs within ecology, how organisms will respond to changes in ECE patterns is poorly understood. I study phenotypic plasticity in *H. ostralegus* nest elevation as a response to increasingly frequent extreme flooding events, focussing on nest-site selection. I document little evidence of phenotypic change in nest-site selection, suggesting that this will not provide a viable mechanism for *H. ostralegus* to respond to flooding events.

4. *H. ostralegus* may also respond to changing flooding patterns through broader scale territory selection. I next investigate *H. ostralegus* settlement patterns and consider how these patterns may have changed in response to ECEs. *H. ostralegus* show changes in territory settlement, suggesting that this species may respond to changing patterns of ECEs at a broader spatial and temporal scale than we originally predicted.

5. Without a rapid response, increased ECE frequency is likely to drive a decline in *H. ostralegus* population density. This may lead to increased nest predation due to reduced neighbour vigilance and mobbing effectiveness. I investigate how changes in *H. ostralegus* density will impact nest predation, using both artificial and real nests. *H. ostralegus* nest predation is negatively related to conspecific nest density. This raises the possibility of a nest predation driven Allee effect in *H. ostralegus*.

This thesis fills a number of key knowledge gaps present in ECE research. Chapters 1 and 2 provide practical tools for designing future ECE studies, while chapters 3 and 4 represent a unique investigation of phenotypic plasticity in response to ECEs. Finally in chapter 5, I document the population consequences of ECE changes using our unique long-term dataset. In combination, these chapters provide a broad investigation of ECEs in an ecological context.

THESIS OUTLINE

The following chapters compose this thesis:

1. Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events.
Liam D. Bailey & Martijn van de Pol
Journal of Animal Ecology (2016) 85 (1): 85 - 96.
2. *climwin*: An R Toolbox for Climate Window Analysis.
Liam D. Bailey & Martijn van de Pol
PLoS ONE (2016) 11 (12): e0167980.
3. Phenotypic plasticity in nest-site selection as a response to extreme flooding events.
Liam D. Bailey, Bruno J. Ens, Christiaan Both, Dik Heg, Kees Oosterbeek & Martijn van de Pol
Philosophical Transactions of the Royal Society B (in press)
4. Changing habitat selection of a long-lived shorebird in response to extreme climatic events.
Liam D. Bailey, Bruno J. Ens, Christiaan Both, Dik Heg, Kees Oosterbeek & Martijn van de Pol
Manuscript under preparation
5. Negative density-dependent nest predation in a threatened mobbing bird species.
Liam D. Bailey, Naomi E. Langmore, Martijn van de Pol
Manuscript under preparation
6. Synthesis and general conclusions

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Introduction

Since the Industrial Revolution, there has been a growing recognition that human society has gained the ability to shape the earth at a planetary level, dramatically shifting our relationship with the natural world. Anthropogenic impacts on natural systems have become so pervasive that there are suggestions we have entered a new human driven geological era, the Anthropocene (Steffen *et al.* 2011). A major element of global change in the Anthropocene period will be human induced climatic change. Greenhouse gas emissions are predicted to shift the mean, inter- and intra-annual variability of the global climate, with changes in temperature, rainfall, sea ice, snow cover and sea-level rise predicted (IPCC 2013). While these climatic shifts will invariably impact human communities, they will also have profound impacts on the world's ecosystems. Many of the predicted changes in climate will be irreversible on a human time scale (IPCC 2013), and it is therefore vitally important that we understand how climate change will impact natural systems and how these systems may respond.

Already, broad scale changes across taxa and geographic regions have been attributed to shifting climatic conditions (Walther *et al.* 2002; Parmesan & Yohe 2003). The distributional range of many species is shifting to track climatic optima, both across latitude and altitude (Hickling *et al.* 2006; Lenoir *et al.* 2008; Chen *et al.* 2011). Similarly, phenological shifts have been observed in both plants and animals, with phenological mismatches arising between previously synchronous species (Visser & Both 2005; Both *et al.* 2006; Charmantier *et al.* 2008; Wolkovich *et al.* 2012; Reed *et al.* 2013). Climate change has also been identified as a key driver of population decline and increased extinction risk across taxonomic groups (Carpenter *et al.* 2008; Both *et al.* 2009; Urban 2015), contributing to what is being termed the "sixth mass extinction" (Barnosky *et al.* 2011; Bellard *et al.* 2012; Ceballos *et al.* 2015).

Although there has been a rapid increase in our understanding of climate change impacts, attention has mostly focussed on the impacts of increasing climatic means rather than the potential impacts of more frequent climatic extremes (Jentsch *et al.* 2007). In response, the last decade has seen a growing interest in the topic of extreme climatic events (Jentsch *et al.* 2007; Moreno & Møller 2011; Smith 2011). Changing patterns of ECEs are expected to have distinct impacts on natural systems compared to those predicted by changing climatic means. ECEs have been shown to drive rapid changes in both species reproduction (Tryjanowski *et al.* 2009; van de Pol *et al.* 2010)

and mortality (Bragazza 2008; Garrahou *et al.* 2009). Increased mortality driven by ECEs may act as intense selection episodes (Bryant & Jones 1995; Brown & Brown 1998; Chevin *et al.* 2013; Jenouvrier *et al.* 2015), exemplified beautifully in the shifting morphology of Darwin's finches on Daphne Major where finch populations showed noticeable changes in beak morphology following precipitation extremes (Price *et al.* 1984; Gibbs & Grant 1987). In fact, the selective role of ECEs has been suggested as a more important driver of evolutionary change over the long-term than gradual shifts in climatic means (Gutschick & BassiriRad 2003). However, simulations suggest that the occurrence of such 'catastrophic events' can increase extinction risk (Kokko & Sutherland 2001; Schwager *et al.* 2006), a prediction likely supported by observed population extinctions in the field (Parmesan *et al.* 2000). Furthermore, as ECEs become more common the temporal auto-correlation of environmental conditions is also expected to decline, disrupting the predictability of natural environments and potentially shifting behavioural patterns (Doligez *et al.* 2003; Schmidt *et al.* 2015). With such a broad range of potential impacts it is important that we understand the consequences of more frequent ECEs that is likely to accompany increases in mean climatic conditions.

This thesis focusses broadly on the topic of ECEs. Chapter 1 provides a review of our current knowledge concerning ECE impacts on natural systems. In particular, I focus on how we describe an ECE and the type of questions we seek to answer when conducting ECE research. I emphasise the importance of conducting long-term studies of ECE impacts, targeting those systems where ECEs are predicted to occur more frequently. It should be noted, however, that ECE studies, especially those conducted over a longer time frame, are likely to require large investment of both time and money. Therefore, in Chapter 2, I introduce a novel statistical method used for identifying periods of climatic sensitivity in natural systems. This tool will allow us to more effectively target our limited resources to encompass biologically significant time periods in which ECEs and other aspects of climate are likely to have an effect.

One particular topic that has received limited attention has been the prevalence of phenotypic plasticity as a response to ECEs (Chapter 1). The occurrence of phenotypic plasticity will alter the responses of populations to ECEs over time, as individuals adjust their phenotype to better cope with future climatic perturbations. This will be

particularly important in long-lived species, where rates of micro-evolutionary change will be limited. Therefore, after considering the theoretical and technical background of conducting ECE studies, I undertake three field based projects to study the impacts of ECEs in a natural system with a particular focus on phenotypic plasticity. I use a 32 year study on the breeding behaviour of a long-lived shorebird, the Eurasian oystercatcher (*Haematopus ostralegus*), experiencing increasingly common occurrences of extreme flooding events, with long-term consequences for reproductive success and population viability. In Chapters 3 and 4, I hypothesise that *H. ostralegus* may exhibit phenotypic plasticity in reproductive behaviour as a response to increased flooding frequency. In Chapter 3, I use nest elevation data to investigate within-individual changes in *H. ostralegus* nest site selection. I consider a potential trade-off between nest concealment and nest elevation which may limit individual responses to flooding changes. In Chapter 4, I study between-individual changes in nest elevation driven by territory selection, with a consideration of the cues individuals may use to inform territory settlement decisions. Furthermore, I consider the effectiveness of territory selection changes as a long-term response to increasing flooding frequency.

Changes in ECE frequency, along with a broad range of other anthropogenic impacts, has driven steep declines in *H. ostralegus* numbers over our 32 year study period (van Roomen *et al.* 2012; van de Pol *et al.* 2014). In Chapter 5, I explore the potential consequences of these population declines on nest predation in our breeding population. Using both an artificial nest experiment and data from our long-term study population, I consider the possibility that mobbing behaviour in *H. ostralegus* will drive negative density-dependent nest predation, where nest predation rates increase with decreasing conspecific density. Additionally, I discuss how density-dependent relationships in nest predation may shape the long-term viability of our study population and mobbing bird species more broadly.

Finally, in my last chapter I provide a synthesis of the aims and main findings of this thesis, and provide an insight into potential future research which may stem from this body of work. In conjunction, the work in this thesis provides a broad investigation of the impacts of ECEs on natural systems, tackling conceptual (Chapter 1), methodological (Chapter 2) and empirical problems (Chapter 3-5).

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Chapter 1

Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events.

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FORUM

Tackling extremes: challenges for ecological and evolutionary research on extreme climatic events

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Summary

1. Extreme climatic events (ECEs) are predicted to become more frequent as the climate changes. A rapidly increasing number of studies – though few on animals – suggest that the biological consequences of ECEs can be severe.

2. However, ecological research on the impacts of ECEs has been limited by a lack of cohesiveness and structure. ECEs are often poorly defined and have often been confusingly equated with climatic variability, making comparison between studies difficult. In addition, a focus on short-term studies has provided us with little information on the long-term implications of ECEs, and the descriptive and anecdotal nature of many studies has meant it is still unclear what the key research questions are.

3. Synthesizing the current state of work is essential to identify ways to make progress. We conduct a synthesis of the literature and discuss conceptual and practical challenges faced by research on ECEs.

4. We consider three steps to advance research. First, we discuss the importance of choosing an ECE definition and identify the pros and cons of ‘climatological’ and ‘biological’ definitions of ECEs. Secondly, we advocate research beyond short-term descriptive studies to address questions concerning the long-term implications of ECEs, focussing on selective pressures and phenotypically plastic responses and how they might differ from responses to a changing climatic mean. Finally, we encourage a greater focus on multi-event studies that help us understand the implications of changing patterns of ECEs, through the combined use of modelling, experimental and observational field studies.

5. This study aims to open a discussion on the definitions, questions and methods currently used to study ECEs, which will lead to a more cohesive approach to future ECE research.

Key-words: climate change, climate events, climate variability, extreme climate, multi-event study, phenotypic plasticity, predictability, selective pressure, threshold responses, truncation selection

Introduction

Anthropogenic climate change is predicted to alter the mean, intra- and interannual variability of the global climate (Schär *et al.* 2004; IPCC 2013). A likely and prominent consequence will be an increase in the occurrence of currently rare extreme climatic events (henceforth ECEs; Easterling *et al.* 2000; IPCC 2012, 2013). For example, there has been an increase in the frequency and length of heatwaves observed across Europe (Kuglitsch *et al.* 2010;

Coumou & Rahmstorf 2012), growing intensity of heavy precipitation events in the Northern Hemisphere (Min *et al.* 2011), and longer fire seasons in both Australia and the United States (Westerling *et al.* 2006; Clarke, Smith & Pitman 2011).

Extreme climatic events can have impacts at the individual, population and community level (e.g. Parmesan, Root & Willig 2000; van de Pol *et al.* 2010b; Hoover, Knapp & Smith 2014). Understanding the long-term impacts of changes in ECEs and how individuals, populations and communities respond is, therefore, an important goal in ecological research. ECEs have received increasing

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interest in the ecological community over the past two decades (Fig. 1a; see reviews by Jentsch, Kreyling & Beierkuhnlein 2007; Moreno & Möller 2011; Smith 2011b), yet this research has suffered from a lack of cohesiveness and structure.

A key problem in the biological literature is the use of unclear definitions of ECEs, limiting the applicability of research findings and the possibility for comparison among studies. Furthermore, some research has equated the impacts of changing ECEs directly with those of increasing climatic variability (e.g. Jiguet, Brotons & Devictor 2011; Roland & Matter 2013), thereby overlooking the influence that other climatic characteristics (e.g. mean and skew) can have upon patterns of ECEs, as well as ignoring the fact that increased climatic variability can have biological impacts distinct from those of ECEs (Lawson *et al.* 2015). In addition, research into ECEs has

predominantly focussed on the short-term impacts of single extreme events, while the impacts of multiple extreme events and long-term responses remain poorly understood. A critical assessment of the literature that clarifies misconceptions and sharpens research focus could thus help advance this study area.

This forum paper aims to stimulate a broad discussion of ECE research. Specifically, the goals of the paper are threefold. First, we discuss alternative definitions of ECEs, with a focus on comparing 'climatological' and 'biological' definitions. In doing so, we clarify the relationship between ECEs and climate variability. Secondly, to advance research beyond predominantly descriptive studies, we identify research questions that help us understand the long-term adaptive responses of biological systems to ECEs, such as selective pressures and phenotypically plastic responses, and how these responses might differ from responses to a changing climatic mean. Finally, we highlight the limitations of anecdotal studies which focus on the short-term consequences of single ECEs, and propose a shift towards multi-event research through the combined use of experimental, observational and modelling studies. Since the majority of ECE research is conducted on non-animal species, we will integrate work in both plant and animal systems to gain a more comprehensive understanding of the state of the research field.

Defining an 'extreme climatic event'

Over a quarter of ECE studies neglect to clearly outline how they define an ECE (28%; Appendix S1, Supporting information) or use vague definitions (Gutschick & BassiriRad 2003; Lloret *et al.* 2012), making it difficult to compare studies and form a cohesive picture of the research. Various papers have proposed broad ECE definitions (Gutschick & BassiriRad 2003; Jentsch, Kreyling & Beierkuhnlein 2007; Smith 2011a), yet there has so far been no detailed discussion of the usefulness of these different definitions. The complex nature of climate and biological systems may make the implementation of a single ECE definition difficult (Beniston & Stephenson 2004), so it is important that we understand the circumstances in which particular definitions may be of use. For example, Jentsch, Kreyling & Beierkuhnlein (2007) consider an ECE to be abrupt, having a large biological magnitude over a short duration relative to the life span of the organism. Although this definition works well for rapid climatic events (e.g. hurricanes, heatwaves, flash flooding), it does not for events that gradually worsen over time and are extreme due to their persistence (e.g. cumulative events such as droughts).

CLIMATOLOGICAL DEFINITIONS

In the biological sciences, the most common way to define an ECE has been to use the same definition as climatologists, where climate is classed as extreme based on its rar-

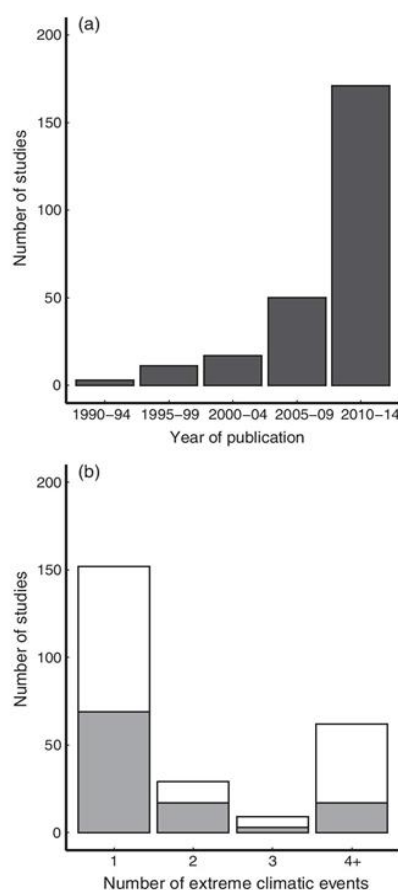


Fig. 1. (a) The number of studies focused on extreme climatic events since 1990. (b) The number of extreme climatic events considered in ecological studies, separated between studies focussing on plant species (white) or other species (grey). Other species included both animal and microbial studies. Data collection methodology outlined in Appendix S1.

ity (e.g. occurring 5% of the time or less. Note that a historical climate distribution is often used as a reference; otherwise, ECEs by definition can never become less rare; Easterling *et al.* 2000; IPCC 2013). Climatological definitions are easily applicable to any study system where sufficient climate data are available, even those systems in which we lack detailed biological information (i.e. opportunistic studies; Section 'Approaches for investigating extreme climatic events'). In addition, the ability to standardize ECEs based on a fixed climate distribution easily facilitates the comparison of ECE responses between systems through both space and time.

However, concerns have been raised over the arbitrary nature of the climatic threshold used to determine ECEs (e.g. $\leq 5\%$), as this may lead to an underestimation of the impacts of climate. For example, the threat of climate to a species may be underestimated if the organism is detrimentally impacted by more common climatic conditions that have been overlooked (e.g. $\geq 5\%$). Furthermore, climatological rareness will have a different biological interpretation for long-lived and short-lived species (Section 'Long-term responses to extreme climatic events'), inhibiting comparison between species (but see Jentsch, Kreyling & Beierkuhnlein 2007). As such, it has been argued that ECEs do not need to be rare by definition, but should instead be considered extreme based on 'biologically relevant thresholds', such as those that control mortality or dominance shifts within communities (Gutschick & BassiriRad 2003; Beier *et al.* 2012).

Hybrid definitions have sought a middle ground by describing ECEs as both climatologically rare and biologically meaningful (e.g. Jentsch, Kreyling & Beierkuhnlein 2007; Smith 2011a). Jentsch, Kreyling & Beierkuhnlein (2007) require ECEs to be both statistically extreme and biologically abrupt. In their definition, Smith (2011a) focusses on a 'statistically rare or unusual climatic period' that has a biological effect 'well outside the bounds of what is considered typical or normal variability'. Yet although these hybrid definitions do consider biological responses, by including statistical extremeness, they still employ an arbitrary climate cut-off (e.g. $\leq 5\%$). Purely biological definitions represent an alternative (e.g. Gutschick & BassiriRad 2003), yet these have rarely been used in the ECE literature.

BIOLOGICAL DEFINITIONS

Biological definitions are focussed on understanding under which circumstances climate will trigger severe biological outcomes, regardless of rarity. For example, Gutschick & BassiriRad (2003) define an ECE as an episode where the acclimation capacity of an organism is exceeded and the subsequent physiological or developmental response of the organism is significantly different than normal acclimation.

It may seem counter-intuitive to completely remove rarity from the definition of an ECE, but this removes the requirement for climatic conditions to be arbitrarily cate-

gorized often before we possess an intimate understanding of how the biological system responds to climate. Ultimately, the biological responses considered are still likely to be triggered by uncommon climatic conditions. On an eco-evolutionary time scale, if climatic conditions create severe biological consequences for organisms, populations that frequently experience extreme conditions are likely to either become extinct if they are incapable of adapting, or adapt so that such conditions no longer produce a strong biological response, and are no longer ECEs. However, although extreme biological responses are likely to be driven by rare climate, rare climate will not *necessarily* produce an extreme biological response.

The removal of a frequency threshold may also raise concerns of a tautology. One can no longer investigate the biological effect of an ECE as, by definition, we already define an ECE as having a strong biological effect. However, this issue can be overcome by reshaping the research questions used to investigate ECEs. When using a climatological definition, ECE research asks 'What was the effect of this extreme (i.e. rare) event?' while when employing a biological definition we can ask 'Was this (rare) climatic event an ECE?' Both questions allow a focus on a specific climate event, but the latter does not assume that the climate in question is extreme until it has been shown to produce a strong biological effect. The use of a climatological or biological question (and corresponding definition) will depend on whether one is interested specifically in *rare* climate or if one is more focussed on understanding the biological effects of climate.

In addition, a biological definition does not assume that the same climatic conditions will always elicit similar responses. Climatic variables are likely to interact with biotic and abiotic factors, making the occurrence of ECEs context-dependent. In *Haematopus ostralegus* (Eurasian oystercatcher), for example, severe winter conditions had little impact on survival in years with abundant food. However, when similar conditions occurred in conjunction with food shortage, adult mortality was much greater than would be expected by either cold weather or food shortage in isolation (Camphuysen *et al.* 1996; Atkinson *et al.* 2003).

Even when other environmental factors remain constant, the seasonal timing at which climatic conditions occur may have a distinct effect on the incidence of a biological response due to the climate window of a species (the time when individuals are most sensitive to climate; van de Pol & Cockburn 2011). For example, *Gadus morhua* (North Atlantic cod) were more sensitive to thermal extremes just prior to and during spawning than outside of this breeding window (Mantzouni & MacKenzie 2010). Similarly, *Ovis aries* (Soay sheep) survival is more sensitive to poor weather conditions between February and April than other months (Hallett *et al.* 2004). Due to the predominantly climatological nature of previous ECE research, there has been a bias towards understanding changes in ECE frequency. Changes in other

characteristics of ECEs, such as timing and magnitude, may also be important but are rarely considered (Box 1).

These characteristics of biological definitions allow them to employ a more discriminative approach to ECEs. However, effectively using a biological definition requires large amounts of detailed biological information on the system of interest, including information on both the desired biological response and other possible biotic and abiotic interactions. Realistically, this is not always possible or may not be of particular interest. Furthermore, the more complex nature of biological ECEs can make them difficult to use for predictive studies, as any context dependence could make predictive models too complex.

AN ALTERNATIVE BIOLOGICAL DEFINITION

Gutschick & BassiriRad's (2003) biological definition succeeds in overcoming the arbitrary nature of climatological definitions, yet as part of their definition, they specify that an ECE includes a long recovery period with hysteresis. Although a long and abnormal recovery period could be

appropriate when studying physiological processes, such a requirement may be less appropriate for studies considering demographic or population consequences of ECEs. For example, while an ECE may cause reproductive failure in a population, this will not necessarily lead to reduced reproductive success in future, non-ECE, years. As such, other studies may find an alternative less restrictive definition more appropriate.

When integrating the biological response into their hybrid definitions, both Smith (2011a) and Jentsch, Kreyling & Beierkuhnlein (2007) considered 'abrupt' or 'extreme' biological responses to be of interest. This point is not present in the definition of Gutschick & BassiriRad (2003), as they focus predominantly on the recovery period following an ECE. We suggest that classifying the biological response as either extreme or non-extreme is only reasonable if there is some distinguishable difference between these two categories. Where there is a linear relationship between the climate and biological response, changes in climate will have the same impact regardless of whether they occur in 'extreme' or 'non-extreme' conditions. In comparison, where responses to climate are nonlinear the consequences of a change in the climate will vary depending on where it occurs in the climate distribution. Therefore, we consider a biological response to be extreme when a nonlinear response to climate is present and define an ECE as:

An episode where climate or climate driven conditions trigger a negative threshold-like (non-linear) biological response.

Box 1. Changing characteristics of ECEs

The most commonly considered characteristic of ECEs is their frequency, while other characteristics of ECEs have often been overlooked. For example, changes in ECE magnitude (e.g. duration of droughts and heatwaves, intensity of precipitation events) are likely to change in a future climate (Coumou & Rahmstorf 2012). However, the consequences of changing magnitude are likely to vary between biological systems. In systems, where the impact of ECEs is already comprehensive, such as populations experiencing total reproductive failure (Bolger, Patten & Bostock 2005), increasing ECE magnitude will have little effect. Yet in other systems, changes in magnitude may have serious impacts on ecosystems or populations, even if the frequency of ECEs remains constant.

In addition, the temporal nature of ECEs may be altered. The seasonal timing of rare climatic conditions may change so that extreme conditions begin to occur at times they have not before. For example, the North American fire season has been starting earlier and lasting longer (Westerling *et al.* 2006). As the sensitivity of populations or organisms to climate may vary within a year, biological systems that currently seem resilient to climatic change may suffer from unprecedented ECEs if the timing of extreme climatic conditions changes. In addition, temporal autocorrelation between ECEs may begin to change (e.g. Hurrell & van Loon 1997). If extreme conditions occur in closer succession, the overall biological impact of these events may become more severe, as there will be less time for systems to recover between events (Schwager, Johst & Jeltsch 2006; Dreesen *et al.* 2014).

The presence of threshold-like biological responses has already been documented in some studies. For example, *Petrochelidon pyrrhonota* (cliff swallow) showed little response to cold spells lasting 2–3 days, but experienced high mortality when cold weather lasted 4 days or more (Brown & Brown 1998). Similarly, Bragazza (2008) reported that *Sphagnum* hummocks that experienced precipitation and temperature conditions past a threshold value displayed irreversible desiccation.

However, threshold-like responses to climate will not be present in all systems. For example, *Eubalaena australis* (Southern right whale) calving output increased linearly with positive sea surface temperature anomalies (Leaper *et al.* 2006). Under our new definition, the occurrence of rare climate in these systems (e.g. high sea surface temperature anomalies) would not be considered an ECE. In most of the literature, however, the presence of a biological threshold has not been explicitly tested. In these cases, our existing biological knowledge can be used to predict where a threshold response may occur. For example, Altwegg *et al.* (2006) focussed on winter snow cover, as snow was known to inhibit the hunting ability of *Tyto alba* (barn owl). In addition, thermal performance curves can be used to predict the vulnerability of organisms to changes in temperature (Huey *et al.* 2012; Deville *et al.*

2014). However, when testing for threshold responses, it is important to realize that observing a threshold-like change over *time* (e.g. Harrison 2000; Tryjanowski, Sparks & Profus 2009) does not necessarily mean the biological response to *climate* will be threshold-like, as other ecological drivers and population state transitions may explain these temporal trends. The applicability and effectiveness of our proposed definition will depend on the frequency with which threshold-like responses to climate occur in natural systems.

CHOOSING A DEFINITION

Regardless of the definition chosen, being explicit about this choice is a necessary first step to increase the possibility for comparison and synthesis within the ECE literature. The choice of definition will depend on the research question (e.g. whether one is interested in physiological, demographic, population or community responses; whether one is interested in rare climate or climate that produces a biological impact), and we thus do not advocate the use of a universal definition. However, we do feel that the dominant focus on climatological definitions within the ECE literature has placed a disproportionate focus on rare, rather than biologically meaningful, climatic conditions.

Possibly, the most useful approach would be for climatological and biological definitions to be used in collaboration, though differently to that considered in hybrid definitions (Jentsch, Kreyling & Beierkuhnlein 2007; Smith 2011a). Specifically, a biological approach may be used to select conditions that generally produce an 'extreme' response, which can then be used to select an informed cut-off point for climatological predictive work. This combination of approaches allows studies to undertake large scale, comparative or predictive work, for which climatological definitions are best suited, without requiring an *a priori* chosen arbitrary cut-off point. Whether such a two-step approach will be feasible will depend largely on how strongly context-dependent the biological impact of rare weather will generally be.

CLIMATIC VARIABILITY AND EXTREME CLIMATIC EVENTS

It has been suggested that climate at the tails of the climate distribution is relatively more sensitive to changes in interannual climatic variability than the climate mean (Katz & Brown 1992). Consequently, the literature tends to associate changes in ECEs mostly with changing climatic variability. However, changes in the occurrence of extreme climatic conditions will ultimately be driven by a combination of changes in the mean, variability and skew of the climate distribution (Fig. 2; Coumou & Rahmstorf 2012). For instance, the European heatwave of 2003 was attributed to an increase in both the mean and variability of summer temperatures (Schär *et al.* 2004).

By focussing predominantly on climate variability, we may risk misinterpreting future changes in ECEs. A rise in the climate mean will result in more frequent extremes in the upper tail but less in the lower tail (e.g. more hot extremes and less cold extremes; Fig. 2a), whereas greater climatic variability will increase the frequency of both high and low extremes (e.g. more hot and cold extremes; Fig. 2b). Even if climatic extremes may be more sensitive to changes in variability, the magnitude of future change in climatic means may outweigh that in variability, so that changes in the mean ultimately play a greater role in altering the occurrence of ECEs (Katz & Brown 1992). This is all the more relevant as recent modelling suggests that increased climate variability under future climate scenarios may be geographically inconstant and less prominent than previously predicted (Huntingford *et al.* 2013).

Ideally, we should consider any change in ECEs to be the product of changes in a variety of characteristics of the climatic distribution. ECEs and climate variability, although often considered interrelated, should be viewed as two distinct concepts, with changing climatic variability only one potential cause of changing patterns of ECEs. This is all the more appropriate when considering that the impacts of ECEs and climate variability on population dynamics will be distinctly different. While ECEs can have a profound effect on the mean arithmetic population growth rate, due to their nonlinear impact, interannual climatic variability can affect the geometric long-term growth rate even when the arithmetic growth rate is unaffected (Boyce, Haridas & Lee 2006). There can be interactive effects between climate mean and variability when populations display a strong nonlinear response to climate, a possible case of ECEs (Lawson *et al.* 2015). This complex and interrelated nature of climatic variability, climate means and ECEs makes it difficult to distinguish any one of these factors as most important under a changing climate; ultimately, they should be considered in conjunction (Lawson *et al.* 2015). Although it is important to focus on ECEs independently to understand their distinct ecological and evolutionary impacts (Section 'Long-term responses to extreme climatic events'), this should not preclude studies that assess and model the impacts of changes in the entire climate distribution, which is currently rare.

Long-term responses to extreme climatic events

Previous ECE research has mostly involved short-term, descriptive studies with an emphasis on the impacts on individual survival and reproductive output (e.g. Garrott *et al.* 2003; Leaper *et al.* 2006; van de Pol *et al.* 2010b). However, these studies tend to focus on a limited number of biological questions, and there is a growing need to move away from descriptive studies to further expand our understanding of ECEs. There are few studies investigating the long-term adaptive responses and lasting

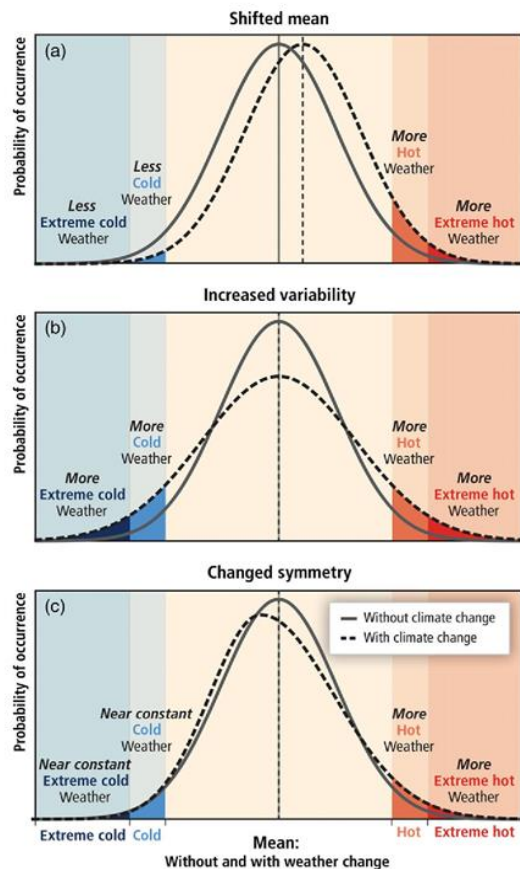


Fig. 2. Effect of changes in the mean, variability and skew of the global climate on the frequency of rare climatic conditions (IPCC 2012).

consequences of ECEs. Below, we discuss the possible effects of ECEs on the selective landscape and phenotypic plasticity of organisms, with particular emphasis on how effects of ECEs might be different from the effects of changes in other aspects of the climate.

RESPONSES TO SELECTION

The consequences of ECEs on the selective landscape are still poorly understood. ECEs may affect all phenotypes equally, but may also impact one phenotype more strongly than another, thereby acting as an intense selection episode (Brown & Brown 1998; Chevin, Collins & Lefèvre 2013), an example of rapid episodic peak movement within the selective landscape (Arnold, Pfender & Jones 2001). In *P. pyrrhonota* (cliff swallow), severe cold weather selected for larger bodied individuals that were able to survive the extreme conditions and reproduce (Brown & Brown 1998). *Riparia riparia* (sand martin) in

Scotland experienced a sharp population decline in response to drought (Jones 1987), which was associated with strong selection for smaller keel length (Jones 1987; Bryant & Jones 1995). More recently, both Jenouvrier, Peron & Weimerskirch (in press) and Lescroël *et al.* (2014) found that extreme sea ice conditions strongly favoured 'high-quality' individuals in Antarctic bird populations, with 'poor-quality' individuals failing to breed or skipping breeding all together. It has been argued that selective pressures imposed by ECEs may be a major driver of evolutionary change over longer time scales, even outweighing the importance of selection acting throughout non-extreme periods (Gutschick & BassiriRad 2003). Yet the vast majority of studies have not considered whether ECEs affect phenotypes differently.

When selective pressure is particularly strong, ECEs may impose 'truncation selection', where the impact of the ECE changes abruptly across phenotypes so that all individuals below a threshold are negatively impacted and all those above this threshold are not. For example, flooding events caused complete reproductive failure in all *H. ostralegus* pairs showing a preference for low nest elevation, but had no effect on the reproductive success of birds nesting above the flooding level (van de Pol *et al.* 2010b). Truncation selection is more efficient at shifting the population phenotype than linear selection as fewer individual deaths or reproductive failures are required to achieve the same change in mean phenotype (Kimura & Crow 1978; Crow & Kimura 1979), although such strong selection may increase a population's extinction risk (Vincenzi, De Leo & Bellingeri 2012). ECEs may be more likely to produce truncation selection in short-lived or rarely reproducing organisms, as a single ECE may have a disproportionately large effect on lifetime fitness in species with few lifetime reproductive opportunities. Although the concept of truncation selection was established almost 40 years ago (Kimura & Crow 1978), there is still little empirical evidence of truncation selection in wild populations. ECEs may provide excellent conditions to study truncation selection in the wild (Moreno & Møller 2011).

In many systems, the frequency of ECEs is rare in relation to the generation time of the organism. In these cases, the average phenotype of the population will shift back to its original state, where individuals that cope better with average, rather than extreme, conditions are favoured. For example, the keel length of *R. riparia* decreased significantly during drought years, but increased in subsequent generations (Bryant & Jones 1995). In addition, if individuals are exposed to ECEs in opposing directions, the selective pressure from one ECE may be offset by the next. In *Geospiza fortis* (ground finch), strong drought conditions selected for individuals with greater mass (Price *et al.* 1984), but extreme wet weather selected for smaller birds (Gibbs & Grant 1987). Therefore, we need to look beyond the selective pressure imposed by a single ECE and attempt

to understand how the frequency of repeated ECEs will change the long-term selective landscape, both during the lifetime of organisms as well as across generations. Potential episodic peak shifts driven by ECEs may threaten population viability due to increased genetic load (Arnold, Pfrender & Jones 2001), and it is important to understand the potential for a population to cope with multiple changes in the peak of the selective landscape. This echoes recent calls in the literature for long-term perspectives of the selection landscapes imposed by ECEs to understand their strongly fluctuating nature (Cockburn, Osmond & Double 2008; van de Pol *et al.* 2010a).

PHENOTYPIC PLASTICITY

Phenotypic plasticity has been posited as a rapid and effective mechanism through which organisms can cope with climate change (Chevin, Lande & Mace 2010; Chevin, Collins & Lefèvre 2013). Plasticity may provide a short-term 'buffer' that will allow individuals to cope with a changing climate, while slower evolutionary processes are able to act (Ghalambor *et al.* 2007; Chevin, Lande & Mace 2010). In fact, it has been suggested that plasticity has been more prevalent in responses to contemporary climate change than microevolution (Gienapp *et al.* 2008). Yet the role of plasticity in response to ECEs is still poorly understood.

For plasticity to be effective, an individual must possess a reliable cue that can allow it to accurately predict the future environment, allowing a phenotypic adjustment to meet the new phenotypic optimum (DeWitt, Sih & Wilson 1998; Tufto 2000). In situations of high uncertainty, where future conditions cannot be reliably predicted, plasticity can become maladaptive as an individual will tend to 'overshoot' the optimal phenotype (Tufto 2000; Reed *et al.* 2010).

Generally, ECEs are considered unpredictable (e.g. Tryjanowski, Sparks & Profus 2009; Chiu *et al.* 2013), suggesting that plasticity will not provide an adaptive advantage to cope with such events (Lloret *et al.* 2012). In some studies, this unpredictability is associated with the lack of a reliable cue. For example, the relationship between climatic conditions and ECEs may vary unpredictably, so that conditions that produce an ECE in one year may not do so in the next (Burger 1982; also see Section 'Defining an 'extreme climatic event)'). There is also a tendency to class ECEs as unpredictable simply because they are rare (e.g. Burger 1982; Chiu *et al.* 2013); however, the rarity and predictability of an event are fundamentally different. An ECE may exhibit reliable cues but simply be too rare for the development of a plastic response to be advantageous. As ECEs become more frequent, however, plasticity may become more advantageous and may be more strongly selected for. Understanding whether ECEs are in fact unpredictable, as is often assumed, or are simply rare will have important implica-

tions for predicting the response of organisms to ECEs in future climates.

Even if organisms possess a reliable cue for ECEs, the efficacy of plasticity as a response may be limited by the lag-time between when an ECE is detected and when the plastic response can occur (Padilla & Adolph 1996; Valladares, Gianoli & Gómez 2007). Plastic responses to ECEs may be most common in labile traits where plasticity exhibits a small lag-time, such as behaviour or physiology, and occur less often in more inflexible traits, such as morphometry (DeWitt, Sih & Wilson 1998). Furthermore, plasticity is likely to be less effective in response to ECEs triggered by rapid or abrupt changes in climate (e.g. cold snaps, flash floods), as the time between the cue and onset of conditions may be too short for response.

Species may overcome the uncertainty associated with ECEs through the use of learning; a special case of behavioural plasticity that allows individuals to respond to novel stimuli (Dukas 2013). Learning may allow individuals that have survived previous non-lethal ECEs to adjust their behaviour to cope with similar future conditions. However, for learning to be effective, ECEs must occur frequently enough that an individual is likely to experience multiple events in a lifetime, most likely in long-lived species. Furthermore, plasticity may be more crucial for long-lived species to respond to ECEs, as the rate of micro-evolution in these species will be slow (Munday *et al.* 2013). So far, reported examples of learning in response to ECEs have been inconclusive. *Rynchops niger* (black skimmer) did not alter their colony location in response to flooding (Burger 1982), whereas *Larus atricilla* (laughing gull) and *Platalea leucorodia* (Eurasian spoon-bill) moved their colony location after flooding, but returned to their original sites the following year (Burger & Shisler 1980; van de Pol *et al.* 2012).

However, while phenotypic plasticity could potentially play a role in ECE adaptation, the evolution of phenotypic plasticity within a population will be influenced by its selective past. It has been suggested that a major change in the environment like an ECE should prompt an increase in the occurrence of phenotypic plasticity (Lande 2009). Yet, other work has shown that populations that evolve under fluctuating selection can exhibit less phenotypic plasticity and lower genetic variation (Hallsson & Björklund 2012). The impact of the selective past on the occurrence of plasticity may depend on the predictability of these past changes in environmental conditions and selection (Hallsson & Björklund 2012).

The occurrence of plasticity and its effectiveness in response to ECEs is still poorly understood, and rigorous tests of the occurrence of phenotypic plasticity as a response to ECEs are still lacking. The role played by plasticity in response to ECEs may be quite different to what we know about similar responses to changes in climatic means, yet to test the effects of ECEs independently, it is important that we are able to clearly define

those conditions that we consider to be extreme (Section 'Defining an 'extreme climatic event'').

FUTURE QUESTIONS

In the previous sections, we have detailed areas that could benefit from greater discussion within ECE research. Box 2 attempts to synthesize the previous sections into a number of specific research questions that can be used to go beyond descriptive studies and tackle the issues needed most to advance research into ECEs.

To better understand biological definitions of ECEs (see Section 'Defining an 'extreme climatic event''), we first need to understand how often and under what circumstances climate may trigger 'biologically relevant thresholds'. Questions 1 to 3 aim to understand what conditions will trigger these thresholds, including an exploration of context dependence, and how ECEs may change as these conditions are altered. Questions 4 through 6 aim to investigate the occurrence and effectiveness of phenotypic plasticity as a response to ECEs, while questions 7 to 9 focus on the impacts of ECEs on the selective landscape. Finally, in question 10, we consider the possible impacts of ECEs at the population level, as discussed in Section 'Defining an 'extreme climatic event'').

Approaches for investigating extreme climatic events

Currently, 60% of ECE studies in the literature encompass only one extreme event (Fig. 1b), possibly due to the inherent unpredictability and rarity of many ECEs and the short duration of many studies (Weatherhead 1986). Previous research has often been 'opportunistic' in nature, with studies initiated in response to an ECE or when an ECE occurs during a pre-established study (Jentsch, Kreyling & Beierkuhnlein 2007; Smith 2011a). The unplanned nature of such studies means they are typically anecdotal, as there is limited information on the study system before the ECE occurred to allow for effective comparison (Gutschick & BassiriRad 2003; Smith 2011a). Furthermore, studies on single ECEs give us little knowledge on the long-term consequences of changes in ECEs. As such, there is a need for a greater focus on multi-event ECE studies, particularly on non-plant systems which have received less focus within the literature (Fig. 1b).

Extrapolating from a single event to draw conclusions on multiple events will overlook the possibility for ECEs to alter the phenotypic composition of the population and fails to consider the impacts of plasticity or learning, which may become more important as ECEs become more frequent (Section 'Long-term responses to extreme climatic events'). Furthermore, the occurrence of ECEs may often be context-dependent (Section 'Defining an 'extreme climatic event''). Therefore, ECE research would benefit greatly from studies that explicitly encompass multiple ECEs.

Box 2. Key questions for future research

Defining ECEs

1. How often do rare climatic events trigger 'biologically relevant thresholds' and can this be used to better inform climatological definitions?
2. How does climate interact with other abiotic and biotic factors to trigger biologically relevant thresholds?
3. How will the frequency, magnitude and timing of ECEs change under future climates?

Individual level responses: phenotypic plasticity

4. Do ECEs exhibit reliable cues for phenotypically plastic responses to act upon?
5. Can learning provide a mechanism for dealing with ECEs, particularly in long-lived species?
6. Could the abrupt nature of certain ECEs preclude the effectiveness of a phenotypically plastic response?

Population level responses: selection, growth rate and extinction risk

7. How often do ECEs affect the selective landscape?
8. What type of selective landscape do ECEs impose (e.g. truncation)?
9. Are ECEs major drivers of evolutionary change outweighing the importance of selection acting throughout non-extreme periods, as suggested by Gutschick & BassiriRad (2003)?
10. How will changes in the frequency, magnitude or timing of ECEs affect the extinction risk of populations?

The inherent rarity and unpredictability of ECEs makes it difficult to implement multi-event studies, but there are a number of strategies that can be undertaken. Possible options include the use of ecological experiments (e.g. Jentsch, Kreyling & Beierkuhnlein 2007), theoretical modelling approaches (e.g. Mooij *et al.* 2002) or observational field studies (e.g. Altwegg *et al.* 2006). Each of these approaches has strengths and limitations; however, if used in conjunction, they can provide powerful tools to enhance our knowledge on ECEs.

Experimental studies are generally restricted to work on plants or animals with limited mobility (Jentsch, Kreyling & Beierkuhnlein 2007), but are ideal for understanding the mechanisms through which climate may impact biological systems (Beier *et al.* 2012). Experimental studies allow for more precise manipulation of environmental conditions and permit us to test the impacts of multiple future climate scenarios by manipulating the frequency, magnitude or timing of climatic conditions. However, experiments may underestimate the biological response, as

it is difficult to replicate the context dependence of natural systems in artificially controlled conditions (Wolkovich *et al.* 2012).

Theoretical modelling can also allow us to test the impacts of various future climate scenarios by altering the characteristics of ECEs (e.g. Mooij *et al.* 2002; Heijmans *et al.* 2013). Modelling approaches are not practically limited by the nature of the study system, but will require knowledge of the biological system beforehand. This requires the input of data from experimental or observational studies. Validation of theoretical models can often be difficult as data may be scarce or modelled conditions may be yet to occur (Araújo *et al.* 2005; van de Pol *et al.* 2010c). Furthermore, when modelling future climatic conditions, accurate regional climatic models will be required as commonly used global climate models fail to effectively predict patterns of ECEs at a regional scale (Marengo *et al.* 2009). Moreover, projecting what will happen at the tails of climate distributions is methodologically challenging (AghaKouchak *et al.* 2013).

Long-term observational field studies may provide the most accurate account of biological responses to multiple ECEs (Wolkovich *et al.* 2012). Yet, practically, not all populations will be appropriate for such studies, as some populations may experience ECEs too infrequently. In addition, long-term field studies require a prolonged investment of both time and resources. One means of overcoming these issues is through the use of historical long-term data sets, where multiple ECEs may have already been documented (e.g. dendrochronology). Another approach may be to use 'model' study populations that experience ECEs frequently enough to make a long-term study worthwhile. Examples may include coastal populations subject to regular storm events (e.g. Frederiksen *et al.* 2008; van de Pol *et al.* 2010b), populations that experience frequent fires (e.g. Westerling *et al.* 2006) or riparian populations that face regular flooding (e.g. Tryjanowski, Sparks & Profus 2009). Yet this enforces a limitation on the questions and variables we can investigate.

Space for time substitution may be used as a surrogate for long-term studies, where the impact of an ECE is measured across multiple populations, rather than within the same population over time. However, such short-term studies will provide less information on the cumulative impacts of ECEs within a single population. Furthermore, their effectiveness depends entirely on the extent to which we can extrapolate spatial environmental gradients to predict future environmental changes over time, of which we still know very little (Phillimore *et al.* 2010). The context-dependent nature of ECEs and local adaptation may limit our ability to compare the responses of different populations.

An example illustrating the insight gained from combining different approaches is the study of *H. ostralegus*. Camphuysen *et al.* (1996) conducted a longitudinal study on the impact of extreme winter temperatures on adult

mortality of Dutch birds. Their results suggested that winter severity and food abundance had an interactive effect on mortality, yet the relatively short time period ('only 25 years') and limited geographic range made it difficult to apply this conclusion more generally. Future field studies in the region were able to verify this result in both the Netherlands and Germany (van de Pol *et al.* 2010c; Schwemmer *et al.* 2014), but work in the United Kingdom, where winters are milder, showed no such interaction (Atkinson *et al.* 2000). Information on the behaviour and energetics of the shorebirds was used to generate a model which helped explain these differences, concluding that an interactive effect would be likely in the United Kingdom if winter severity was to increase (Stillman *et al.* 2001). Ultimately, the use of multiple long-term studies combined with predictive modelling provided detailed information on the relationship between *H. ostralegus* mortality, winter severity and food abundance over a wide geographic scale.

In another example, results from experimental studies investigating the impacts of global change on *Sphagnum* spp. (Weltzin *et al.* 2000; Gunnarsson, Granberg & Nilsson 2004) were compiled and utilized to design a model that investigated the response of peat bog ecosystems to climate change (Heijmans *et al.* 2008). With the information gathered from the experimental work, this model was able to predict the impacts of drought and temperature change on the structure of peat bog communities (Heijmans *et al.* 2013). The detailed information gained from experimental studies enhanced the predictive power of the model, improving the quality of the results.

CONCLUSIONS

The goal of ECE research should not only be to understand the direct implications of single ECEs, but also the long-term consequences of changing patterns of ECEs. While many studies have tackled the former goal, the latter has been largely unstudied. Therefore, there is a need for a change in the way we approach ECE research. We have outlined some of the key areas in which we feel improvement is necessary. First, we discussed the importance of selecting an appropriate ECE definition and considered the available biological and climatological definitions within the literature. Next, we considered biological questions that address the long-term implications of ECEs, such as impacts on the selective landscape or phenotypic plasticity. Finally, we contended that a greater use of multi-event studies is essential to understand how biological systems will be impacted by ECEs in future climates, best achieved through a combination of experimental studies, theoretical modelling and observational field studies. It is imperative that those working on ECEs actively critique the definitions used, questions addressed and approaches employed to ensure they are the most effective. We hope this article will stimulate discussion on this topic.

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Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.cq83b> (Bailey & van de Pol 2015).

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Supporting Information

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

Appendix S1. Literature review methodology.

Chapter 2

***climwin*: An R toolbox for climate window analysis**

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RESEARCH ARTICLE

***climwin*: An R Toolbox for Climate Window Analysis**

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Abstract

When studying the impacts of climate change, there is a tendency to select climate data from a small set of arbitrary time periods or climate windows (e.g., spring temperature). However, these arbitrary windows may not encompass the strongest periods of climatic sensitivity and may lead to erroneous biological interpretations. Therefore, there is a need to consider a wider range of climate windows to better predict the impacts of future climate change. We introduce the R package *climwin* that provides a number of methods to test the effect of different climate windows on a chosen response variable and compare these windows to identify potential climate signals. *climwin* extracts the relevant data for each possible climate window and uses this data to fit a statistical model, the structure of which is chosen by the user. Models are then compared using an information criteria approach. This allows users to determine how well each window explains variation in the response variable and compare model support between windows. *climwin* also contains methods to detect type I and II errors, which are often a problem with this type of exploratory analysis. This article presents the statistical framework and technical details behind the *climwin* package and demonstrates the applicability of the method with a number of worked examples.

Introduction

With the growing importance of climate change there are an increasing number of studies seeking to understand the impact of climate on biological systems (e.g., [1–5]). However, in many study systems the impacts of climate are likely to be different at different times of the year (e.g., [4–6]) making it necessary for researchers to subset their climate data to encompass a particular period of interest, here termed the climate window (e.g., spring temperature, winter precipitation). However, this subsetting decision is often made with little *a priori* knowledge on the relationship between climate and the biological response, leading to the arbitrary selection of one, or few, climate windows [7].

The use of a limited number of arbitrarily selected climate windows hinders our ability to make meaningful biological conclusions. If a trait, such as body mass or offspring number,

displays no response to an arbitrary climate window we cannot determine if this is evidence of climatic insensitivity in our response variable or if the choice of climate window is flawed. Even where we detect a relationship between climate and our response, we cannot know whether there may be another point in time at which climate has a much stronger and more biologically meaningful impact. With flawed conclusions there is a potential to overlook key periods of biological importance, leading us to focus limited management and conservation resources in the wrong areas.

To overcome these issues, there is a need to test a greater number of climate windows with fewer *a priori* assumptions. One solution is the use of a sliding window approach [5, 8–11], where one varies (or slides) the start and end time of a climate window to compare multiple possible windows and select a best window (Fig 1). However, as these analyses are often done manually, comparison of a large number of climate windows can be cumbersome and time consuming. Additionally, there is currently no standardised method for testing or comparing climate windows, and we have no knowledge on the performance of sliding window approaches, including the possibility for false positives and false negatives (type I and II errors); precision and bias of parameter estimates and model statistics (e.g., R^2); and how these errors and biases might depend on sample size and climate signal strength. There is a need for a standardised and automated approach that can help streamline these frequently performed analyses and make the testing and comparison of multiple climate windows easy and accessible to the general scientific community. The package *climwin*, built in R, creates a best practice method for this process.

In a previous paper, van de Pol et al. [7] provide a broad introduction to climate window analysis for a general scientific audience, with practical details on how the method can be applied using *climwin*. It proposes a step-wise approach for *climwin* implementation that encourages users to identify all potential competing hypotheses, including different potential climate variables (e.g., rainfall, temperature), climate window types (relative or absolute; see Section 1.2), response functions (e.g., linear, quadratic), and aggregate statistics (e.g., mean or maximum temperature). Each of these hypotheses should then be tested and compared using a climate window analysis, with the intention of identifying those hypotheses that are best supported by the data.

This paper is complementary to van de Pol et al. [7], building on the general introduction to *climwin* by discussing the technical details of the package, both the design of the package code and the statistical reasoning behind the proposed methods. We discuss a number of topics not covered in the previous paper, including the difference between absolute climate windows (e.g., May to June) and relative climate windows (e.g., two preceding months; Section 1.2); and the potential use of multi-model inferencing in climate window analysis (Section 1.4). We expand upon the commonly used sliding window analysis, discussed in van de Pol et al. [7], and propose an alternative method for analysing climate, a weighted window analysis (Section 2); we then consider the mechanisms available to account for errors and biases in both methods (Section 3). Finally, we run through a worked example to demonstrate both methods using a real world dataset (Section 4).

In combination, this paper and van de Pol et al. [7] provide a comprehensive overview of *climwin*; its strengths and weaknesses; and potential future directions for the package. While *climwin* has been designed with climate analysis in mind, the package can be applied to any analysis over a continuum (e.g., time or distance) using climatic or non-climatic predictors. For example, climate window methods like those provided in *climwin* have been used to analyse plant neighbourhood competition [12]. Therefore, we expect *climwin* to have broad applicability both in climate change ecology and more broadly within the scientific community.

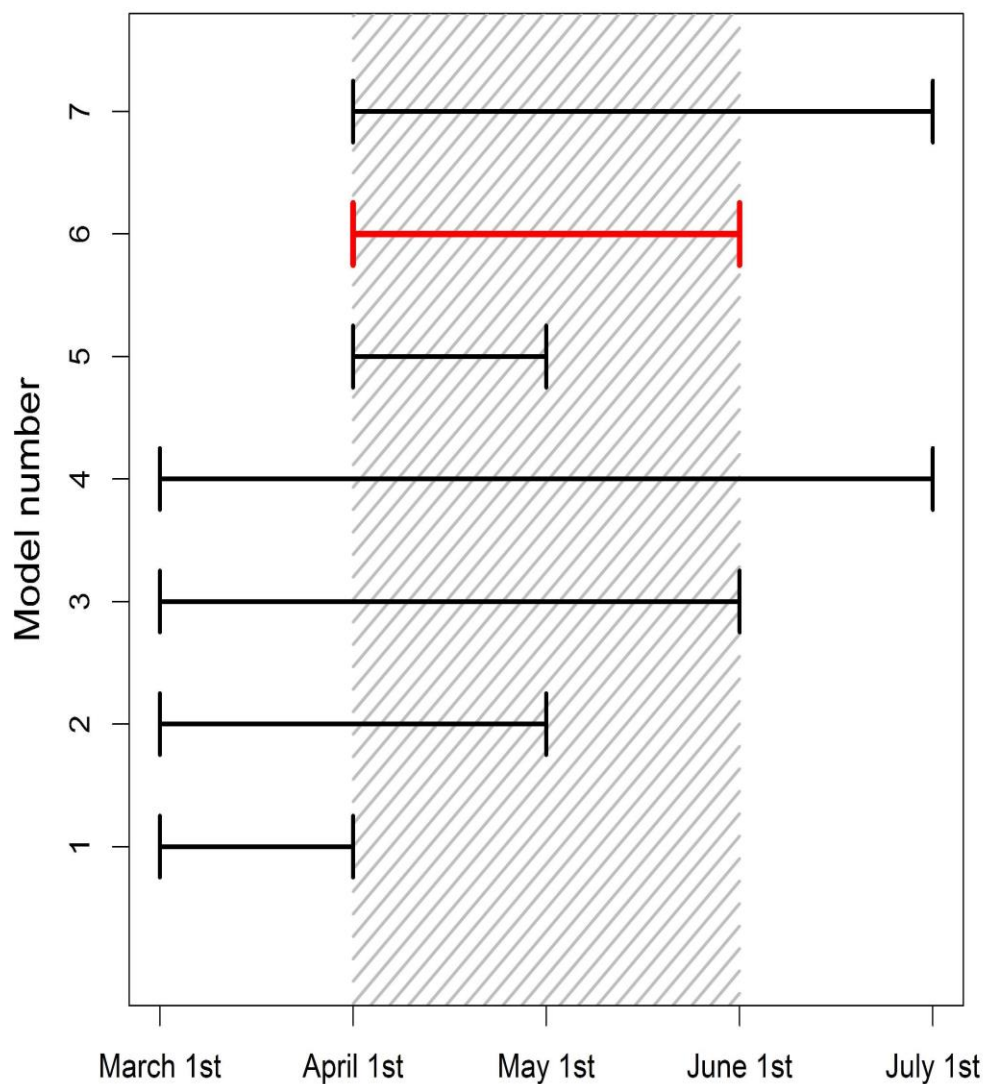


Fig 1. Illustration of a sliding window approach. Shaded region represents a climate signal (April 1st–June 1st), where a climatic predictor has the strongest impact on the biological response. Each line represents a tested climate window. The start and end time of windows is varied until we identify the best window (in red). This figure demonstrates a sliding window analysis conducted at a monthly resolution, but such analyses can use finer scale daily data.

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1 Sliding window analysis

1.1 Introduction

Model selection metrics. Early sliding window analyses used Pearson's correlation coefficient to select among different climate window models, where the best window was considered to be the one with the strongest correlation between the climatic predictor and response (e.g.,

[8–10]). Yet this method only works in simple Gaussian regression models, and there is no possibility to include additional covariates or random effects terms or consider non-linear effects of climate.

Later sliding window studies have used information criteria (IC; [13–15]) as a metric for model selection among competing climate windows (e.g., [5, 11]). An IC-based approach compares all candidate models (i.e. climate windows) and ranks them using a chosen Information Criterion (e.g., Akaike, Bayesian or Deviance Information Criterion; AIC, BIC and DIC respectively). This allows for comparison of any type of multiple regression models, rather than correlation between two variables, and allows users to assess model uncertainty and conduct multi-model inferencing (see Section 1.4). These characteristics make an IC approach more suitable for analysis of climate windows, where it is necessary to compare hundreds or thousands of different models with the aim of determining a best window or group of best windows. An IC approach forms the basis for all climate window comparisons in *climwin*.

Function *slidingwin*. *climwin* provides the function *slidingwin* for sliding window analysis. *slidingwin* requires two separate datasets: one containing climate data (ideally at a daily scale) covering the entire period of interest and one containing information on the response variable, as well as any potential covariates. To properly test the relationship between our biological response and climatic predictor, it is necessary for us to take measurements that have different climatic histories. Ideally, this will involve a combination of temporal and spatial replication, where we measure our response variable over multiple years and/or sites. However, combining these two forms of replication assumes that climatic sensitivity is consistent across time and space, which may not always be the case (e.g., [16]).

A key feature of *climwin* is the ability for users to define a baseline model into which climate data will be added. This versatility allows for the analysis of data with a variety of error distributions (e.g., Gaussian, binomial, Poisson), the inclusion of multiple covariates, the use of mixed effects modelling, and different types of regression models. Currently *climwin* is known to work with base R functions *lm* and *glm* [17], mixed effects model functions from the package *lme4* (*lmer*, *glmer*; [18]), and the cox proportional hazard function from package *survival* (*coxph*; [19]). Technically, any model that returns a log-likelihood or IC value can be integrated into *climwin*; however differences in syntax between different modelling packages have hindered our ability to integrate more modelling functions. We aim to provide a greater number of options for model fitting in future versions.

As highlighted in the introduction, it is possible to vary a broad range of climate window characteristics in *slidingwin* (e.g., temporal resolution of climate data, aggregate statistic, model function). Varying different characteristics of the sliding window analysis allows users to test a variety of climate window hypotheses and help identify potentially novel relationships between climate and the biological response. For example, while we commonly consider mean climate, recent studies have highlighted the potential importance of climatic range [20], rate of climate change [21, 22], and climatic thresholds [23]. However, although it is important to consider a diversity of climate window characteristics in our analyses, changes in many of these characteristics can slightly alter the technical details of the methods used in *climwin*; therefore, we will focus specifically here on the use of mean climate at a daily resolution.

1.2 Relative and absolute climate windows

It is possible that the date of measurement for each record in the response dataset will vary within a sampling group (e.g., year or site). This may be due to constraints on the expression of the response variable (e.g., the date at which offspring size can be measured will depend on birth date) or practical limitations involved in data collection. In cases where the variation in

measurement time is small it is reasonable to assume that all records will be influenced by climatic conditions at the same point in time; however, as variation increases this assumption becomes less realistic.

To address this issue, *climwin* allows for the use of both absolute and relative climate windows [24, 25]. In an absolute climate window, we assume that all records are influenced by climate at the same absolute point in time, allowing us to define windows using calendar dates (e.g., mean March temperature). Absolute windows require the user to provide a reference date, used as the start point for all fitted climate windows. By contrast, a relative climate window assumes that each record will be impacted by climate at different times depending on the time of measurement. Unlike absolute window analysis, a relative window analysis will test the impact of climate x days before the date of measurement.

Absolute climate window analysis is most useful for sampling populations with little temporal variation or data sets where we lack any information on within-group variation in trait expression (e.g., datasets with one aggregate measurement per group; mean body mass of a population). However, relative windows become more appropriate as temporal variation in the data increases, particularly when searching for short-lag climate signals. For example, large variation in moult timing of superb fairy wrens (*Malurus cyaneus*) makes the use of an absolute climate window inappropriate as many individuals will already have completed moulting before the start point of the absolute climate window. In this case, a relative climate window (e.g., the 25 days before moulting) is much more useful [25]. It should be noted however, that the output of relative windows can often be more difficult to interpret at the population level as individuals will vary in their climatic sensitivity. Thus the choice of an absolute or relative window involves a trade-off between biological realism and ease of interpretation.

Within-group centring. As an absolute window approach assumes no variation in response within a group it can usually only explain between-group variation in the response variable. In comparison, a relative window approach can explain both within- and between-group variation in the response, potentially improving the explanatory power of any fitted climate window model. In certain cases, users may wish to disentangle these within- and between-group climate effects, as they may not necessarily be of equal interest or of the same magnitude. For example, spawning dates of frogs showed a weaker within population response to temperature than that observed across the whole of Britain [26]. *climwin* can distinguish both effects by separating climate variables using a technique called within-group centring [27] with the parameter *centre*, such that both the within- and between-group climatic sensitivity are estimated for each given time window. Whether one is interested in differentiating between these two types of variation will inform the choice of window type.

1.3 How it works

Linking climate and biological data. The first step of the *slidingwin* function involves the linking and manipulation of the date information provided in the climate and biological response data frames. As R cannot automatically read date data, *climwin* converts this data into an R date format using the function `as.Date`. Date information must be provided in a standard dd/mm/yyyy format to ensure this process is successful. At this point, we also take into account whether an absolute or relative window is used. Where an absolute window is chosen, the date values of all biological records are changed to the reference day and month provided by the user, with year remaining unchanged.

Using this new date information, *slidingwin* creates a data matrix containing the relevant climate data for each record in the response data frame. For each biological record we extract the climate data needed to fit all potential climate windows (e.g., climate up to 365 days

Table 1. Example of a climate matrix built using *slidingwin*.

RecordID	Measurement date (x)	Climate on day x	Climate on day x - 1	Climate on day x - 2	...	Climate on day x - n
1	01/01/2015	5.2	6.0	2.4	...	23.1
2	02/02/2015	4.8	5.2	6.0	...	22.0
3	21/01/2015	4.5	2.4	7.5	...	23.9

Climate data is stored for each day before the biological data was collected. Data will be stored up until day $x-n$, where n is set by the user with the parameter *range*.

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before measurement; Table 1). The amount of climate data stored in this matrix will depend on the minimum and maximum number of days considered in the analysis, determined by the *range* parameter.

Model fitting. With a completed matrix we now possess all the necessary information to test different climate windows. *slidingwin* uses nested for-loops to vary the start and end time of climate windows. Where start and end time are acceptable (i.e. start time occurs before end time) *slidingwin* will subset the climate matrix to include only climate data which corresponds to the tested window. We use this data subset to calculate the aggregate statistic (e.g., mean, max, slope), set using the *stat* parameter.

```
R> apply(climateMatrix[, windowstart:windowend], 1, FUN = stat)
```

Where *windowstart* and *windowend* refer to the columns in the climate matrix from which climate data is extracted. The user can decide to test a linear effect of climate, or use more complex model structures (e.g., quadratic, logarithmic, inverse). The function used to test climate is determined by the user with the *func* parameter. Before the for-loops begin, we update the baseline model structure to be consistent with the level of *func*, using a dummy climate variable. Carrying out this structure update before entering the for-loops helps to reduce computational time.

```
R> func <- "quad"
R> baseline <- glmer(Response ~ 1 + (1|ID), data = BiolData,
  family = poisson)
R> BiolData$climate <- rep(1, times = nrow(BiolData))
R> baseline <- update(baseline, . ~ . + climate + I(climate^2),
  data = BiolData)
```

Once inside the for-loops, we can replace the dummy climate data with the climate data extracted from the climate matrix. Using the *update* function we then refit our model.

Information criterion. Once we have updated our model to replace the dummy climate data we can extract a sample size corrected measure of AIC (AICc), using the function *AICc* from the package *MuMIn* [28]. However, AICc does not tell us whether a fitted climate window improves upon the baseline model (i.e. a model containing no climate). Therefore, we subtract the model AICc from the AICc value of the baseline model. This creates a metric ($\Delta AICc$) that can be used to both compare individual climate windows to one another and determine how well climate in any given window improves upon the explanatory power of the baseline model. Currently all *climwin* functions use AICc as their information criterion; however, there is potential for other criteria to be used in the future.

Output. *slidingwin* returns three distinct objects. Firstly, *slidingwin* will return a data frame containing information on the entire model set reflecting all fitted climate windows. This data is sorted by $\Delta AICc$, so that the best model (i.e. smallest $\Delta AICc$ value) is listed

at the top. With this data frame, the function `plotdelta` can be used to produce a heat map representing the landscape of $\Delta AICc$ values for all fitted climate windows (see Section 4). By examining the $\Delta AICc$ landscape the user can determine whether multiple peaks of climatic sensitivity may be present in the data. Additionally, `slidingwin` returns the best model (i.e. the model with the lowest value of $\Delta AICc$) as well as the climate vector used to fit this best model.

1.4 Multi-model inferencing

Until this point we have only discussed extracting a single best model from our `slidingwin` analysis; however, we must be aware that there will be uncertainty in the estimation of the best model. An IC approach provides well established methods to deal with this uncertainty, using Akaike model weights (w_i ; the probability that model i is in fact the best model within the model set; [15]). In practice, we often have little certainty that the model with the lowest $\Delta AICc$ is in fact the best model, as a number of top models can have very similar values of w_i . This is particularly likely in climate window analysis as climate data will often be strongly auto-correlated. Our worked examples illustrate that the top models can have very similar values of both $\Delta AICc$ and w_i (see Section 4). Is it reasonable, therefore, to extract a single best window from a sliding window analysis?

Ultimately, this will depend on one's reason for using *climwin*. Although we often discuss climate as the key point of interest, in some cases users may be more interested in simply accounting for the effect of climate on their response variable, without much concern for the exact nature of the climatic signal. In such a case, it makes sense to extract and use the best climate window as this is, by definition, the climate window that can best explain variation in the response variable.

In other cases, we may be more interested in accurately calculating the timing of a climate signal and/or the relationship between climate and our response. In these scenarios, it makes much less sense to pick a single window as the difference in w_i between the top windows is likely to be small. As an alternative we can take a group of models that make up a cumulative sum of w_i . For example, we may group all those models that include the top 95% of w_i . With such a subset we can be 95% confident that the best model is located within our new model set. This model set is often called a 'confidence set' [15]. We can then report values calculated from this subset of top models using multi-model inferencing.

Measuring the percentage of windows included within a confidence set (C) can help users determine confidence in a given climate signal. If the models within the set make up a small percentage of the total models tested (C is low; e.g., Fig 2a) we can be much more confident that we have observed a real climate signal; however when no climate signal occurs, the confidence set is likely to be much larger (C is high; e.g., Fig 2b). *climwin* includes the plotting function `plotweights` that visualises different confidence sets for a sliding window analysis and calculates the percentage of models within the 95% confidence set (by default `plotweights` uses the 95% confidence set although users can adjust this cut-off if desired).

When we are interested in estimating the timing of a climate window, it may be useful to determine a median start and end time for all windows within the confidence set. This can be achieved using the function `medwin`. Additionally, the function `plotwin` can generate box plots illustrating the variation in start and end times within the 95% confidence set. These median values allow users to account for model uncertainty when estimating climate window timing. Similarly, when a user is interested in estimating the relationship between climate and the biological response we can draw information from a subset of potential climate windows using model averaging [15]. A model averaged parameter estimate is simply the sum of

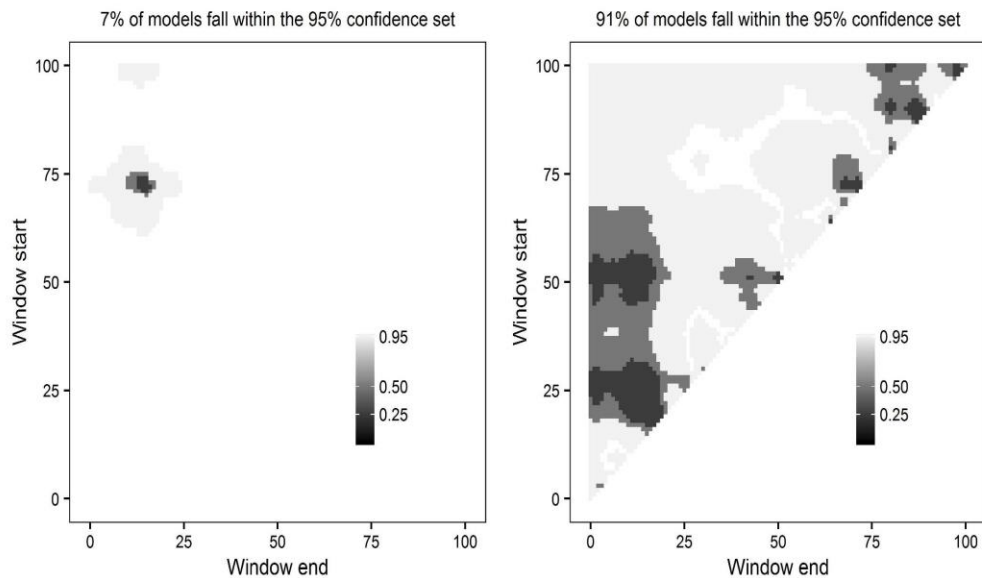


Fig 2. Heat-map of 95%, 50% and 25% confidence sets for *slidingwin* analysis. Where a strong climate signal occurs, models within the confidence sets make up a small percentage of total models (a; 7%). Where there is no climate signal the confidence set is much larger (b; 91%). A point with window start of 100 and window end of 50 represents a climate window fitted using mean climate 50–100 days before measurement date. Figures generated using *plotweights*.

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parameter estimates weighted by w_i . With such model averaging we can determine the average relationship between climate and our response variable within the confidence set. Users can conduct model averaging using the parameter estimates and model weight values presented in the *slidingwin* output.

Multi-model inferencing is fairly straight forward for datasets with a clear climate signal, where the value of C is small, yet this will not always be the case. Large values of C may occur when multiple climate signals are present in the data or when the climate signal is weak (i.e. low R^2), exacerbated by low sample size (Fig 3). Both the median window location and model averaged parameter estimates are less informative in situations where C is large as the 95% confidence set may include poor models with spurious parameter estimates [29]. Where multiple peaks are present it can be reasonable for users to adjust the *range* parameter within their *slidingwin* analysis to approach each climate signal separately. However, when a large value of C is caused by a weak signal model averaging is not advisable.

2 Weighted window analysis

2.1 Introduction

When testing climate windows using mean climate one effectively fits a weight function to the climate data. Using a sliding window approach, we assume that all points between the start and end time of a climate window influence the biological response equally (i.e. a uniform weight distribution with sum of 1). Outside the window, climate is assumed to have no influence on the response (i.e. a uniform distribution with sum of 0; Fig 4a). As we group time into discrete units (i.e. days, weeks, months), assuming a uniform distribution leaves us with a finite number of potential climate windows to test, allowing us to undertake a brute-force approach

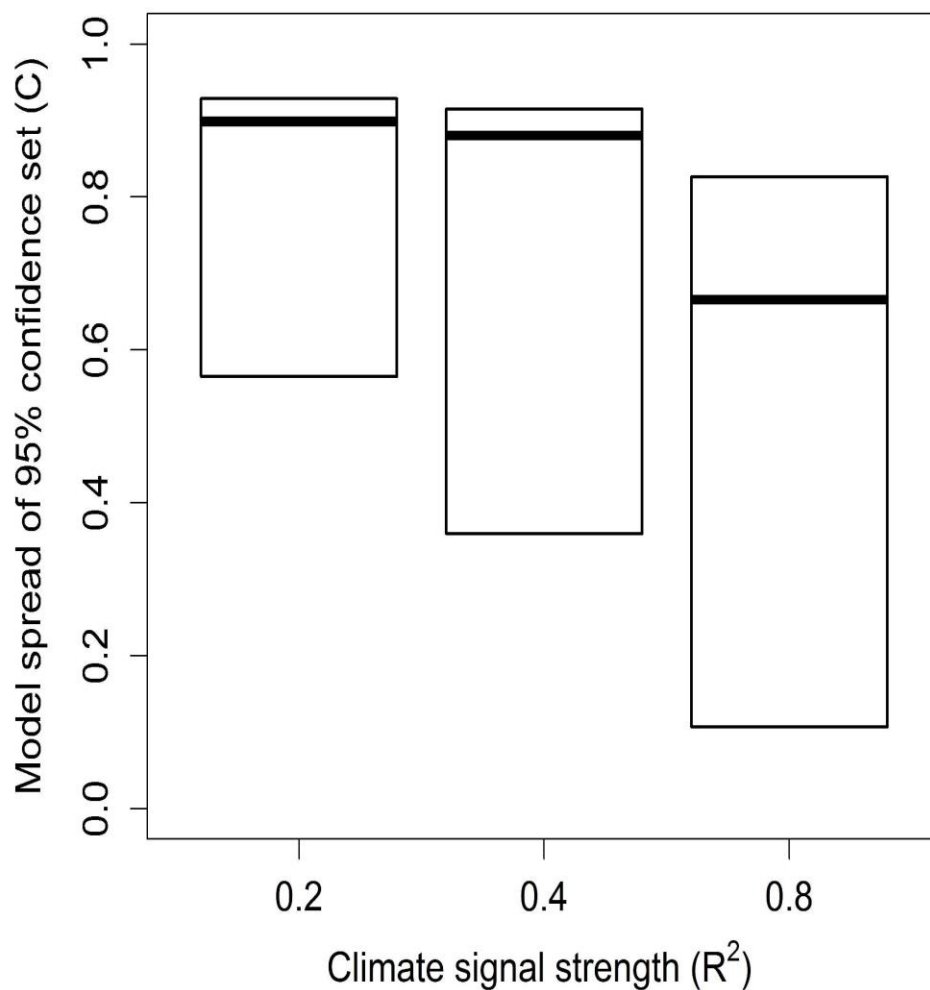


Fig 3. Relationship between the percentage of models in the 95% confidence set and climate signal strength. Percentage of models in the 95% confidence set (C) are shown for a very strong ($R^2 = 0.8$), strong ($R^2 = 0.4$), and moderate climate signal ($R^2 = 0.2$). Boxes represent median and inter-quartile range. Data from 2,000 simulated datasets, see Section 3 for methods.

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for climate window analysis, where we systematically test all possible combinations of start and end time sequentially.

Realistically however, the assumption that all points within a time window contribute equally to a climate signal may not be true. The importance of climate will likely change gradually, not abruptly, over time. As an alternative, one can determine a weighted climate mean using a single fitted weight distribution, allowing each climate record to take any weight value between 1 and 0. This allows for more biologically realistic relationships between climate and the biological response. We call this method a 'weighted window approach'.

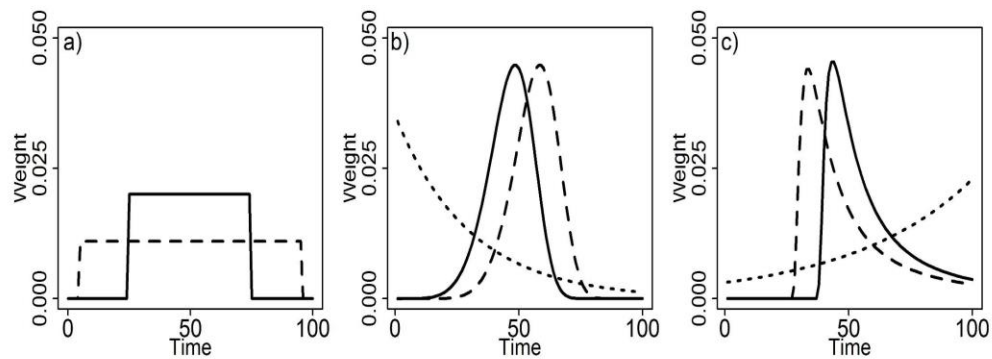


Fig 4. Examples of weight distributions generated with a) uniform, b) Weibull, and c) Generalised Extreme Value probability distribution functions.

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climwin includes the function `weightwin`, based on the methods outlined in van de Pol and Cockburn [25], which allows for the calculation of weighted climate means using more complex weight distributions fitted using three parameters: scale, shape and location. The location parameter allows users to adjust where the peak of the distribution sits, similar to a sliding window approach (e.g., Fig 4b solid and dashed lines). Unlike a sliding window analysis however, the scale and shape parameters allow for users to also adjust the width (duration of window) and shape (e.g., exponential decay or bell-shaped) of the distribution respectively. These three parameters are optimised to achieve the lowest possible value of ΔAIC_c .

As the type of data used is the same, users can apply both the `slidingwin` and `weightwin` function to the same set of data with no changes required. This allows these two approaches to be used in complement to one another and directly compared (section 2.4).

2.2 Weight distribution

In principle, any type of probability distribution function can be used to model a weight distribution. So far two probability distribution functions are implemented in `weightwin` that specifically reflect aspects of weight distributions that we think are biologically relevant. The Weibull function is described by the three parameters shape, scale and location and allows for a wide range of weight distributions (Fig 4b). Moreover, for specific values of shape and location the Weibull weight function reduces to an exponential distribution, producing a weight distribution that reflects gradual decay/fading memory effects (Fig 4b; [25]).

The second function is the Generalized Extreme Value (GEV) probability distribution function, which allows for even greater flexibility as it includes functions from the Frechet, Gumbel, and reverse Weibull families (Fig 4c). The GEV function also has a shape, scale and location parameter but, in contrast to the Weibull, includes left-skewed, right-skewed, as well as fairly non-skewed functions, which allows for the comparison of even more refined competing hypotheses. In practice, the GEV function can be harder to fit, as it is more likely to get stuck on local optima during convergence due to the asymptotic nature of the shape parameter around the value zero [25].

Importantly, both the Weibull and GEV probability distribution functions enforce smoothing on the weight distribution. This is of particular importance when analysing climate data, as data is likely to show strong auto-correlation. Furthermore, by imposing smoothing the weight

distributions are less likely to be impacted by single extreme climatic events thus reducing the potential for overfitting bias.

Although Weibull and GEV are useful for modelling climate windows, additional probability distribution functions (e.g., Gaussian) may provide reasonable alternatives. Future updates in *climwin* will seek to expand the range of weight distributions available to users, increasing the versatility of the *weightwin* function.

2.3 How it works

weightwin works in a similar way to *slidingwin*. However, rather than varying window start and end time using nested for-loops, *weightwin* varies the values of scale, shape and location to minimise the value of $\Delta AICc$, using the base optimisation function *optim* in R. By default, we use a quasi-Newton method of optimisation, described by Byrd et al. [30]. This allows for bounding of the shape, scale and location parameters; however, users can employ alternative optimisation methods through the *method* parameter in *weightwin*. Each set of scale, shape and location values is used to generate a weight distribution using either the Weibull or GEV function. This distribution is then used to calculate a weighted climate mean, which is added to the baseline model with the *update* function. A value of $\Delta AICc$ is returned for the optimisation function to assess.

Once the optimisation function has converged, the user will be provided with an output showing the optimised weight distribution and a corresponding best model. Additionally, users will be shown technical details of the optimisation procedure, which can help users to adjust and improve the optimisation process if needed (e.g., alter the initial values with parameter *par* or change the settings of the optimisation routine with parameter *control*).

2.4 Comparing approaches

Using a weighted window approach provides a number of benefits over *slidingwin* when assessing the impacts of climate. Firstly, by allowing for an infinite number of potential weight distributions, *weightwin* can provide greater detail on the relationship between climate and the response, such as the occurrence of exponential functions reflecting fading memory effects of past climate. Additionally, by using more diverse weight distributions, *weightwin* will often generate models with better $\Delta AICc$ values, which may be especially important when users are most interested in achieving high explanatory power, although one should be aware of potential over-fitting bias (Section 3). Furthermore, by using an optimisation routine *weightwin* often needs to test far fewer models than *slidingwin*, allowing for more rapid analysis.

Despite these benefits, *weightwin* will not always be the most appropriate function for all scenarios. Firstly, the nature of the fitted weight distributions means that *weightwin* can only detect single climate signals, which forces users to detect and compare potential climate signals with separate analyses. While step-wise peak comparison is also required in *slidingwin*, the brute-force approach allows for the detection of multiple climate signals with a single analysis by observing the full $\Delta AICc$ landscape. *weightwin* can also be more technically challenging, with users needing to adjust starting values and optimisation settings (e.g., step size, optimisation method) to find the global optimum (i.e. lowest value of $\Delta AICc$). Such technical requirements may limit the accessibility of the *weightwin* function to the general user. Additionally, *weightwin* can only be used for testing mean climate, with no capacity to consider other aggregate statistics. Therefore, whether one chooses to use *weightwin* or *slidingwin* will depend on the aggregate statistic of interest, the level of detail desired, and the user's technical knowledge.

Ideally, we recommend the use of `slidingwin` and `weightwin` in conjunction to improve our understanding of climate windows. The `slidingwin` approach can be used to explore general trends in the climate data and broadly identify climate signals, including circumstances where multiple climate signals are present. When climate signals are detected using mean climate, the `weightwin` function can then provide greater detail on the specific climate signals observed in the `slidingwin` approach.

2.5 Alternative approaches

As discussed above, a limitation of using `weightwin` is the inability to detect and compare multiple climate signals in a single analysis. This issue is a necessary consequence of the assumptions built into the Weibull and GEV functions, forcing us to identify and analyse each climate signal separately. Although `slidingwin` improves upon this issue somewhat by allowing for multiple signal detection, step-wise signal comparison is still required. Yet multiple climate signals may be fairly common and the ability to test and compare these simultaneously would be useful.

With advances in computing and statistics a number of data-driven methods to tackle high-dimensional problems like climate analysis have become common, such as machine learning, least absolute shrinkage and selection operator (LASSO) and functional linear models using splines [12]. These alternative methods offer additional flexibility compared to Weibull and GEV functions, by allowing for the detection of multiple signals with a single analysis (e.g., [12]). Furthermore, they open up the possibility of multi-dimensional climate window analysis, analysing multiple climate variables at the same time, potentially improving upon the uni-dimensional analysis currently employed in *climwin*.

Splines in particular may provide a suitable alternative for weighted window analysis, as they are ideally suited for modelling a smooth function over a continuum (e.g., time; [12, 31]). In their work, Teller et al. [12] successfully apply a spline function to assess climate signals, demonstrating the ability to detect multiple climate signals within a single weight distribution. Encouragingly, the spline method was able to outperform functions generated by random forest machine learning and LASSO methods, especially at higher climatic resolution that will be common in climate window analyses (e.g., weeks instead of months). The use of splines may reduce the limitations currently encountered by `weightwin`, and incorporating splines is a priority for future *climwin* versions.

However it should be noted that the effectiveness of spline functions, in comparison to LASSO and machine learning, was found to vary depending on the characteristics of the data used ([12]; their Fig 6). Users of *climwin* will likely analyse a wide variety of data types and seek to answer a broad range of questions. One should be aware that no single method may be ideal for all questions, and it may be more appropriate to consider a range of possible climate window methods and provide a mechanism to compare them. By incorporating a range of alternative methods, such as sliding and weighted window methods, *climwin* offers a broad toolbox for analysis of a wide range of questions.

3 Assessing method performance

Although sliding and weighted window approaches can help us identify climate signals, there has so far been limited systematic testing of the performance of these methods and no way to assess the likelihood that a detected signal is genuine. While Teller et al. [12] employed some method comparison using model correlation (i.e. the correlation of observed parameter estimates with predicted estimates), we still possess little knowledge on potential bias inherent to climate window analyses; the precision of the climate window coefficients and model statistics

(e.g., slope, R^2 , window duration); or the rates of type I and type II errors. *climwin* includes mechanisms to test and account for many of these potential errors and biases, providing a standard method for testing current and future climate window approaches.

In this section, we will discuss two of these mechanisms, data randomisation and k-fold cross-validation, and quantify their ability to reduce type I and II errors and R^2 bias respectively. Although we focus here on only two potential biases, users should be aware that biases in other metrics also occur (e.g., slope and window duration bias) and the approaches to account for these biases may differ [7]. Ultimately, the mechanisms one employs to account for potential bias will depend on which metric we most accurately want to predict.

3.1 Data randomisation

To estimate the probability that a given result represents a false positive (type I error) we can calculate the expected distribution of ΔAIC_c values in a data set where no relationship exists between climate and our response variable. *climwin* provides the function `randwin`, which randomises a given dataset (i.e. removes any climate signal) and conducts a sliding window analysis to extract a value of ΔAIC_c . `randwin` reorders the date variable in the original response data frame, allowing us to maintain any relationship between the response variable and other covariates and maintaining auto-correlation within the climate data while still removing any relationship between climate and the response. Following this randomisation procedure, `randwin` will run a climate window analysis on this new set of data from which we extract the ΔAIC_c of the best model.

The randomisation process is repeated a number of times, defined by the user with the parameter `repeats`. We recommend a large number of randomisations (e.g., 1,000) to best estimate the distribution of ΔAIC_c values that could be obtained from a climate window analysis on a dataset with no climate signal ($\Delta AIC_{c,rand}$). We can then determine the percentile of $\Delta AIC_{c,rand}$ that exceeds the value of ΔAIC_c observed in our analysis, allowing us to calculate the likelihood that a given ΔAIC_c value might occur by chance (termed $P_{\Delta AIC_c}$). $P_{\Delta AIC_c}$ can be obtained using the function `pvalue`.

Although conducting a large number of randomisations is the best method to guard against false positives, running this many randomisation can be impractical. Many analyses will use large datasets and/or complex models that can take multiple hours to run. Running time will also be impacted by the range over which the analysis covers, with the number of models run during a sliding window analysis increasing approximately quadratically with analysis range (Eq 1).

$$models = \frac{range * (range + 1)}{2} \quad (1)$$

For a sliding window analysis covering a year (`range = c(365, 0)`) *climwin* will fit over 67,000 models.

Consequently, carrying out 1,000 or even 100 randomisations may simply take too long for many users. Yet it is still important that we are able to protect against the possibility of false positives. As an alternative, *climwin* includes a metric that can be used to estimate the probability of false positives with a limited number of randomisations (e.g., 5–10).

To empirically derive an alternative metric, we analysed a range of simulated datasets where the occurrence of a real signal was known. We generated groups of 2,000 datasets, each with a range of sample sizes (10, 20, 30, 40, or 47 datapoints) and levels of climate signal strength (climate signals with an R^2 that was very high [0.80], high [0.40], moderate [0.20], or where no signal was present). Our simulated datasets were intentionally small, which allowed

us to derive a potential metric that is able to function well in challenging situations. Many climate analyses will use datasets with many more data points by employing temporal and spatial replication. The performance of the metric will often be much better in these circumstances.

We assigned each dataset a binary value (*SignalTrue*) depending on whether it contained a real signal (1) or no signal (0). For every dataset, we then ran a full `slidingwin` analysis and extracted metrics for the best model, here after termed the observed result (R^2 , sample size, $\Delta AICc$, and the percentage of models within the 95% confidence set [C]). In addition, we ran each dataset either with k -fold cross-validation (with $k = 10$ folds; see Section 3.2) or without. In total, we tested 80,000 different datasets. For each of these datasets we then used `randwin`, with $repeats = 5$, to determine the median value of $\Delta AICc$ and C from randomised data. From this we calculated two new metrics:

$$\Delta D = \Delta AICc_{\text{observed}} - \text{median}(\Delta AICc_{\text{randomizations}}) \quad (2)$$

$$\Delta C = C_{\text{observed}} - \text{median}(C_{\text{randomizations}}) \quad (3)$$

We divided our simulation results in half to generate a training and test dataset that we could use to calculate our new metric. We expected that the effectiveness of ΔD and ΔC would vary with both sample size and the use of cross-validation. We therefore divided our training dataset again to separate those datasets that used cross-validation and those that didn't. For each of these two training datasets we then fitted two potential models:

$$\text{Logit}(\text{SignalTrue}) \sim \beta_0 + \beta_1 \Delta D + \beta_2 N + \beta_3 \Delta D * N \quad (4)$$

$$\text{Logit}(\text{SignalTrue}) \sim \beta_0 + \beta_1 \Delta C + \beta_2 N + \beta_3 \Delta C * N \quad (5)$$

where N is the sample size of the dataset used to calculate the values of ΔC and ΔD .

Both with and without cross-validation, Eq 5 was clearly the best supported ($\Delta AICc < -2,500$), suggesting that ΔC is the best metric to determine the likelihood of a real signal. Therefore, we determine the likelihood that a given value of $\Delta AICc$ has occurred by chance with our new metric (P_C) to be:

$$P_C = \frac{1}{1 + \exp(-0.54 + 1.95 * \Delta C + 0.08 * N + 0.31 * \Delta C * N)} \quad (6)$$

for datasets analysed without the use of cross-validation, and

$$P_C = \frac{1}{1 + \exp(-0.62 + 11.56 * \Delta C + 0.06 * N + 6.88 * \Delta C * N)} \quad (7)$$

for datasets analysed with the use of 10-fold cross-validation.

Finally, we used our test dataset to determine the rate of misclassification for our new metric, P_C . Specifically, we calculated the rate of false negatives in datasets where we knew a signal was present and the rate of false positives in those datasets where no signal existed.

P_C was able to provide a good estimate of the reliability of a signal, with average rates of misclassification generally low (Fig 5; mean false negative rate = 0.10, mean false positive rate = 0.17). The effectiveness of P_C was strongly influenced by both sample size (Fig 5) and climate signal strength (Fig 6), with misclassification rates dropping well below the overall average when sample size and signal strength increased (e.g., false negative rate = 0.02 when $N = 30$, $R^2 = 0.4$; Fig 6). Sample size also had a strong influence on false positive rates which decreased with increasing sample size (Fig 5b). These results are not necessarily surprising as misclassification is common when dealing with weak effects and small sample sizes, but it

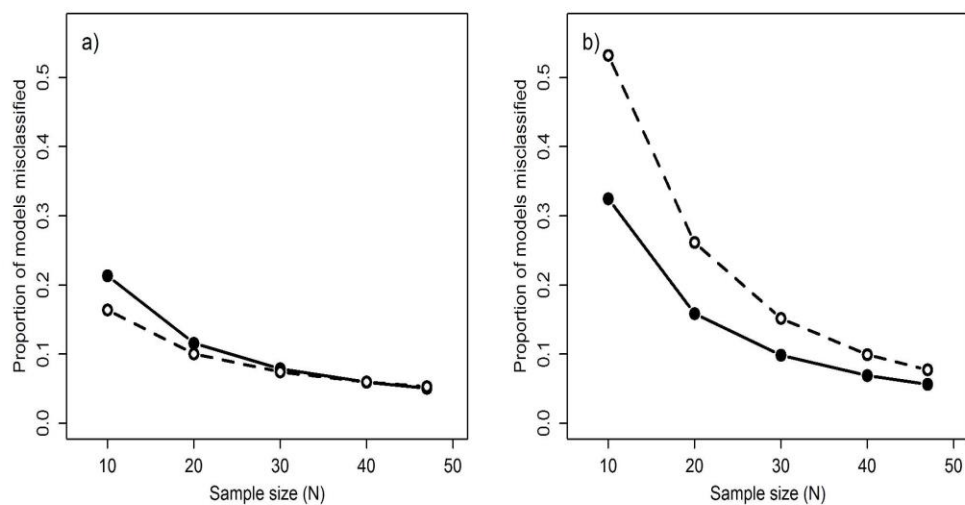


Fig 5. Relationship between sample size (N) and misclassification rate of climate signals. Misclassification rate calculated using the metric P_C both with 10-fold cross-validation (dashed line) and without cross-validation (solid line). Metric tested on datasets where a) a climate signal is present and b) a climate signal is missing. Note that misclassification in a) denotes false negatives while in b) it denotes false positives.

doi:10.1371/journal.pone.0167980.g005

highlights the importance of using large sample sizes when conducting these types of exploratory analyses and the need for caution when interpreting results from small datasets.

For this exercise, we considered a signal to be identified when $P_C < 0.5$ (i.e. when P_C calculated that there was a better than even chance that a given signal was real). The point that one

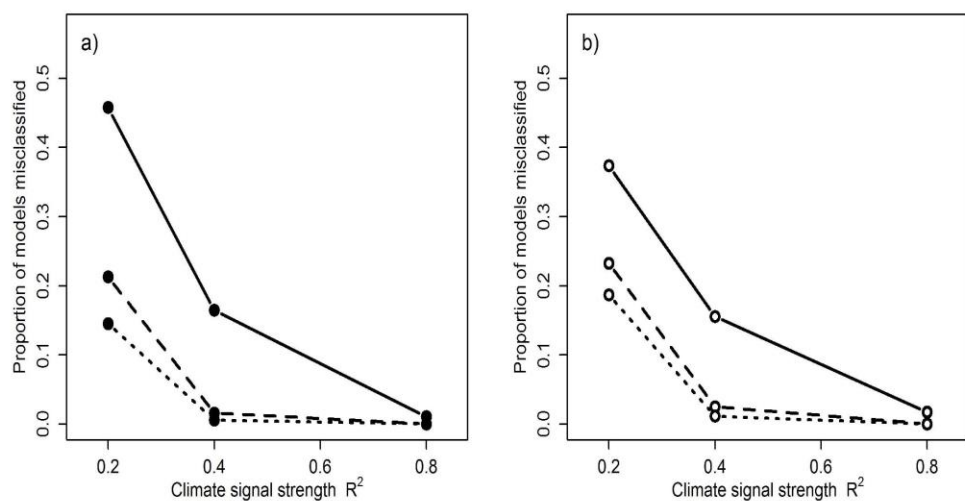


Fig 6. Relationship between climate signal strength (R^2) and misclassification rate of climate signals. Misclassification rate (false negative) calculated using the metric P_C at sample sizes of 10 (solid line), 30 (dashed line) and 47 (dotted line) with a) no cross-validation and b) 10-fold cross-validation.

doi:10.1371/journal.pone.0167980.g006

chooses to distinguish between real and false signals will ultimately involve a trade-off between false positive and negative rates. A lower more conservative cut-off would reduce the chance of false positives but simultaneously increase false negative rates. As an alternative to cut-off values, we encourage the reporting of the full values of P_C and $P_{\Delta AICc}$ as a means of documenting the confidence in a given result, rather than trying to classify signals as either real or not.

3.2 k-fold cross-validation

While P_C and $P_{\Delta AICc}$ can help test the rates of false positives and negatives, they give us no indication of the reliability of the parameter estimates and model statistics derived from our best model (e.g., R^2 , slope, window duration). k-fold cross-validation, provided in `slidingwin`, can be a key tool to help account for any potential biases in these estimates that might arise from overfitting [32]. k-fold cross-validation involves the division of a dataset into k training datasets (of length $N - \frac{N}{k}$) and k test datasets (of length $\frac{N}{k}$, with $k \leq N$), where N represents sample size. Once these training and test datasets are partitioned, `slidingwin` fits each climate model to one of the training datasets and its predictive accuracy is then tested on the corresponding test dataset. To measure predictive accuracy, mean square error (MSE) of the training fit to the test data is used to calculate the AICc:

$$AICc_{model} = N * \log(MSE) + 2\rho + \frac{2\rho(\rho + 1)}{N - \rho - 1} \quad (8)$$

(where ρ is the number of estimated model parameters) and subsequently compared to the AICc of the baseline model, also determined using the training dataset, to obtain $\Delta AICc_{model}$. This procedure is repeated k times (once for each test dataset), after which the $\Delta AICc_{model}$ is averaged across all folds to obtain the cross-validated $\Delta AICc_{model}$. The total number of folds used, is set by the user with the parameter k in the `slidingwin` function.

Cross-validation is used in `slidingwin` to improve the $\Delta AICc$ predictions of each climate window, the out-of-sample $\Delta AICc$, which is then used to improve the model selection process. Each climate window is ultimately fitted to the full dataset, so all other parameter estimates and model statistics (e.g., R^2) have not been cross-validated. However, our more conservative model-selection process is able to greatly reduce the bias in the estimation of climate signal R^2 , reducing the inherent optimistic bias observed in climate window analyses conducted without cross-validation (Fig 7).

To determine the optimum value of k for R^2 estimation, we generated groups of 1,200 datasets each with a known climate signal ($R^2 = 0.22$) and varying sample sizes (10, 20, 30, 40, or 47 datapoints). For each sample size group, `slidingwin` analysis was conducted varying the value of k (0, 2, 4, 6, 8, and 10-folds), so that 200 datasets were tested for each level of sample size and k -folds. Because k cannot exceed N , $k = 10$ was used as the largest number of folds. We found that increasing the number of folds consistently improved estimation of R^2 across all sample sizes, with $k = 10$ providing the best estimate of R^2 (Fig 8).

Although cross-validation greatly improves R^2 estimation, users should be aware that R^2 bias is not completely removed by cross-validation and the goodness-of-fit of the best model from `slidingwin` may still be overly optimistic. Additionally, like data randomisation, k-fold cross-validation can substantially increase the computational time of `slidingwin`, and users will need to consider a trade-off between reducing R^2 bias and analysis time.

While data randomisation and k-fold cross-validation improve our detection of climate signals and our estimates of climate signal R^2 , neither of these methods can be reliably used to simultaneously combat all potential biases in climate window analysis. For example, although cross-validation can effectively reduce bias in R^2 it will also increase false positive rates,

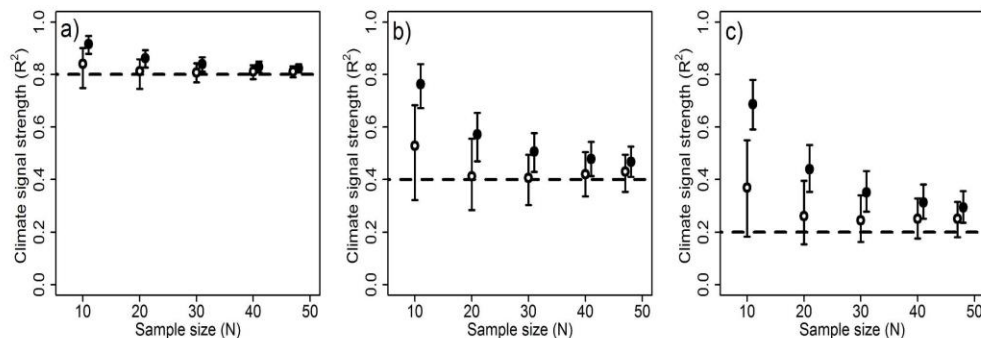


Fig 7. Performance of *slidingwin* in estimating the true R^2 value of a climate signal. Performance determined at varying sample sizes with very high R^2 (0.80; left), high R^2 (0.40; centre), and moderate R^2 (0.20; bottom) both without cross-validation (black) and with 10-fold cross-validation (white). Points represent median R^2 estimates from 2,000 simulated datasets. Error bars represent inter-quartile range. The horizontal dashed line shows the true value of R^2 used to generate the simulated datasets.

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particularly at low sample sizes (Fig 5b). Ultimately, therefore, the methods chosen to reduce bias in climate window analysis will differ depending on the particular parameters of interest.

4 Worked examples

This section provides examples applying the *climwin* package to real data. We use the *Chaff* and *ChaffClim* datasets, included with the package, to run both a sliding window and weighted window analysis. As part of this analysis, we demonstrate the use of multi-model inferencing to determine the median start and end time of a climate signal and conduct model averaging on parameter estimates. In addition, we conduct k-fold cross validation and data randomisation to determine P_C and $P_{\Delta AIC}$.

4.1 Analysis with *slidingwin*

Our analysis of the *Chaff* dataset focuses on the impact of mean temperature on the annual average laying date of the common chaffinch (*Fringilla coelebs*) over a 47 year period (1966–2012; with data provided by the British Trust for Ornithology). We first carry out a sliding window analysis on our data using *slidingwin*.

Function syntax. To begin, we set the structure of our baseline model using the base *lm* function.

```
R>baseline = lm(Laydate ~ 1, data = Chaff)
```

Although we use a simple baseline model for illustration, it is possible to include covariates and random effects terms into the baseline model, as well as using different model functions (e.g., *lmer*, *coxph*). We next specify the climatic variable of interest using the parameter *xvar* (`xvar = list(Temp = Chaff$Temp)`), and include both the climate and biological date data with the parameters *cdate* and *bdate* (`cdate = ChaffClim$Date`, `bdate = Chaff$Date`). As our *Chaff* dataset contains no within-year variation, we conduct our analysis using absolute climate windows (`type = "absolute"`) with a reference day of April 24th (`refday = c(24, 4)`), equivalent to the earliest biological record in our data.

As we have no *a priori* knowledge on when a climate signal might occur, we test all possible climate windows over the period of a year (`range = c(365, 0)`), considering the linear

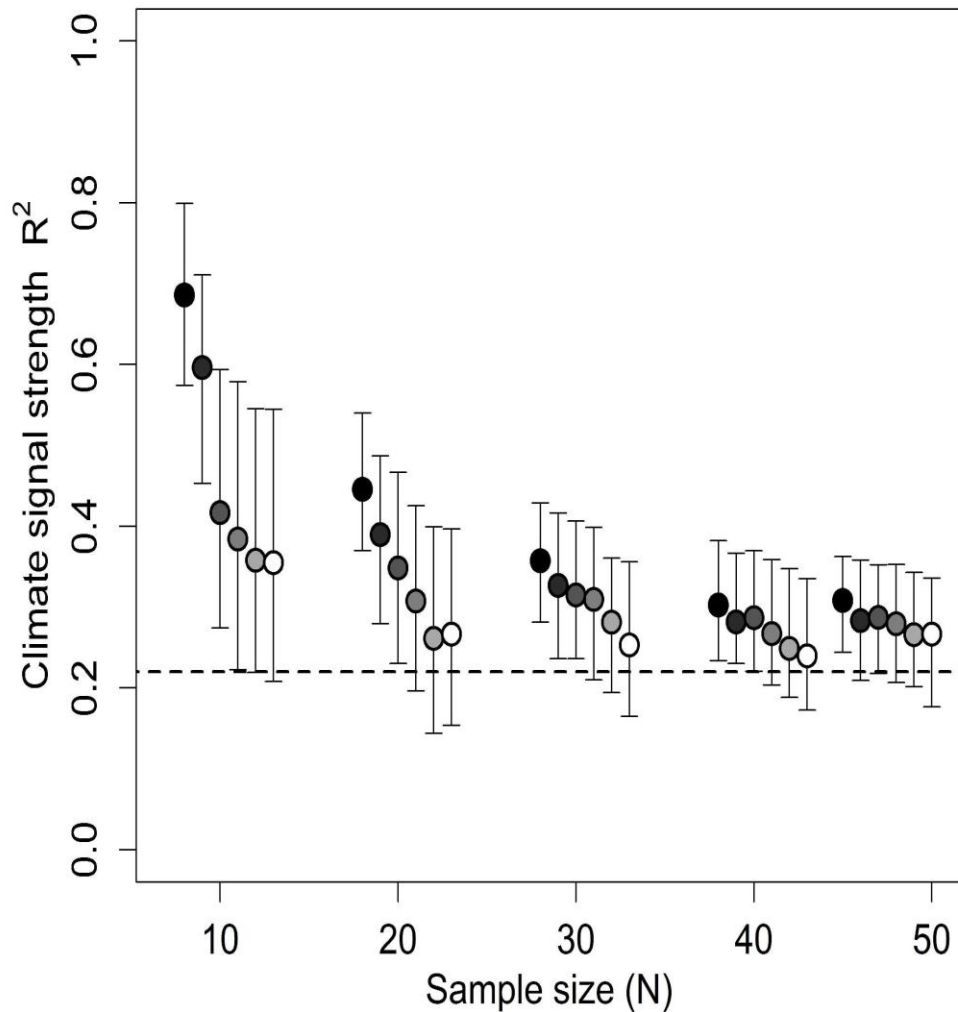


Fig 8. Effect of cross-validation folds (k) on the median R^2 estimation of k -fold cross-validated *slidingwin* analysis. Each point generated using 200 simulated datasets. The horizontal dashed line shows the true value of R^2 used to generate the simulated datasets ($R^2 = 0.22$). R^2 was estimated using 0, 2, 4, 6, 8, or 10-folds (black to white respectively). Sample sizes of 10, 20, 30, 40, and 47 were used. Error bars represent inter-quartile range.

doi:10.1371/journal.pone.0167980.g008

effect (func = "lin") of mean temperature (stat = "mean"). With all these elements, our final function is shown below:

```
R> SLIDING<- slidingwin(baseline=lm(Laydate ~ 1, data=Chaff),
  xvar=list(Temp=ChaffClim$Temp),
  cdate=ChaffClim$Date, bdate=Chaff$Date,
  type="absolute", refday=c(24, 4),
  range=c(365, 0), func="lin", stat="mean")
```

Table 2. Output of *combos* item from an absolute sliding window analysis.

response	climate	type	stat	func	$\Delta AICc$	Start	End	betaL
Laydate	Temp	absolute	mean	lin	-84.01	46	0	-3.86

Testing the relationship between mean temperature and laying date in the common chaffinch (*Fringilla coelebs*) using a reference day April 24th.

doi:10.1371/journal.pone.0167980.t002

By default, *slidingwin* will assume daily climate data is used to test climate windows. However, in cases where the resolution of climate data is coarser, users can alter the parameter *cinterval* to use either weeks or months.

Results. The object *SLIDING* is a list item with two separate elements. We can firstly examine a summary of our results using the *combos* item, a truncated version of which can be seen in Table 2.

```
R> SLIDING$combos
```

The *combos* item provides a summary of our sliding window analysis and a brief overview of the best fitted climate window, showing us the $\Delta AICc$, start and end time, and slope of the best window. It should be noted that *climwin* allows for multiple hypotheses to be tested in a single function (e.g., effect of mean and maximum temperature), in which case the *combos* item will provide a summary of all tested hypotheses. For this example, we can see that the best climate window detected in our analysis falls 0–46 days before our reference date (April 24th), equivalent to mean temperature between March 9th and April 24th.

We can look at the results further in the full model selection dataset, a truncated version of which can be seen in Table 3.

```
R> head(SLIDING[[1]]$Dataset)
```

In Table 3 we can see that there are a number of climate windows that exhibit similar model weights (w_i) to our best window. To understand how these other windows influence our result we can determine the median window size of the 95% confidence set with our function *medwin* and calculate model averaged parameter estimates for the same confidence set.

```
R> medwin(SLIDING[[1]]$Dataset)
R> dataset <- SLIDING[[1]]$Dataset
R> ConfidenceSet <- dataset[which(cumsum(dataset$ModWeight)
  <= 0.95), ]
R> sum(ConfidenceSet$ModelBeta*ConfidenceSet$ModWeight)
```

Median window size from the 95% confidence set is slightly wider than our best window (73—1; February 11th–April 23rd), although the median and best window still contained over

Table 3. Top five climate windows detected using *slidingwin* with an absolute window approach.

Window start	Window end	$\Delta AICc$	Temperature β (days/°C)	Standard error	w_i
46	0	-84.01	-3.86	0.25	0.06
47	0	-83.46	-3.85	0.25	0.05
74	0	-83.41	-3.79	0.25	0.05
75	0	-83.20	-3.78	0.25	0.04
73	0	-83.13	-3.80	0.25	0.04

Window start and end time are measured in days before April 24th.

doi:10.1371/journal.pone.0167980.t003

60% of the same days. The best window shows a strongly negative relationship between temperature and laying date ($\beta = -3.86$ days/ $^{\circ}\text{C}$, 95% CI = -4.35 – -3.37 ; Table 3), very similar to the model averaged relationship ($\beta = -3.60$ days/ $^{\circ}\text{C}$). Multi-model inferencing tells us that the average laying date of *F. coelebs* advances by 3.6 days for every 1°C increase in mean temperature between February 11th and April 23rd.

Although these results point to the presence of a strong climate signal in *F. coelebs* laying date, we cannot be sure that this result has not occurred due to chance. To test this possibility, we next run the randomisation procedure using the function `randwin`, with `repeats = 5`.

```
R> SLIDING.RAND <- randwin(repeats = 5,
  baseline = lm(Laydate ~ 1, data = Chaff),
  xvar = list(Temp = ChaffClim$Temp),
  cdate = ChaffClim$Date, bdate = Chaff$Date,
  type = "absolute", refday = c(24, 4),
  range = c(365, 0), func = "lin", stat = "mean")
```

The output of the `randwin` function can then be used to run the function `pvalue` to return a value of P_C .

```
R> pvalue(dataset = SLIDING[[1]]$Dataset,
  datasetrand = SLIDING.RAND[[1]], metric = "C", sample.size = 47)
```

From this function, we can conclude that the likelihood of observing such a climate signal by chance is very small ($P_C = 5.89 \times 10^{-16}$).

Although this provides us with information on the best model, it does not tell us whether multiple peaks may be present. Our final step should therefore be to examine the ΔAICc and model weight landscape (Fig 9). In this case, there is only a single clear ΔAICc peak (red; Fig 9a), which is mirrored in the small size of the confidence set (C) (Fig 9b). We can therefore discount the possibility of multiple peaks.

Using k-fold cross-validation. Above, we have focused on estimating the window duration and slope using multi-model inferencing. However, in other circumstances we may be more interested in determining the strength of the detected climate signal (R^2). As R^2 estimations using `slidingwin` can be biased at low sample size and/or effect size, k-fold cross-validation should be employed to improve the accuracy of our R^2 estimate. To conduct our `slidingwin` analysis with k-fold cross-validation we incorporate the parameter `k` into the `slidingwin` function (`k = 10`).

```
R> SLIDINGK <- slidingwin(baseline = lm(Laydate ~ 1, data = Chaff),
  xvar = list(Temp = ChaffClim$Temp),
  cdate = ChaffClim$Date, bdate = Chaff$Date,
  type = "absolute", refday = c(24, 4),
  range = c(365, 0), func = "lin", stat = "mean",
  k = 10)
```

Looking at the `combos` object, we can see that the best model selected using cross-validation has a very similar window duration and slope to that calculated using multi-model inferencing in our first sliding window analysis (Window duration: 75–0, February 9th–April 24th; window slope: -3.78 days/ $^{\circ}\text{C}$, 95% CI = -4.27 – -3.30 ; Table 4).

```
R> SLIDINGK$combos
```

Although window duration and slope are similar to our previous analysis, the value of ΔAICc is much less negative, due to the conservative nature of ΔAICc calculation when using

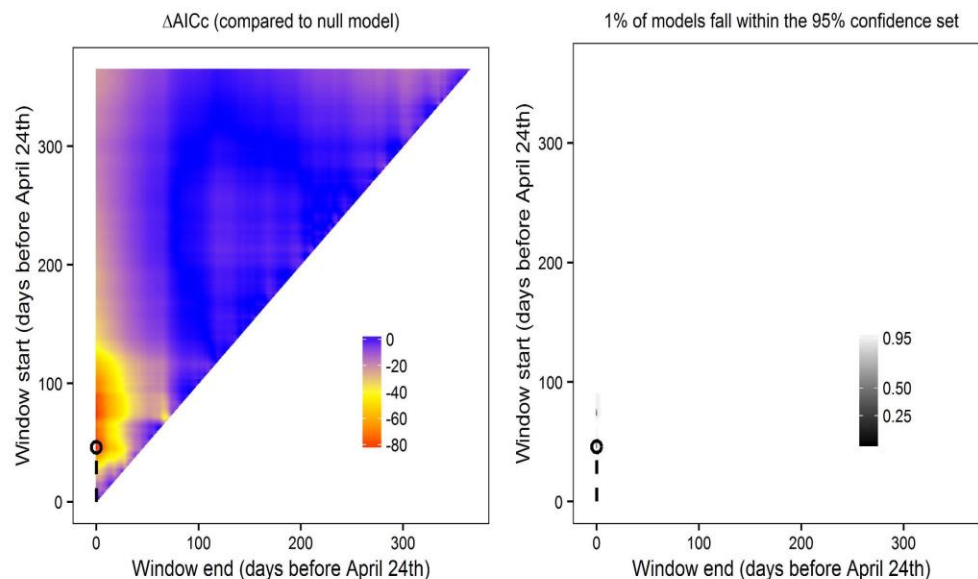


Fig 9. Output of absolute sliding window analysis. Analysis testing the relationship between mean temperature and laying date in the common chaffinch (*Fringilla coelebs*) using a reference day April 24th. (Left) Heat map of $\Delta AICc$ ($AICc$ of null model— $AICc$ of climate model) for all fitted climate windows. (Right) 95%, 50% and 25% confidence sets for all fitted climate windows. The best fitted climate window (lowest value of $\Delta AICc$) is circled. Plots generated using `plotdelta` and `plotweights` functions.

doi:10.1371/journal.pone.0167980.g009

cross-validation (i.e. $\Delta AICc$ is calculated on a smaller test dataset). This more conservative $\Delta AICc$ estimation will also lead to much larger values of C (Fig 10), which will often remove the possibility for users to conduct multi-model inferencing. However, even though the model weight landscape shows less compelling evidence of a climate signal, by running `randwin` with cross-validation and calculating P_C , we find that the likelihood of getting such a value of C by chance when using 10-fold cross-validation is still very small ($P_C = 1.10e^{-11}$).

Once we are confident in our climate signal result we can then examine the summary of the best model to gain an estimate of strength for the climate signal.

```
R> summary(SLIDINGK[[1]]$BestModel)
```

In this case, the strength of the climate signal detected in *F. coelebs* laying date is particularly strong ($R^2 = 0.83$).

4.2 Analysis with weightwin

Using `slidingwin` we have been able to identify a negative relationship between mean temperature and *F. coelebs* laying date. Yet we have so far assumed a uniform weight distribution

Table 4. Output of `combos` item from an absolute sliding window analysis.

response	climate	type	stat	func	$\Delta AICc$	start	end	betaL
Laydate	Temp	absolute	mean	lin	-11.07	75	0	-3.78

Testing the relationship between mean temperature and laying date in the common chaffinch (*Fringilla coelebs*) using a reference day April 24th and 10-fold cross-validation.

doi:10.1371/journal.pone.0167980.t004

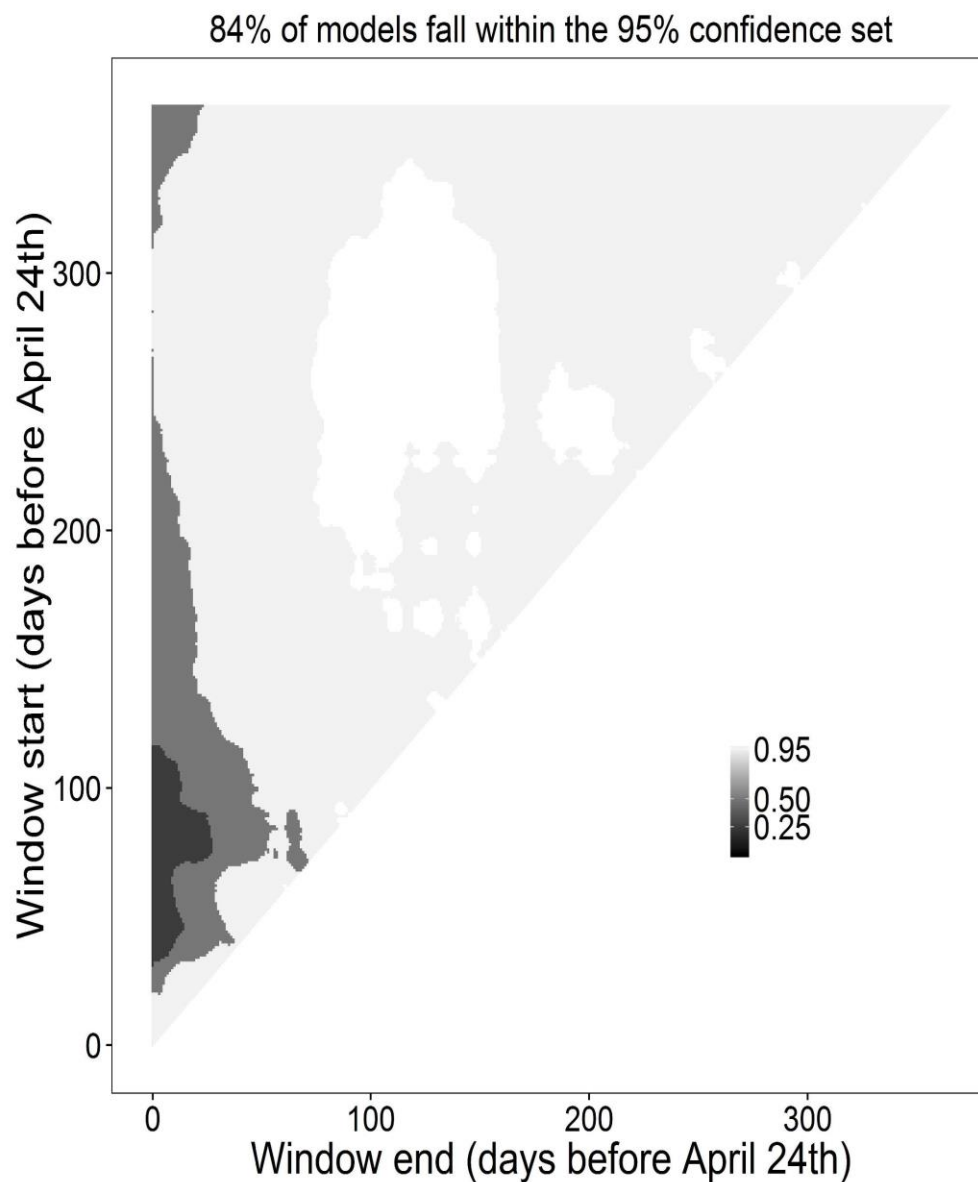


Fig 10. Heat-map of 95%, 50% and 25% confidence sets for an absolute sliding window analysis. Analysis testing the relationship between mean temperature and laying date in the common chaffinch (*Fringilla coelebs*) using a reference day April 24th and 10-fold cross-validation. Shading levels represent 95%, 50% and 25% confidence sets for all fitted climate windows. Plots generated using the `plotweights` functions.

doi:10.1371/journal.pone.0167980.g010

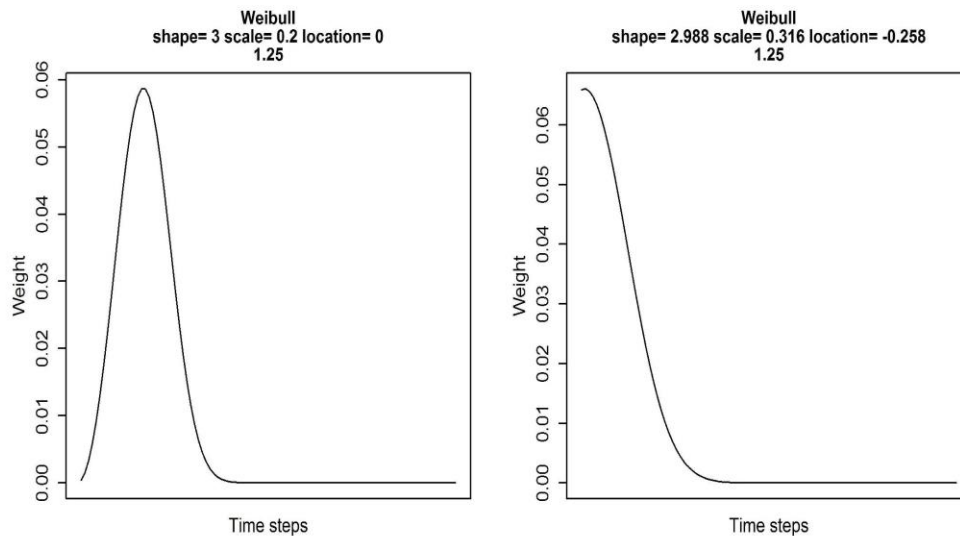


Fig 11. Weight distribution calculated using a Weibull probability distribution function. Distribution shows the relative importance of climate over time (days). (Left) Values of shape, scale and location used as starting parameters for weighted window analysis. (Right) Output from weightwin analysis showing the relative influence of temperature on the average annual laying date of the common chaffinch (*Fringilla coelebs*). Weight distribution shows that temperature has the strongest influence on laying date immediately before the reference date (April 24th) but slowly decays as we move further into the past. Plots created using the function explore.

doi:10.1371/journal.pone.0167980.g011

when calculating mean temperature. To gain more insight into the detected climate signal, we can next run a weighted window analysis using `weightwin`.

Firstly, we want to determine the best starting distribution to use for the `weightwin` optimisation procedure, using the included `explore` function. We can experiment with the shape, scale and location parameters for a Weibull distribution to determine a reasonable starting weight distribution for our optimisation procedure (Fig 11).

```
R> explore(shape=3, scale=0.2, loc=0, weightfunc="W")
```

Most of the parameter values will be the same between `weightwin` and `slidingwin`, but we must provide additional information on the type of probability distribution function being used (in this case Weibull, `weightfunc="W"`) and the starting values of our three optimisation parameters, taken from the `explore` function (`par=c(3, 0.2, 0)`). Additionally, both the parameters `k` and `stat` are not used in `weightwin`.

```
R> WEIGHT <- weightwin(baseline=lm(Laydate ~ 1, data=Chaff),
  xvar=list(Temp=ChaffClim$Temp),
  cdate=ChaffClim$Date, bdate=Chaff$Date,
  type="absolute", refday=c(24, 4),
  range=c(365, 0), func="lin",
  weightfunc="W", par=c(3, 0.2, 0))
```

In contrast to the uniform distribution assumed by `slidingwin`, our analysis with `weightwin` returned a rapidly decaying weight distribution, with temperature having the largest impact on laying date close to April 24th and rapidly declining further into the past (Fig 11). Furthermore, by examining the `WeightedOutput` item generated by `weightwin`, we

Table 5. Output of an optimised weight distribution (Weibull function) testing the relative influence of temperature on the laying date of the common chaffinch (*Fringilla coelebs*).

$\Delta AICc$	shape	scale	location	model β	standard error
-100.42	2.99	0.32	-0.26	-4.28	0.23

doi:10.1371/journal.pone.0167980.t005

can see that the explanatory power of this weight distribution ($\Delta AICc$) is much greater than that generated with the uniform distribution assumption in `slidingwin` (-84.01 v. -100.42; Table 5).

```
R> WEIGHT$WeightedOutput
```

Once again, however, we cannot be sure that such a result could not occur by chance and so we can compare our result to those from a randomised dataset using `randwin`. In this case, however, the smaller computational time required to run `weightwin` allows us to increase repeats to 1,000. Note, however, that we must specify we are running a weighted window analysis with the argument `window = "Weighted"`.

```
R> WEIGHT.RAND <- randwin(repeats = 1000, window = "weighted",
  baseline = lm(Laydate ~ 1, data = Chaff),
  xvar = list(Temp = ChaffClim$Temp),
  cdate = ChaffClim$Date, bdate = Chaff$Date,
  type = "absolute", refday = c(24, 4),
  range = c(365, 0), func = "lin",
  weightfunc = "W", par = c(3, 0.2, 0))
```

With 1,000 randomisations, we are able to use the more reliable $P_{\Delta AICc}$ to estimate the probability that we would observe such a largely negative value of $\Delta AICc$ by chance.

```
R> pvalue(dataset = WEIGHT$WeightedOutput,
  datasetrand = WEIGHT.RAND[[1]], metric = "AIC")
```

Once again, we find that the probability of observing such a weight distribution by chance is very small ($P_{\Delta AICc} < 0.001$). Therefore, our analysis using *climwin* provides good evidence that laying date in *F. coelebs* is strongly impacted by temperature over late winter and early spring (February–April) with a decaying relationship over time.

4.3 Replication

The worked examples above can be replicated using functions and data included with *climwin*. The full release version of *climwin* (version 1.0.0) is available from the Comprehensive R Archive Network at <http://CRAN.R-project.org/package=climwin>. The current pre-release version of the package can be accessed on GitHub <https://github.com/LiamDBailey/climwin>. The worked examples above use the `Chaff` and `ChaffClim` datasets included with the full release version of the package. All code was written by Liam D. Bailey and Martijn van de Pol and can be used freely according to the General Public License (GPL), version 2.

5 Conclusion

The way in which previous research has tested and compared the effects of climate has tended to require arbitrary *a priori* selection of a limited number of climate windows, curtailing our ability to make meaningful conclusions. Climate window analyses, such as sliding and weighted window analyses, improve on these methods by reducing the need for *a priori*

assumptions. Yet until now, we have lacked a standardised and accessible way in which to carry out such analyses, nor any way to assess method performance. We introduced the R package *climwin*, which provides an easy and versatile toolbox for analysing the impacts of climate using a number of potential methods and includes metrics to assess the performance of these methods. This toolbox will allow for the greater utilisation of more sophisticated climate analyses within the general scientific community and consequently improve our understanding of the impacts of climate.

Supporting Information

S1 File. Simulated data used to test misclassification rates. Simulated data used to generate Figs 5–7.
(TXT)

S2 File. Simulated data used to test optimum cross-validation folds. Simulated data used to generate Fig 8.
(CSV)

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Author Contributions

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Funding acquisition: MvdP.

Investigation: LDB MvdP.

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Software: LDB MvdP.

Supervision: MvdP.

Validation: LDB MvdP.

Visualization: LDB MvdP.

Writing – original draft: LDB.

Writing – review & editing: LDB MvdP.

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Supplementary Material

Chapter 2 supplementary material includes large datasets that are inappropriate for inclusion within the printed thesis. All supplementary material can instead be accessed through BioRxiv (<http://dx.doi.org/10.1101/069427>).

Chapter 3

Phenotypic plasticity in nest-site selection as a response to extreme flooding events

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Research



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No phenotypic plasticity in nest-site selection in response to extreme flooding events

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Phenotypic plasticity is a crucial mechanism for responding to changes in climatic means, yet we know little about its role in responding to extreme climatic events (ECEs). ECEs may lack the reliable cues necessary for phenotypic plasticity to evolve; however, this has not been empirically tested. We investigated whether behavioural plasticity in nest-site selection allows a long-lived shorebird (*Haematopus ostralegus*) to respond to flooding. We collected longitudinal nest elevation data on individuals over two decades, during which time flooding events have become increasingly frequent. We found no evidence that individuals learn from flooding experiences, showing nest elevation change consistent with random nest-site selection. There was also no evidence of phenotypic plasticity in response to potential environmental cues (lunar nodal cycle and water height). A small number of individuals, those nesting near an artificial sea wall, did show an increase in nest elevation over time; however, there is no conclusive evidence this occurred in response to ECEs. Our study population showed no behavioural plasticity in response to changing ECE patterns. More research is needed to determine whether this pattern is consistent across species and types of ECEs. If so, ECEs may pose a major challenge to the resilience of wild populations.

This article is part of the themed issue 'Behavioural, ecological and evolutionary responses to extreme climatic events'.

1. Introduction

One of the most prominent aspects of global climate change is the more frequent occurrence of extreme climatic events (ECEs), such as droughts and floods [1,2]. ECEs can have consequences for biological systems at the population [3], community [4] and ecosystem level [5], but ultimately these impacts are driven by individual changes [6]. Organisms may respond to changing ECE frequencies through inter-generational micro-evolutionary change or intra-generational phenotypic plasticity in labile traits.

Phenotypic plasticity in response to gradual changes in mean climate is a well-studied topic [7,8], and has been suggested as the key mechanism through which organisms can respond to recent climate change [8]. By contrast, consideration of phenotypic plasticity as a response to ECEs has been mostly theoretical [9–12]. Phenotypic plasticity may allow individuals to respond pre-emptively to upcoming ECEs or adapt once the extreme conditions arise through behavioural or physiological change [12–14]. To pre-empt future ECEs, individuals must possess a reliable cue to predict future conditions [15]. When a reliable cue is absent, or the reliability of a cue deteriorates, phenotypic plasticity becomes maladaptive as

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individuals can 'overshoot' optimal conditions [15–17]. ECEs are often considered unpredictable in the biological literature, but it is possible that ECEs may simply be rare rather than unpredictable [10]. In this case there may still be reliable cues available to individuals that will allow them to predict oncoming ECEs and respond accordingly. Climatological work has highlighted the potential for ECEs to show predictability under certain circumstances [18]; but whether these reliable cues are detectable by organisms and will facilitate responses to ECEs is still unknown.

Even without reliable cues, individuals may exhibit plasticity through learning, where an individual remembers previously experienced conditions and adjusts its future response. For example, nesting blue tits (*Cyanistes caeruleus*) learnt to adjust their laying date when they experienced a mismatch with their food source in the previous spring [19]. Unlike other types of plasticity, which will generally require exposure to environmental conditions across multiple generations to evolve, learning allows individuals to generate responses to novel environmental conditions [20]. For example, Australian marbled frogs (*Limnodynastes convexiusculus*) learned to avoid toxic cane toads (*Bufo marinus*) following a first novel encounter [21]. For learning to occur however, environmental conditions must be stochastic enough to make learning worthwhile but not so much that the relationship between a stimulus and response are highly changeable [22]. Therefore, while climate change could select strongly for learning responses, such selection will require that conditions in one year are generally indicative of conditions in the next [23].

Learning is unlikely to evolve in response to ECEs if such events are infrequent compared to the lifespan of an organism; yet as climatic conditions change, learning responses to ECEs could become more common or previously evolved learning responses may be expressed. Learning responses to other types of stochastic events, such as predation, have previously been documented in birds [24,25], fish [26] and amphibians [27], and some studies in nesting birds have suggested that learning responses to ECEs can occur [28–30]. Yet, as with much of the ECE literature, these studies are often anecdotal (i.e. only consider a single ECE) making it difficult to generalize the results from one event to the next and reliably estimate responses [10]. Therefore, whether learning can act as a response to changing patterns of ECEs is still an open question.

In this study, we use detailed longitudinal behavioural information on individual Eurasian oystercatchers (*Haematopus ostralegus*) over two decades to test for behavioural plasticity in nest-site selection as a response to changing patterns of extreme flooding events. Since 1971 maximum high tides during the *H. ostralegus* breeding season have increased at twice the rate of mean high tides over the same period (0.8 versus 0.4 cm yr⁻¹; electronic supplementary material, figure S1), driven by sea-level rise and changing wind and storm patterns [3]. Consequently, the frequency of historically rare extreme floods (defined using a biologically informed cut-off; see [10] and Methods for details) has more than doubled from once every 7.0 years, between 1971 and 1991, to once every 2.7 years since 1991.

These flooding events strongly impact *H. ostralegus* reproductive success, washing away eggs and drowning young chicks [3]. Over the two decades of this study, 51% of nests were located on sites that were inundated at some point during the breeding season. Although many vulnerable nests are predated or fledged before flooding can occur, on average

14% of nests are inundated annually during the incubation period. A large number of nests (42%) fail when covered by water, increasing to almost 60% once water is 15 cm or more above the nest. Even those nests that remain following flooding may fail to hatch after being submerged [31].

Van de Pol *et al.* [3] outline three traits that may be used by *H. ostralegus* to reduce flooding risk. Increasing nest elevation will allow breeding pairs to reduce the chance that a nest will be inundated during a flooding event. Alternatively, as flooding risk is known to increase across the season, individuals may lessen flooding risk through laying date advancement. Finally, breeding pairs may shorten the incubation and early chick phase to reduce the length of time at which nests are at risk of flooding. Of these three behavioural traits, variation in nest elevation provides the most effective mechanism through which *H. ostralegus* pairs can mediate flooding risk [3]. For example, an increase in nest elevation of only 18 cm (equivalent to the median standard deviation of elevation within a territory; see Results) would completely alleviate *H. ostralegus* flooding risk in comparison to 1990–2008 levels. However, to achieve a similar reduction in flooding risk *H. ostralegus* would need to advance laying date by 34 days or reduce the length of the incubation and early chick phase by more than half (24 days) [3]. Importantly, *H. ostralegus* pairs also have plenty of opportunity to increase nest elevation, as chosen nesting sites are typically around half a metre lower than the highest available point within a territory (see Results).

Empirical field data further highlight the importance of nest elevation as a mediator of flooding risk. During flooding events, low nesting *H. ostralegus* experience greatly reduced nest success, in turn limiting the reproductive success of the breeding population as a whole. If the nesting behaviour of our population remains unchanged, increased frequency of such flooding events will pose a serious threat to population viability [3]. This is likely to be a common scenario among many coastal (beach and saltmarsh) nesting species [32–34]. However, it should not be assumed that nest elevation will remain static. As the frequency of flooding events increases we would expect directional selection to favour higher nest elevation, working via the fitness component of nest success. Encouragingly, our study population has shown an increase in mean nest elevation over time at half the rate of change seen in maximum high tide [35], providing evidence that changing nest elevation as a response to flooding may be possible.

Due to the long generation time of *H. ostralegus* (11–13 years; [36]), it is unlikely that micro-evolutionary changes in nest elevation will explain the rapid changes we observe in our population. Instead, phenotypic plasticity in nest-site selection provides a more plausible mechanism by which such changes may be explained, with individuals selecting higher elevation nest sites over their lifetimes. The current study system is perfectly suited to test for the presence of such phenotypic plasticity. Our extensive dataset on a long-lived species with high site fidelity includes many individuals that have been followed over multiple years, allowing us to detect small within-individual changes that might otherwise be missed. Importantly, by testing for the presence of phenotypic plasticity in *H. ostralegus* nest elevation we can also provide a test on the role of phenotypic plasticity as a response to ECEs more generally.

To assess the presence of phenotypic plasticity in nest-site selection we investigated three questions. First, do individuals

exhibit a change in nest elevation over their lifetime? Any changes across our study period would provide initial evidence for phenotypic plasticity as a driver of nest elevation change.

Second, do reliable cues exist that predict extreme flooding events and do *H. ostralegus* adjust nest elevation in response to such environmental cues? If *H. ostralegus* exhibits phenotypic plasticity in response to changing flooding patterns then reliable cues are likely to exist that will allow for the prediction of future flooding risk. Both the lunar nodal cycle, a predictable 18.6 year cyclical pattern in water heights [37,38], and water levels in the preceding breeding season might act as such reliable cues. We predicted that individuals would increase nest elevation as lunar nodal cycle position advanced (i.e. as water heights increase) and as water heights in the preceding breeding season increased. Additionally, we tested the relationship between individual nest elevation and water heights in the upcoming breeding season to account for the presence of unknown reliable cues that may be correlated with flooding risk but were not directly measured.

Finally, do *H. ostralegus* demonstrate a learning response by changing their nest elevation following a flooding event? Even without the presence of reliable environmental cues, *H. ostralegus* may exhibit changes in nest elevation through learning. We predicted that individuals that experience a flooding event would increase the elevation of their next nest, with individuals whose nests were destroyed by flooding increasing more than those that survived a flood. Since random nest-site selection may also result in a positive change in nest elevation following flooding (see Methods), we specifically tested whether any increase in nest elevation was greater than that expected under random nest-site selection.

2. Methods

(a) Defining an extreme climatic event

To study ECEs it is important to define what conditions are classed as 'extreme'. This definition will depend on the question of interest and the spatial, temporal and biological scale at which one works [39]. For this study, we are interested in investigating how climate-driven processes (i.e. tidal flooding) might impact individual behaviour, with a focus on the local spatial scale (a single study population) and short-term temporal scale (1–2 years). We use a 'biological' definition of ECEs [10]: 'An episode where climate or climate-driven conditions trigger a negative threshold-like (non-linear) biological response'. Setting an ECE baseline using a 'biological' definition allows us to document changes in the frequency of extreme conditions that are biologically meaningful, removing the need for definitions based purely on historical climatological frequency [10].

We used our current biological knowledge of the study system to select a standard water height over which we consider a flood to be 'extreme'. Specifically, we considered data from 1995 and defined an extreme flooding event as water heights that exceeded 95% of all nests laid in this year (electronic supplementary material, figure S2), equivalent to 82 cm above 1971 mean high tide (here after MHT; source www.live.waterbase.nl). The year 1995 is the earliest in which both nest elevation and tidal data are available, providing us with a measure of tidal extremeness that pre-dates any phenotypic plasticity in nest elevation that may be present within our dataset.

(b) Study system

H. ostralegus is a ground-nesting shorebird that breeds on salt-marshes and beaches, close to the estuarine intertidal flats on

which they feed. It is a long-lived species (generation time 11–13 years), and forms stable, long-term pair bonds [36]. Pairs have strong site fidelity, returning to the same territories year after year [40,41]. During the breeding season, males construct several nest cups within their territory, from which the female selects a suitable site for egg laying [42]. *H. ostralegus* are not a multi-brooding species, but often lay replacement clutches during a year following nest predation or flooding. As *H. ostralegus* do not construct nest mounds and use limited nesting material, nest elevation will be determined solely by nest-site selection.

Our study population, on the Dutch barrier island of Schiermonnikoog (53.4833°N, 6.1667°E), has been monitored since 1983 (see [43,44] for details). Numbers of *H. ostralegus* have declined sharply, with declines of 3% per annum in the region since 1991 [45]. Consequently, the area of the study was expanded over time to sample a similar number of breeding pairs. Most breeding birds (more than 90%) have been individually colour banded, allowing us to follow their behaviour over multiple years.

(c) Data collection

We monitored nesting activity from April to August annually, with most nests laid between May and June. Nests were located through systematic searching in the field every 2–3 days, with active nests revisited to determine nest fate. We identified nest parents by their colour bands. Nest elevation was recorded over a 20 year period (1995–2014; no data in 1997–1999), and measured in centimetres (± 0.1 cm) above MHT.

We collected nest elevation data from 2912 nests of which 2250 had at least one banded parent. We had nest elevation data from 374 banded males (mean 5.7 nests over 4.2 years per individual) and 404 banded females (mean 4.9 nests over 3.7 years per individual). The methods used to measure nest elevation varied between years. In eight years (1995, 1996, 2008, and 2010–2014) nest elevation was measured directly in the field. Elevation was determined *in situ* using a water level device (1995–1996); laser machine control device (2008); and a differential GPS (2010–2014; ProMark 800 GNSS). All *in situ* methods provide measurement accuracy to within 2 cm, confirmed using existing calibration sites established by Rijkswaterstaat (Dutch Ministry for Infrastructure and Environment). For all other nests, elevation was determined by overlaying nest coordinates on a LiDAR digital elevation map (measured 2008; cell size 0.5×0.5 m; <http://www.ahn.nl/index.html>). This less precise *ex situ* method was used to collect data between 2000–2007 and 2009, as well as supplementing data in predominantly *in situ* measured years. These differences in precision between *in situ* and *ex situ* data collection are explicitly accounted for in all analyses (see below).

The lunar nodal cycle varies considerably in amplitude and phase globally [37], therefore we calculated the shape of the lunar nodal cycle specifically for our study site, employing methods outlined by Houston & Dean [38] and Baart *et al.* [37] with tidal data covering 1971 to 2015. On Schiermonnikoog, we identified a lunar nodal cycle with an amplitude of 2.22 cm and a phase of -0.76 radians (with 1970 set as year 0), representing fluctuations in water height of around 0.5 cm yr^{-1} , a similar magnitude to the rate of sea-level rise recorded in our study region (electronic supplementary material, figure S3). To analyse lunar nodal cycle we gave each year a value based on the 'position' of the cycle, where -1 represents a trough in the cycle and 1 represents a peak.

Water height data were measured at our study site by Rijkswaterstaat (Dutch Ministry for Infrastructure and Environment). All data were collected at 10 min intervals providing an accurate measure of high tide values. To test the response of individuals to tidal patterns during both the preceding and current breeding season we calculated the mean high tide across May and June in all years, the point in time at which nesting activity is most

frequent. To distinguish between the effects of lunar nodal cycle and seasonal differences in water height we then calculated a residual water height variable (the difference between actual water heights and water heights predicted based on the lunar nodal cycle).

To test for the presence of learning we first needed to determine the fate of each measured nest. We considered a nest site to be 'flooded' when recorded water levels exceeded nest elevation. Inspection of nests during and after flooding events showed that this was a suitable rule to determine flooding experience. We considered a nest to be active once the first egg was laid and inactive when no more eggs were present in the nest, either due to hatching, predation or flooding. The point at which a nest was considered inactive was determined as the mid-point between the penultimate and final nest check. We categorized nests into one of three different experiences: failed due to flooding, survived a flooding event, and unflooded. A nest was considered failed due to flooding when the inactive date of the nest was on the day of a flood. Nest checks were generally conducted immediately before and after a flooding tide, allowing us to more accurately estimate nest inactivity date and attribute nest failure due to flooding with high confidence. We then investigated the relationship between flooding experience and changes in nest elevation from one nest to the next. For this analysis we removed all individuals with only one nest, leaving 1508 nests.

As *H. ostralegus* territories vary widely in elevation, we expected that the characteristics of individual territories might be an important modulator of nest elevation. Specifically, we predicted that more variable territories (i.e. larger standard deviation of elevations within a territory; σE) would allow for stronger plastic responses in nest elevation, as such territories would provide more opportunities to nest higher. For each year we determined the known locations of individual pairs (nest locations and territory roosting locations), with which we generated polygons using a Voronoi algorithm in QGIS [46]. This procedure provided an estimate of territory location for each pair, with polygons covering an average of 6781 m² (range: 2–94 537 m²). Territory polygons were overlaid on our LiDAR map to calculate σE . We had no records of *in situ* measured nests less than 20 cm above MHT; therefore, points below 20 cm were considered unviable nesting locations and were excluded from σE calculations.

The frequency of flooding events is also known to increase across the breeding season; therefore, the impact of nest elevation on flooding risk and the potential for phenotypic plasticity is likely to depend on egg laying date [3]. Laying date was incorporated into all analyses, defined as the date that the first egg of a clutch was laid, estimated with a precision of 1–2 days using methods described by van de Pol *et al.* [47].

(d) Geomorphological model

The elevation of nest sites on the salt marsh will increase naturally over time due to sedimentation (primarily driven by winter flooding) and glacial rebound [48]. To distinguish plastic changes in nest elevation from such geomorphological processes we used a geomorphological model designed and parameterized with field data from our study island to determine the annual rate of saltmarsh accretion as a function of elevation (see [3] for model details).

(e) Data analysis

Analyses were conducted using general linear mixed models with a Gaussian distribution (log identity), using the package *nlme* in R [49,50]. Akaike's Information Criterion, with a correction for small sample size (AICc), was used to conduct model selection [51], taking care to avoid the addition of 'uninformative variables' [52]. We carried out a model selection process with package MuMIn [53].

The best supported random effects structure was determined by comparing AICc values of models with varying random effects structures using maximum likelihood. Although *H. ostralegus* tend to form long-term pair bonds, pair divorce and widowhood does occur (8% and 7% per annum respectively; [36,44]); therefore, we initially considered both male and female identity in our random effects structure. In the analysis of environmental cues, we found that male identity explained more of the variation in nest elevation than female identity (see Results); therefore, the rest of our study is focused on male behaviour. In the learning analysis, model comparisons showed no benefit of including any random effects, and all subsequent learning analysis was carried out using general linear (non-mixed) models (electronic supplementary material, table S1).

Over the course of the long-term study the size of the study area was expanded, with more high elevation locations included in later years. Therefore, we included a random intercept term 'AreaID' to account for the potential influence of sub-area on nest elevation trends. We fitted our model error term as a function of 'Method' to account for differences in precision between *in situ* and *ex situ* collection methods.

In both the analysis of environmental cues and changes over time we carried out within-group centring of 'MaleID' [54]. This method allowed us to exclude any potential changes in nest elevation that may be driven by changes in population composition and focus specifically on phenotypic change within individual males over their lifetime. At the edge of our study site some males have the opportunity to nest on a large artificial sea wall (74 males; 20% of our study population). Nest elevation values from these pairs can lead to a violation of the assumption of normality within our data. Therefore, we conducted a Winsorisation procedure, in which nests high on the sea wall were capped at the value of the highest recorded non-sea wall nest (260 cm above MHT). In our analysis of within-individual change over time, those pairs with access to the sea wall were found to behave differently to others within the population (see Results). Variation in individual nest elevation was better explained by access to the sea wall than standard deviation of elevations within a territory (σE). As these two variables are strongly confounded, access to the sea wall (Sea wall) was used in place of σE for further analyses.

For the learning analysis, we determined the difference between the elevation of each nest and the elevation of the following nest belonging to the same male (ΔE). The following nest could be in either the same year or the following year and we included a categorical factor in our model to differentiate between these two scenarios (NextYear). This allows us to account for geomorphological processes that may influence nest elevation between seasons. Models were fitted with a fixed effects term for flooding experience (Exp; levels: failed due to flooding, survived a flood, unflooded), Seawall, LayDate, and NextYear. To account for differences in behaviour between birds with different territory characteristics an Exp*Seawall interaction was included. Furthermore, we included an Exp*LayDate interaction to account for potential seasonal variation in behavioural responses.

It is possible that a relationship could occur between flooding experience and nest elevation change (ΔE) even if individuals are selecting nest sites at random. This is due to the bounded nature of nest elevation data (i.e. individuals have a minimum and maximum potential elevation at which they can nest) [55]. For individuals nesting at the lower bounds of potential elevation the majority of alternative nest sites will be higher than their current site. These low nesting individuals are therefore likely to increase their nest elevation in their next nesting attempt, even if nest-site selection occurs at random. As flooded nests are likely to be much lower than unflooded nests this possibility may obscure any effect of flooding experience. We applied two approaches to account for this concern. Firstly, we quantified

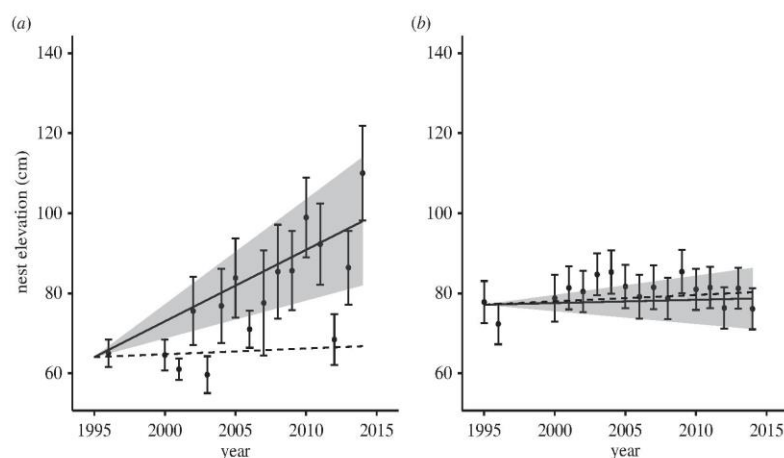


Figure 1. (a) Within-individual change in nest elevation over time for *H. ostralegus* males with access to the artificial sea wall ($1.66 \pm 0.40 \text{ cm yr}^{-1}$; solid line) and rate of nest elevation change predicted by sedimentation (0.13 cm yr^{-1} ; dashed line). Analysis based on 528 *H. ostralegus* nests from 74 individual males (mean 6.5 nests/individual). (b) Within-individual change in nest elevation over time for *H. ostralegus* males without access to the artificial sea wall ($0.07 \pm 0.17 \text{ cm yr}^{-1}$; solid line) and rate of nest elevation change predicted by sedimentation (0.12 cm yr^{-1} ; dashed line). Analysis based on 2384 nests from 311 males (mean 5.3 nests/individual). For both plots, shaded region shows the 95% confidence interval for the slope of observed data.

the relationship between flooding experience and elevation change in randomized data. We conducted 5000 iterations in which we randomized the order of nests for each male, maintaining the association between sea wall, laying date and nest elevation. We then recalculated values of ΔE using this randomly ordered data, estimating the change in nest elevation we would expect under a null hypothesis of random nest-site selection without learning. Additionally, we refitted our top learning model by replacing the experience term (Exp) with a term showing the difference between the elevation of each nest and the median elevation of our study area (140 cm above MHT). We compared our top model with this new model using AICc to test how well distance from the median explains change in nest elevation.

Due to the presence of replacement clutches our data included nests laid by individuals in the same year and across years. Lunar nodal cycle and mean water height measurements were measured at a yearly scale; therefore, analyses of environmental cues consider only changes in nest elevation between years. In comparison, learning analysis considers changes both within the same year and across years. In combination these analyses provide a test of nest elevation changes in *H. ostralegus* both within and between years.

3. Results

(a) Nest elevation consistency within males and females

Male identity better explained variation in nest elevation than female identity, suggesting that males are more likely to determine nest elevation. When both male and female identity were fitted as random effects, male explained 20% of variance in nest elevation while female only explained 5%. Importantly, when male identity was included alone it was able to explain all the variation previously explained by female (26%), but female was only able to explain 19% of variation when included without male. The long-term pair bonds formed in *H. ostralegus* mean that male and female identity will not be

fully independent; therefore, in subsequent analyses we excluded female identity from our random effects structures.

(b) Nest and territory characteristics

Oystercatchers selected relatively high nest sites within their territory, although they did not nest at the highest sites available. On average, *H. ostralegus* laid nests higher than their mean territory elevation (5.7 cm, 95% CI = 4.1–7.2) but far below the maximum territory elevation (–59.4 cm, 95% CI = –56.6 to –62.1). The median mean elevation of *H. ostralegus* territories was 68.2 cm above MHT (range: 20.6–380.8 cm) and the median standard deviation of elevation within a territory was 18.0 cm (range: 0.4–188.4 cm).

(c) Phenotypic change over time

Individual *H. ostralegus* showed an increase in nest elevation over time; however, this change was restricted to those breeding birds with access to the artificial sea wall (74 pairs; 20% of the population). Birds with access to the sea wall showed a strong positive increase in nest elevation, more rapid than geomorphological processes would predict (figure 1a, table 1; $\beta_{\text{TIME}} = 1.66 \text{ cm yr}^{-1}$, 95% CI = 0.88–2.44), while those birds without a sea-wall territory showed no nest elevation change over time (figure 1b, table 1; $\beta = 0.07 \text{ cm/year}$, 95% CI = –0.26–0.40). The presence of the sea wall was able to explain variation in nest elevation more effectively than standard deviation of elevations within the territory (σE ; table 1). *Post hoc* analysis including only those individuals with access to the sea wall showed a significant increase in sea-wall use over time (electronic supplementary material, figure S4); however, these sea-wall nests constituted only 9.2% of all nests laid by sea-wall birds and only 1.6% of all measured nests. Similar results were obtained when we considered changes in nest elevation of females instead of males (electronic supplementary material, table S3).

Table 1. Coefficients of models investigating within-individual change in *Haematopus ostralegus* nest elevation over time (cm $\pm$ s.e.). Models include Time, standard deviation of elevations within territories (σE) and egg laying date (LayDate). All models within the 95% confidence set are displayed plus the null model; for full model selection results see electronic supplementary material, table S2. *Post hoc* analysis includes a categorical term to account for the presence of an artificial sea wall (Seawall). Nests with a sea wall are used as the reference category. k denotes the number of parameters estimated in each model; w_i denotes AICc model weights.

$\Delta AICc$	w_i	k	intercept	time (years)	σE (cm)	time * σE		
0.00	0.91	4	79.56 (± 4.33)	0.38 (± 0.16)	0.06 (± 0.02)	0.01 ($\pm 0.03e^{-1}$)		
5.91	0.05	2	79.58 (± 4.37)	0.32 (± 0.16)	—	—		
6.09	0.04	1	79.52 (± 4.38)	—	—	—		
Post hoc comparison								
$\Delta AICc$	w_i	k	intercept	time (years)	σE (cm)	time * σE	seawall	time * seawall
0.00	0.99	4	81.75 (± 9.51)	1.66 (± 0.40)	—	—	-2.41 (± 10.80)	-1.59 (± 0.43)
10.20	0.01	4	79.56 (± 4.33)	0.38 (± 0.16)	0.06 (± 0.02)	0.01 ($\pm 0.03e^{-1}$)	—	—
16.29	0.00	1	79.52 (± 4.38)	—	—	—	—	—

(d) Phenotypic plasticity in response to environmental cues

Both water levels during the preceding breeding season (May–June) and lunar nodal cycle position showed a positive correlation with water height during the current season (water height: Pearson's correlation 0.70, 95% CI = 0.51–0.83; lunar nodal cycle: Pearson's correlation 0.27, 95% CI = -0.02–0.53), suggesting that these could provide a reliable cue of future flooding risk. The influence of lunar nodal cycle position on nest elevation was included in the best supported model, but the direction of the effect was opposite to our prediction (figure 2a; table 2). Model selection provided little support for a positive relationship between water height in either the preceding or current breeding season and changes in individual nest elevation (figure 2b,c; electronic supplementary material, table S4). Frequency of sea-wall use also showed no change in response to any of the three tested environmental cues (electronic supplementary material, table S5). Similar results were obtained when we considered changes in nest elevation of females instead of males (electronic supplementary material, table S6).

(e) Learning response

Flooding experience had a strong effect on nest elevation change. The top model contained flooding experience, access to the artificial sea wall (Seawall) and an interaction between the two (table 3). Males that experienced no flooding showed no change in nest elevation (figure 3; table 3, $\beta_{\text{UNFLOODED}} = -1.19$ cm, 95% CI = -6.03–3.65). Males that experienced a flood increased their nest elevation more than those that had not experienced a flood, regardless of the ultimate fate of the flooded nest (figure 3; table 3, $\beta_{\text{FAILED}} = 21.24$ cm, 95% CI = 5.19–37.29; $\beta_{\text{SURVIVED}} = 21.61$ cm, 95% CI = 11.07–32.15). Whether the next nest was laid in the same year or the next year had no impact on the change in elevation (table 3, $\beta_{\text{NEXTYEAR}} = 1.02$, 95% CI = -2.76–4.80). In *post hoc* analysis, we found that individuals that had previously experienced flooding, in breeding seasons before the current year, behaved the same as those individuals that had no earlier flooding experience (electronic supplementary material, table S8).

However, a randomization procedure showed that the differences in nest elevation change between flooded and unflooded nests were of the same magnitude as we would expect from birds exhibiting random nest-site selection without learning (figure 3; electronic supplementary material, figure S5). Furthermore, a model including the difference between nest elevation and the median elevation in our study site was able to explain observed changes in nest elevation more effectively than flooding experience (electronic supplementary material, table S9). The differences we observed between flooded and unflooded nests were likely driven by differences in nest elevation between these two groups (electronic supplementary material, figure S6; $\beta_{\text{UNFLOODED}} = 27.47$ cm, 95% CI = 22.56–32.40). Similar results were obtained when we considered changes in nest elevation of females instead of males (electronic supplementary material, table S10).

(f) Fecundity selection landscape

We expected increased flooding risk to impose directional selection on nest elevation via the fitness component of nest success. However, as our results showed no evidence of phenotypic plasticity in *H. ostralegus* nest elevation we went on to specifically test the relationship between nest elevation and annual reproductive success (fledgling production). This *post hoc* analysis provided no evidence for directional selection on *H. ostralegus* nest elevation but did show evidence for stabilizing selection in this trait (figure 4; electronic supplementary material, table S11).

This analysis accounts for the impact of flooding events on *H. ostralegus* nest success [3] as well as selective pressures imposed via other fitness components that may vary with nest elevation (e.g. chick mortality or nest predation). We measured within-territory changes in nest elevation to avoid any potential differences in reproductive success that may be driven by environmental differences between territories. In this way, we considered the impact of *relative* changes in nest elevation (within a territory) on *H. ostralegus* reproductive success. We also included terms to account for variation in reproductive success that may be caused by differences in social status (whether a territory has access to the coast) and flooding risk between territories (mean

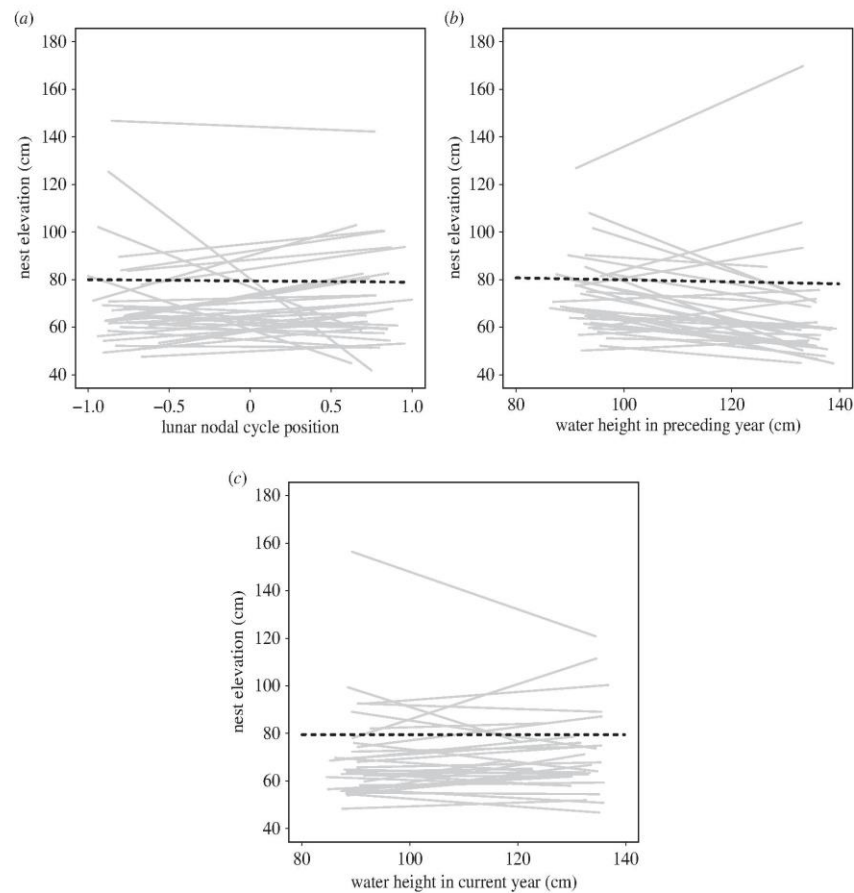


Figure 2. Relationship between *Haematopus ostralegus* nest elevation and (a) lunar nodal cycle position, where a value of 1 represents a water height peak and -1 represents a trough (dashed lines); (b) mean water height in the breeding season before nesting occurred (May–June); and (c) mean water height in the breeding season of nesting (May–June). Solid lines show nest elevation slopes for all male *H. ostralegus* with more than 10 years of data ($n = 32$). All elevation data measured in centimetres above mean high tide in 1971. Analysis conducted using 2912 nests from 1129 males.

Table 2. Coefficients of models investigating the role of potential environmental cues on *Haematopus ostralegus* nest elevation (cm $\pm$ s.e.). Models include within-individual effects of lunar nodal cycle (LNC), water height in the current breeding season (May–June; Water), and sea-wall access (Seawall) where birds with the sea wall are used as the reference category. Top two models based on AICc are displayed plus the null model; for full model selection results see electronic supplementary material, table S4. k denotes the number of parameters estimated in each model; w_i denotes AICc model weights.

ΔAICc	w_i	k	intercept	seawall	LNC	water (cm)	LNC * seawall	water * seawall
0.00	0.99	4	77.86 (± 9.88)	1.56 (± 11.21)	-2.25 (± 0.55)	—	2.72 (± 0.62)	—
17.93	<0.01	4	80.22 (± 9.62)	-0.87 (± 10.92)	—	-0.58 (± 0.54)	—	0.74 (± 0.61)
19.86	<0.01	1	79.52 (± 4.38)	—	—	—	—	—

territory height). We considered both a linear and quadratic relationship between elevation and reproductive success to test for directional and stabilizing selection respectively. Models were compared using AICc. The model structure is discussed in greater detail in supplementary material (see electronic supplementary material, Appendix B).

4. Discussion

This study used an extensive longitudinal behavioural dataset, collected over two decades, to investigate behavioural plasticity in response to increasingly frequent extreme climatic events (ECEs). Despite increases in the mean nest elevation

Table 3. Coefficients of models investigating the role of flooding experience (Exp) on changes in *Haematopus ostralegus* nest elevation from one breeding attempt to the next (cm $\pm$ s.e.). Models include whether individuals have access to the artificial sea wall (Seawall) and a categorical variable specifying whether nest elevation change was measured within the same year or across two consecutive years (NextYear). Unflooded nests in the same year with access to the sea wall are used as the reference category. All models within the 95% confidence set are displayed plus the null model; for full model selection results see electronic supplementary material, table S7. k denotes the number of parameters estimated in each model; w_i denotes AICc model weights.

Δ AICc	w_i	k	intercept	survived	failed	nextyear	seawall	survived * seawall	failed * seawall
0.00	0.65	7	−1.08 ($\pm$ 2.31)	21.61 ($\pm$ 5.38)	21.24 ($\pm$ 8.19)	1.02 ($\pm$ 1.93)	−1.19 ($\pm$ 2.47)	−10.82 ($\pm$ 6.74)	−11.60 ($\pm$ 9.91)
1.40	0.32	6	−0.71 ($\pm$ 2.19)	21.40 ($\pm$ 5.37)	21.35 ($\pm$ 8.19)	—	−1.14 ($\pm$ 2.47)	−10.62 ($\pm$ 6.73)	−11.72 ($\pm$ 9.90)
50.07	<0.01	1	0.42 ($\pm$ 0.95)	—	—	—	—	—	—

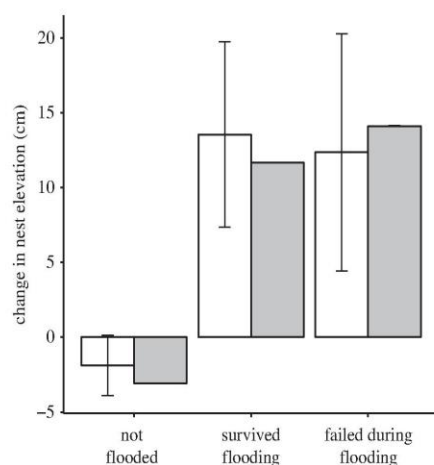


Figure 3. Impact of flooding experience on *Haematopus ostralegus* nest elevation change in both observed data (white) and randomized data reflecting random nest-site selection (grey; see electronic supplementary material, figure S5). Error bars represent 95% confidence intervals for observed data. Analysis conducted using 1508 nests from 297 males.

of our study population we were unable to show evidence of phenotypic plasticity in *H. ostralegus* nest elevation in response to extreme flooding events. We documented within-individual increases in nest elevation over time in a limited subset of our study population; however, we found no evidence that this phenotypic change had occurred in response to flooding. There was no evidence of behavioural plasticity in *H. ostralegus* nest elevation in response to environmental cues or as a learned response to previous flooding experience. Although flooding events disproportionately impact the reproductive success of low nesting birds, *post hoc* evidence of stabilizing selection in the fecundity selection landscape suggests that the general absence of behavioural plasticity may be a consequence of counter-acting selective pressures that disfavour increased nest elevation.

(a) Nest elevation as a repeatable trait

Interestingly, we found that male identity better explained variation in nest elevation than female identity, suggesting

that site choice by males during nest cup building may be a more important mediator of nest elevation than the female decision of which nest cup to use for egg laying. Repeatability of nest elevation within males (26% of variance explained) highlights the potential for heritability to occur in this trait. This repeatability may be driven at least partly by territorial and physical constraints (i.e. males do not have access to nest sites at all potential nest elevations); however, our results suggested that males often have access to a range of elevations within their territory. Encouragingly, all our results were consistent using both males and females showing that our conclusions are not driven by our focus on male identity.

(b) Does phenotypic plasticity occur in response to extreme flooding events?

There was no evidence of increased nest elevation in response to either of our tested environmental cues. Nest elevation showed no positive relationship with either the lunar nodal cycle phase or water heights in the preceding breeding season, irrespective of whether individuals had access to the artificial sea wall. It may be possible that *H. ostralegus* is able to use an alternative environmental cue to track changes in flooding patterns; however, our analyses also showed no relationship between nest elevation and water height measured in the same year, which seems to discount this possibility.

There was also no evidence of learning in response to flooding experience. Although increases in nest elevation following a flooding experience could be interpreted as evidence of learning in *H. ostralegus*, the differences we observed between flooded and unflooded nests were no larger than expected due to random nest-site selection (figure 3; electronic supplementary material, table S9). This strongly suggests that the apparent learning result is due to the fact that flooded nests are found at lower elevations, rather than providing evidence of individual learning. It is worth considering that random nest-site selection could help explain previous reports of learning in response to flooding events [28–30], and will be important to consider in future studies that test changes in bounded data over time.

The lack of both phenotypic plasticity in response to measured environmental cues and lack of learning may be a reflection of the stochastic and unpredictable nature of extreme floods. Although water heights in the previous breeding

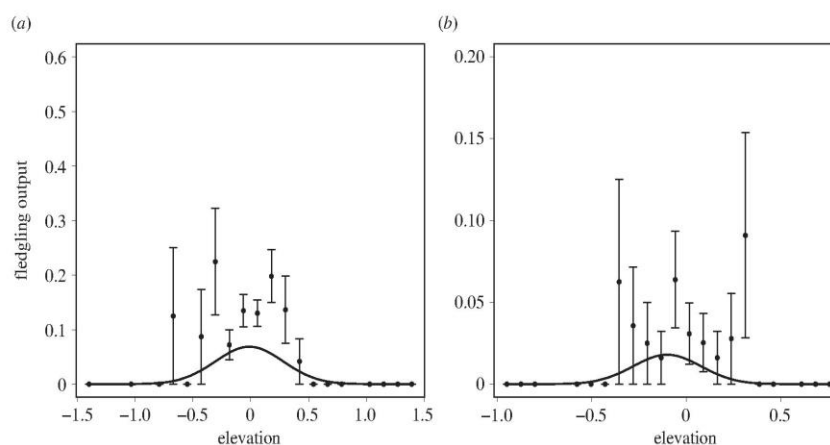


Figure 4. Quadratic relationship between *Haematopus ostralegus* nest elevation (within territories) and reproductive success (fledgling output $\pm$ s.e.) in (a) coastal and (b) non-coastal territories. x axis represents relative change in elevation within territories. See electronic supplementary material, Appendix B, for detailed methods.

season and lunar nodal cycle position were correlated with mean breeding season water height (0.70 and 0.27 respectively), it is possible that these correlations may not be sufficient to act as reliable cues. Theoretical work by Reed *et al.* [15] found that phenotypic plasticity would be maladaptive to population viability where environmental cues showed a reliability (i.e. correlation between a cue and the environmental optimum) of less than 0.5, with this threshold increasing further as environments become more stochastic. Similarly, learning is only likely to evolve when conditions in one year are indicative of conditions in the next [23]. While climate change has driven an increase in mean water heights, whether an extreme flooding event will occur in a given year greatly depends on both wind speed and direction as well as monthly tidal cycles (i.e. spring tides) [3]. Although there is a correlation between mean breeding season water heights (0.70), the correlation between the occurrences of extreme floods from one breeding season to the next between 1971 and 2015 is much smaller (Pearson's correlation 0.38, 95% CI = 0.03–0.56). Indeed, in comparison to other threats, flooding risk is considered to be fairly unpredictable [30]. Therefore, the lack of evidence for both learning and phenotypic plasticity in response to environmental cues potentially supports the idea that ECEs are simply too unpredictable to facilitate the use of phenotypic plasticity.

(c) Counter-acting selection pressures

Although we found no evidence of learning or phenotypic plasticity in response to our tested environmental cues, we did observe an increase in nest elevation over time in those males with territorial access to the artificial sea wall (74 pairs; 20% of our study population). The explanation for this trend is not immediately clear. There is a possibility that such a result stems from geomorphological processes. Sea-wall territories typically encompass habitat in both low-elevation saltmarsh and on the high-elevation sea wall. Over time, territory boundaries are likely to have changed to incorporate a larger proportion of sea-wall habitat, driven by both the disappearance of other pairs that compete for sea-wall space as the population has declined [45] and the loss of available saltmarsh

habitat due to coastal erosion (LD Bailey 2014, personal observation). Population declines and saltmarsh erosion will likely lead to greater utilization of sea-wall nest sites without any need for behavioural plasticity in nest elevation, with individuals selecting sea-wall nest sites more often by chance. However, as the frequency of flooding events, the rate of saltmarsh loss, and reduction in population size have changed concurrently over the study period our ability to distinguish between this possibility and other behavioural mechanisms is limited.

Alternatively, the phenotypic change we observe in sea-wall birds may be evidence of phenotypic plasticity in response to environmental cues unrelated to flooding frequency. What such an alternative cue might be is unclear. It is also not immediately clear why we might observe marked differences in phenotypic change between sea-wall and non-sea-wall birds within our study population. One potential explanation may be environmental differences between sea-wall and non-sea-wall areas. The sea-wall represents a unique nesting habitat for *H. ostralegus*, as it provides high elevation nest sites but is covered in short vegetation, due to both sheep and geese grazing, rather than the tall perennial grasses (e.g. *Elymus athericus*) that dominate natural high-elevation locations [56,57]. *H. ostralegus* are generally known to select nest sites with relatively low vegetation [42], a pattern that has been observed directly in our study population (electronic supplementary material, Appendix C). This preference for low vegetation may be driven by mortality selection, as areas with low vegetation provide incubating adults with good visibility to spot approaching threats [58]. In long-lived species like *H. ostralegus* a preference for increased adult survival at the expense of nest survival, which often decreases in lower vegetation, would be expected [59]. Therefore, the disparity we see between sea-wall and non-sea-wall birds may present evidence for competing fecundity and mortality selection on *H. ostralegus* nest-site selection behaviour. Further study on *H. ostralegus* nest preference may allow for a better understanding of nest elevation responses in sea-wall birds. For example, future studies could consider artificially reducing vegetation height in high elevation areas to observe *H. ostralegus* nesting responses.

In addition to the importance of vegetation height, alternative selection pressures may also exist that will influence

H. ostralegus nest elevation decisions. It is possible that high-elevation sites may make nests more obvious to the avian nest predators that dominate this study system. Similarly, vegetation type may play an important role, with nesting individuals potentially showing a preference for specific ground cover so as to increase nest camouflage [60]. As vegetation type covaries strongly with elevation, due to differences in winter flooding frequency [56,57], it is possible that increasing nest elevation may necessitate nesting in non-preferred vegetation. Therefore, changes in nest-site characteristics at higher elevations may reduce reproductive success through increased predation.

The presence of counter-acting selective pressures on various components of reproductive success would help explain the lack of evidence for directional fecundity selection in nest elevation and thus help explain why the majority of our studied individuals show no change in nest elevation. Although flooding events are known to cause high reproductive failure in *H. ostralegus* [3] alternative selective pressures, such as those discussed above, may be inhibiting any plastic nest elevation response. This may be further exacerbated by the infrequent nature of ECEs, with higher elevation nest sites potentially favoured in flooding years but selected against in non-flooding years [10,30,35]. Although there is currently no clear selection for higher nests, as flooding events become more frequent the selective landscape may begin to change. It will be imperative to consider the possibility of counter-acting selective pressures in other cases where we seek to understand responses to ECEs. While the detrimental impacts of ECEs are clear during extreme years, we must also incorporate factors that drive organismal responses in the more frequent benign conditions [61]. This raises the importance of long-term datasets for studying ECEs as they will provide insights into the responses of organisms in both extreme and non-extreme years.

(d) Alternatives to phenotypic plasticity

As *H. ostralegus* is a long-lived species, we initially hypothesized that phenotypic plasticity in nest-site selection would provide the most likely explanation for the increasing mean nest elevation observed within our population [35]; however, our current analyses provide no evidence to support this prediction, compelling us to consider alternative mechanisms. Micro-evolution in nest elevation is possible, although the long generation time of our study species makes this explanation unlikely. Selective appearance, where new breeders settle disproportionately in higher elevation areas, or selective disappearance, where individuals in low elevation areas leave the population more often, may provide more likely alternative explanations. Importantly, any of these mechanisms would explain observed increases in the population without the need for phenotypic plasticity over the lifetime of an individual [54]. It seems plausible that individuals leaving the population (selective disappearance) will be the more important modulator of population elevation due to the declines observed in this species, although whether this would be driven by adult mortality (i.e. higher mortality at low elevation sites) or dispersal (i.e. abandonment of low elevation territories by breeding individuals) is unclear. A general shift from coastal to inland breeding habitats has been observed in *H. ostralegus* across Europe over the past decades [62], suggesting that dispersal may play an important role; however, to disentangle these

potential mechanisms effectively will require an analysis of settlement, mortality and dispersal patterns across both space and time.

(e) Consequences for shorebird conservation

From our results, it seems unlikely that phenotypic plasticity in nest elevation will provide an effective mechanism by which individuals can reduce their flooding risk. Consequently, the viability of our *H. ostralegus* population is likely to be seriously threatened by increasing sea levels and changing storm patterns [3]. Greater utilization of the sea wall by some individuals (74 pairs; 20% of the population) is unlikely to provide a solution. Although the number of nests laid directly on the sea wall has increased over time (electronic supplementary material, figure S4), the total number of nests on the sea wall is still limited (46 of 528 nests laid by birds with access to the sea wall) and none of these nests have produced fledglings. Greater utilization of the sea wall may therefore represent an example of maladaptive plasticity, providing further evidence that nesting at higher elevations entails potential costs.

The issue of coastal flooding may present a similar threat to other coastal nesting birds if plastic responses to flooding are generally uncommon; however, whether the results observed in *H. ostralegus* will be broadly applicable to other species is still an open question. Other coastal species may experience fewer reproductive detriments from nesting at higher elevations or in taller vegetation than observed in *H. ostralegus*, potentially facilitating greater nest-site movement [30,33,63]. It is also important to consider that responses to flooding risk may occur through other behavioural or physiological traits, such as egg laying date [3], flooding resilience of eggs [31], nest structure [64], or site fidelity [65]. While we focused specifically on nest elevation as the most effective mechanism for combating nest flooding, we cannot rule out the possibility that coastal bird species may respond to extreme flooding through other traits. Future studies that seek to investigate phenotypic plasticity as a response to ECEs should attempt to measure and compare a range of traits to overcome this limitation.

The lack of evidence for phenotypic plasticity in our study population in response to changing patterns of ECEs contrasts with the prevalence of phenotypic plasticity as a response to gradual changes in climatic means [8]. More studies are needed to see if this is a general pattern, or whether responses to ECEs will vary with the type of ECE (e.g. floods or fires) or the study system. Whether or not a population will respond to ECEs may depend on the frequency with which they occur and the presence of counter-acting forces that may select against organismal responses. Long-term, individual-based studies that encompass multiple ECEs, like ours, will be pivotal to improve our understanding of the impacts of future climatic change. If our result is broadly applicable, it is possible that many populations will be vulnerable to changing patterns of ECEs, with long-lived species, such as *H. ostralegus*, that lack the capacity for rapid inter-generational micro-evolutionary change, likely to be the most vulnerable.

Ethics. No ethics approval was required for this project.

Data accessibility. Data available from the Dryad Digital Repository [66].

Authors' contributions. L.D.B. designed the study with the help of M.v.d.P.; L.D.B., K.O., M.v.d.P. and D.H. collected field data; L.D.B. carried out the statistical analysis; L.D.B., M.v.d.P., D.H., B.J.E. and C.B. helped draft the manuscript.

Competing interests. We have no competing interests.

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Supplementary Material

Appendix A: Additional Tables and Figures

Table S1: Comparison of random effects structure for models investigating change in nest elevation between breeding attempts. Random effects included a unique male ID, female ID and area ID.

Random effects structure	$\Delta AICc$	w_i
None	0.00	0.39
MaleID	2.01	0.14
FemID	2.01	0.14
Area	2.01	0.14
MaleID + Area	4.02	0.05
MaleID + FemID	4.02	0.05
FemID + Area	4.02	0.05
MaleID + FemID + Area	6.04	0.02

Table S2: Comparison of models investigating within-individual change in *Haematopus ostralegus* nest elevation over time. Models included a term for Time, standard deviation of elevation within territories (σE) and laying date (LayDate). k denotes the number of parameters estimated in each model. w_i denotes AICc model weights.

Model	$\Delta AICc$	w_i	k
Time * σE	0.00	0.91	4
Time	5.91	0.05	2
Null	6.09	0.04	1
Time * LayDate	20.76	< 0.01	4

Table S3: Parameter estimates of a model investigating within-female change in *Haematopus ostralegus* nest elevation over time (cm $\pm$ SE). Models also considered whether an individual had access to the artificial seawall within their territory (Seawall). Territories including a seawall were used as the reference category.

Intercept	Time (Year)	Seawall	Time * Seawall
81.63 ($\pm$ 9.54)	1.35 ($\pm$ 0.50)	-2.19 ($\pm$ 10.82)	-1.02 ($\pm$ 0.55)

Table S4: Models investigating the role of potential environmental cues on the nest elevation of *Haematopus ostralegus*. Models included terms for within-individual effects of lunar nodal cycle (LNC), mean water heights in the current (Water_t) and previous (Water_{t-1}) breeding seasons (May – June), plus whether an individual has access to the seawall (Seawall) and egg laying date (LayDate). k denotes the number of parameters estimated in each model. w_i denotes AICc model weights.

Model	ΔAICc	w_i	k
LNC * Seawall	0.00	0.99	4
Water_t * Seawall	17.93	< 0.01	4
Water_{t-1} * Seawall	19.03	< 0.01	4
Null model	19.86	< 0.01	1
Water_{t-1}	22.56	< 0.01	2
LNC	22.64	< 0.01	2
Water_t	22.80	< 0.01	2
LNC + Water_{t-1}	25.20	< 0.01	3
Water_{t-1} + Water_t	25.50	< 0.01	3
LNC + Water_t	25.52	< 0.01	3
LNC + Water_t + Water_{t-1}	28.07	< 0.01	4
LNC * LayDate	34.10	< 0.01	4
Water_t * LayDate	36.84	< 0.01	4
Water_{t-1} * LayDate	37.19	< 0.01	4

Table S5: Coefficients from models investigating the effect of lunar nodal cycle (LNC) and water heights in the preceding (Water_{t-1}) and current (Water_t) breeding season (May – June) on the use of the artificial seawall ($\pm\text{SE}$), using a subset of nesting *Haematopus ostralegus* individuals with access to the artificial seawall ($n = 500$).

Intercept	LNC	Water_{t-1}	Water_t
-2.86 (± 0.33)	-0.12 (± 0.06)	-	-
-7.85 (± 10.83)	-	0.03 (± 0.06)	-
2.42 (± 12.60)	-	-	-0.02 (± 0.06)

Table S6: Parameter estimates of a model investigating the role of lunar nodal cycle (LNC) on nest elevation change in female *Haematopus ostralegus* (cm $\pm\text{SE}$). Models included a term for access to the seawall (Seawall), where birds with access to the seawall are used as the reference category.

Intercept	LNC	Seawall	LNC * Seawall
76.07 (± 10.47)	-2.24 (± 0.60)	3.55 (± 11.89)	2.83 (± 0.67)

Table S7: Models investigating the role of flooding experience (Exp) on nest elevation change in *Haematopus ostralegus*. Models included whether individuals had access to the artificial seawall (Seawall), nest laying date (LayDate) and a categorical variable specifying whether nest elevation change is measured within the same year or across two consecutive years (NextYear). k denotes the number of parameters estimated in each model. w_i denotes AICc model weights.

Model	$\Delta AICc$	w_i	k
Exp * Seawall + NextYear	0.00	0.65	7
Exp * Seawall	1.40	0.32	6
Exp * Seawall + Exp * LayDate + NextYear	7.08	0.02	10
Exp * LayDate + Exp * Seawall	8.75	0.01	9
Exp + NextYear	15.07	<0.01	4
Exp	16.34	<0.01	3
Exp * LayDate + NextYear	21.63	<0.01	7
Exp * LayDate	23.14	<0.01	6
Null model	50.07	<0.01	1

Table S8: Model estimates from post-hoc analysis investigating the role of flooding experience on nest elevation change in *Haematopus ostralegus* (cm $\pm$ SE).

Model investigated the impact of current flooding experience (Exp; whether an individual's last nest was unflooded, flooded and survived, or failed due to flooding) and past flooding experience (PastExp; whether an individual has previously experienced a nest flooding event), plus an interaction between the two.

The model also included a categorical variable specifying whether nest elevation change is measured within the same year or across two consecutive years (NextYear), and whether individuals have access to the artificial seawall (Seawall). Individuals nesting over two years with previous flooding experience and access to the seawall were used as the reference category.

Intercept	SurvFlood	FailFlood	PastExp	Seawall	NextYear	SurvFlood * PastExp	FailFlood * PastExp	SurvFlood * Seawall	FailFlood * Seawall
-0.72 ($\pm$ 2.49)	22.69 ($\pm$ 5.85)	20.72 ($\pm$ 9.68)	-0.83 ($\pm$ 2.13)	-1.00 ($\pm$ 2.52)	1.04 ($\pm$ 1.93)	-3.54 ($\pm$ 6.66)	1.09 ($\pm$ 9.28)	-9.88 ($\pm$ 6.96)	-11.76 ($\pm$ 9.97)

Table S9: Model selection results for models investigating changes in *Haematopus ostralegus* nest elevation from one breeding attempt to the next ($\pm$ SE). Models included a term for the effect of flooding experience (Exp; Flooded survived, flooded failed, unflooded) and the difference between nest elevation and median elevation of our study site (Diff; cm). Models also included whether individuals have access to the artificial seawall (Seawall) and a categorical variable specifying whether nest elevation change was measured within the same year or across two consecutive years (NextYear). Nests in different years with access to the seawall are used as the reference category. k denotes the number of parameters estimated in each model. w_i denotes AICc model weights.

Model	Δ AICc	w_i	k
Diff * Seawall + NextYear	0.00	>0.99	5
Exp * Seawall + NextYear	417.82	<0.01	7

Parameter estimates (best model)

Intercept	Diff (cm)	Seawall	NextYear	Diff * Seawall
-44.24 ($\pm$ 2.82)	-0.73 ($\pm$ 0.03)	21.76 ($\pm$ 3.48)	1.79 ($\pm$ 1.68)	0.39 ($\pm$ 0.05)

Table S10: Parameter estimates of a model investigating the role of flooding experience on nest elevation change in female *Haematopus ostralegus* (cm $\pm$ SE). The model considers the impact of current flooding experience (Exp; whether an individual's last nest was not flooded, flooded and survived, or failed due to flooding), whether an individual has access to the artificial seawall (Seawall) and an interaction between the two. In addition, we include a categorical variable specifying whether nest elevation change is measured within the same year or across two consecutive years (NextYear). Nests in different years with access to the seawall are used as the reference category.

Intercept	SurvFlood	FailFlood	Seawall	NextYear	SurvFlood * Seawall	FailFlood * Seawall
-4.74 ($\pm$ 1.92)	18.74 ($\pm$ 4.15)	13.93 ($\pm$ 6.91)	-3.10 ($\pm$ 2.05)	8.72 ($\pm$ 1.60)	-11.94 ($\pm$ 5.11)	-5.34 ($\pm$ 8.36)

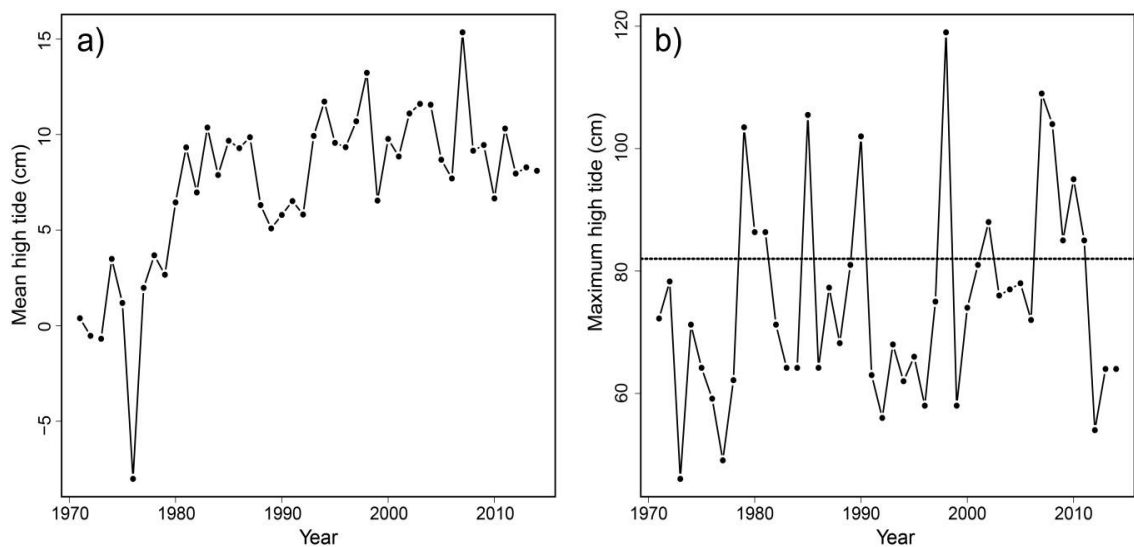


Figure S1: a) Change in mean high tide (cm above mean high tide in 1971) over time on Schiermonnikoog during the breeding season of *Haematopus ostralegus*. b) Change in maximum high tide (cm above mean high tide in 1971) over time on Schiermonnikoog during the breeding season of *Haematopus ostralegus*. Points above the dashed line represent extreme flooding events, defined in methods.

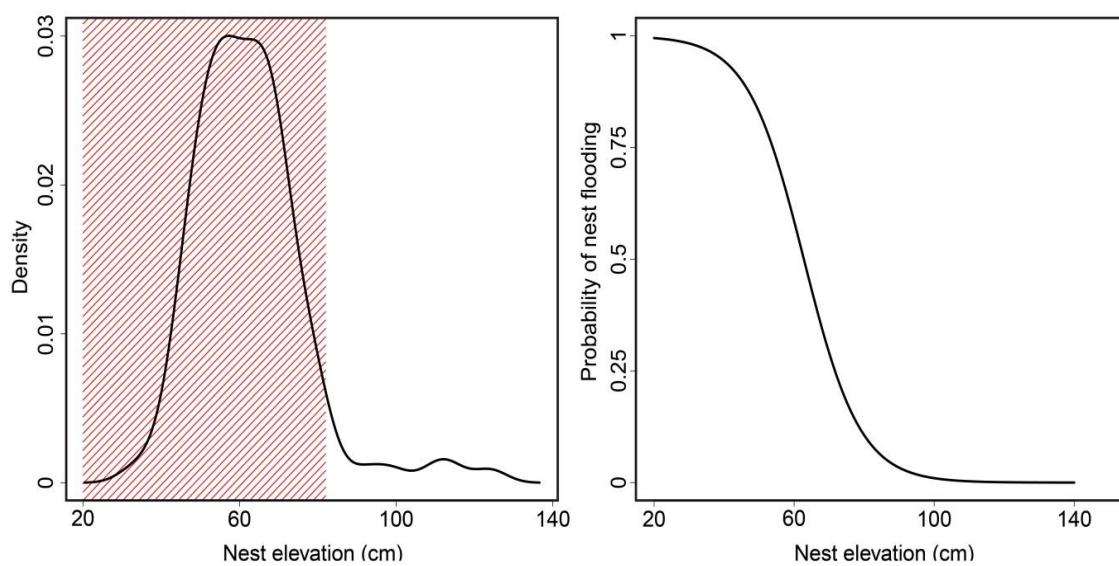


Figure S2: a) Kernel density plot of nest elevation (cm above 1971 mean tide) of *Haematopus ostralegus* in 1995. Shaded area signifies the elevation over which 95% of all nests would be flooded. b) Relationship between *H. ostralegus* nest elevation (cm above 1971 mean tide) and probability of flooding in 1995. Predictions derived from a generalised linear model fitted with a logistic distribution.

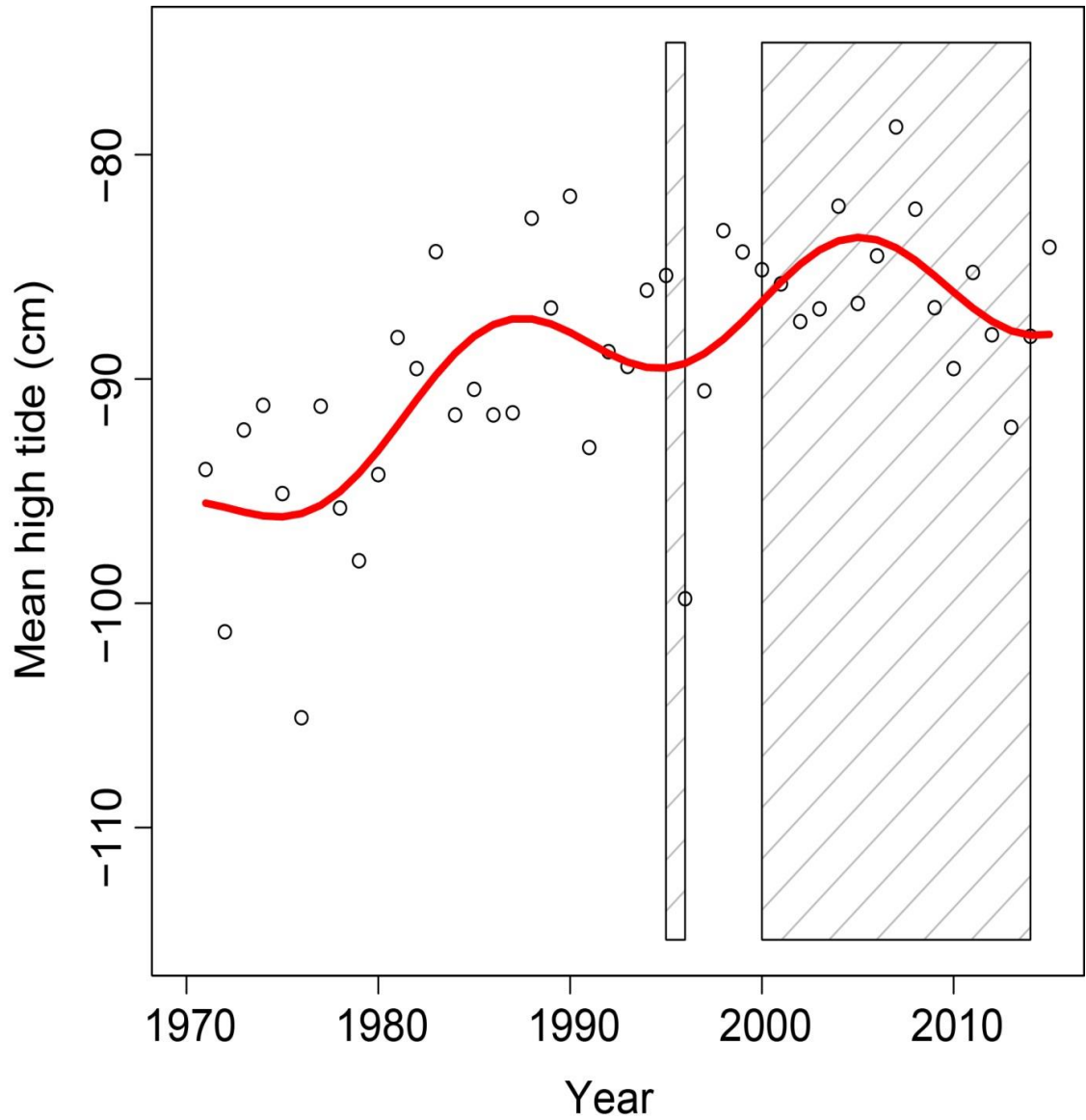


Figure S3: Annual mean high tide (cm above 1971 mean tide) on Schiermonnikoog with fitted lunar nodal cycle trend (Amplitude: 2.22 cm; Phase: -0.76 radians). Shaded boxes show the time period over which *Haematopus ostralegus* nest elevation was measured.

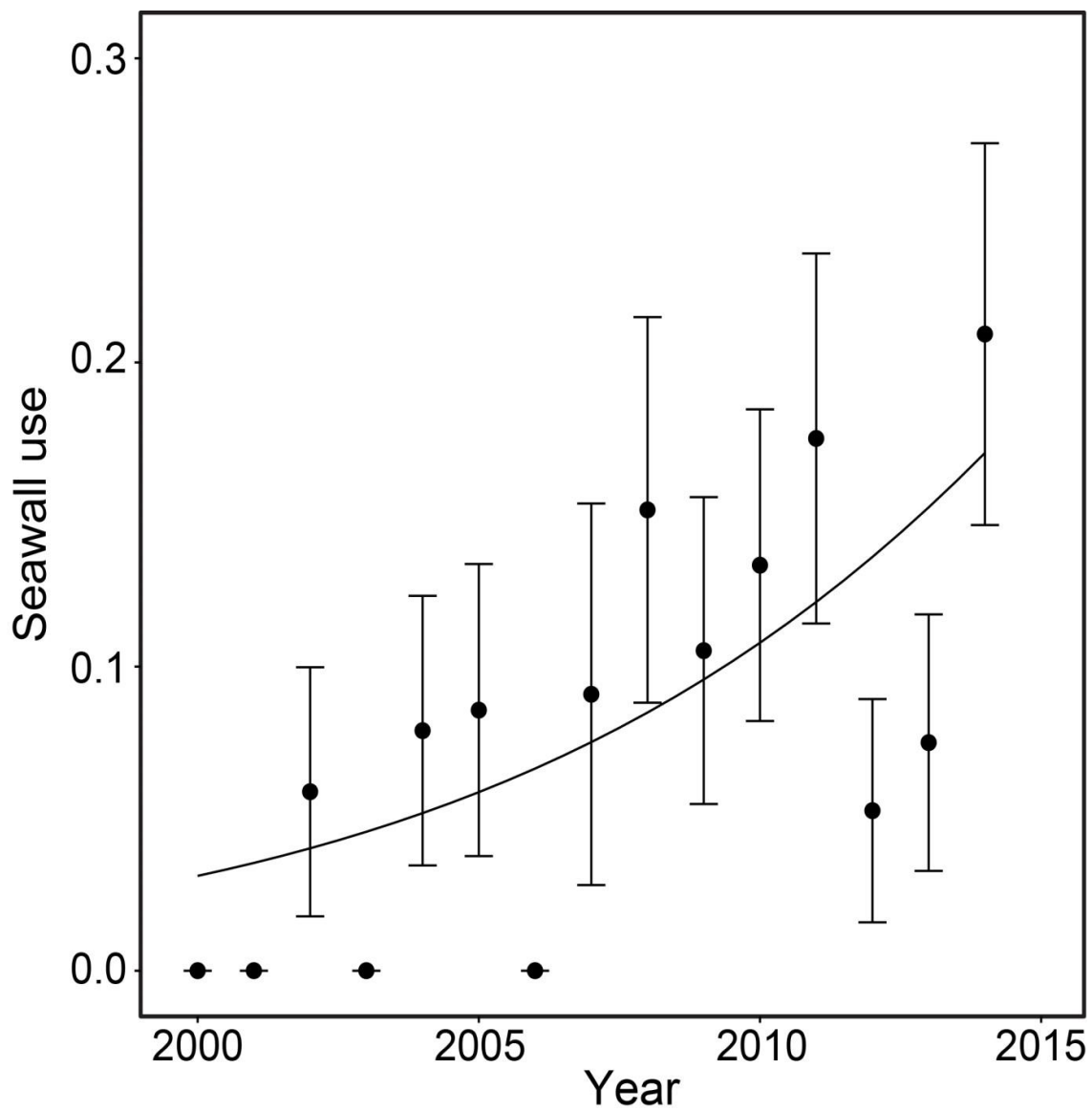


Figure S4: Change in seawall utilisation over time in nesting *Haematopus ostralegus* individuals with access to the artificial seawall ($n = 500$), showing a significant increase in seawall use over time ($\beta_{\text{TIME}} = 0.13$, 95%CI = 0.05 – 0.21). Data modelled using a generalised linear model with a binomial distribution.

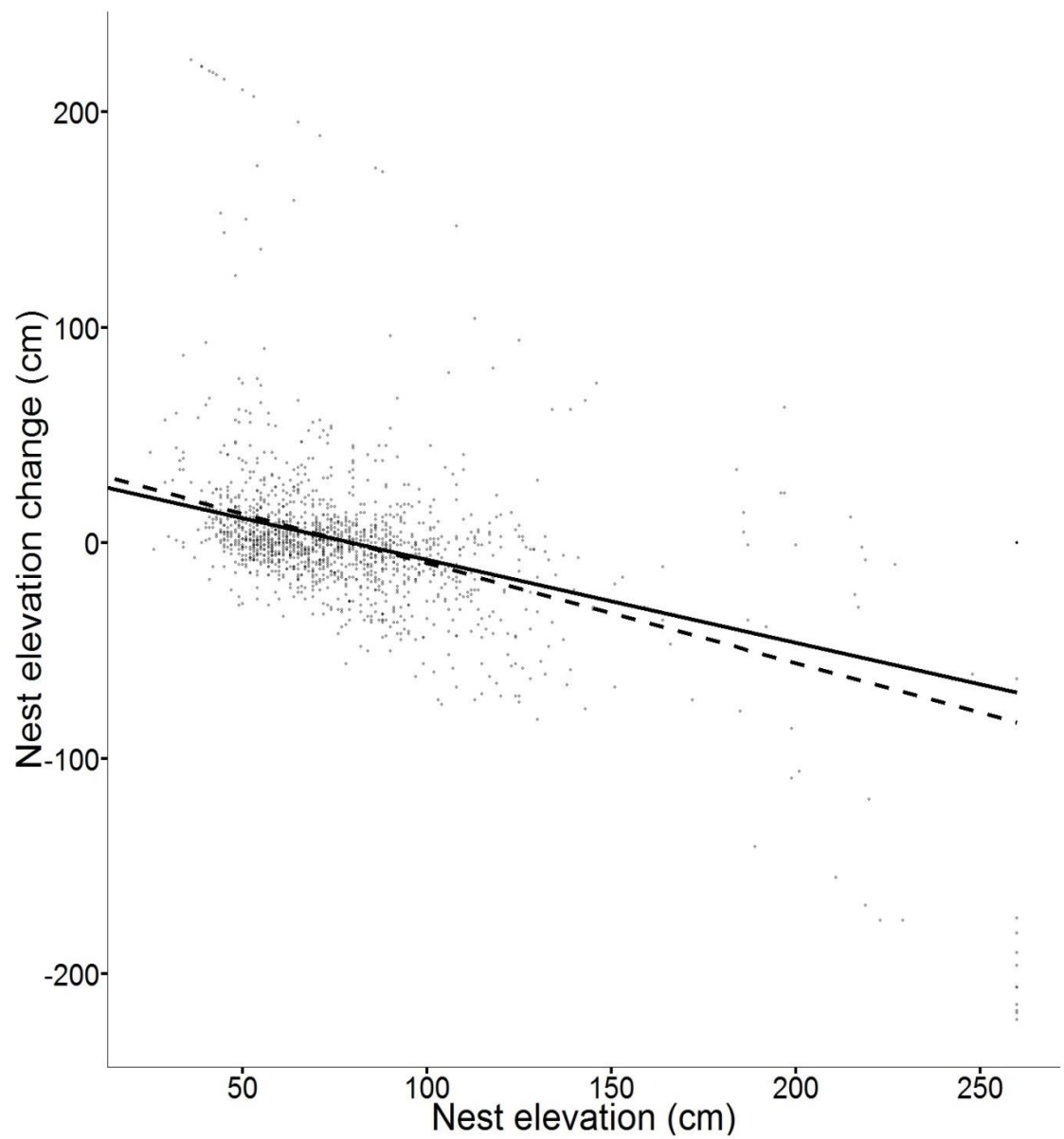


Figure S5: Relationship between nest elevation and change in nest elevation between consecutive breeding attempts for *Haematopus ostralegus*. Lines show observed data (solid line) and randomised data reflecting random nest-site selection (dashed line).

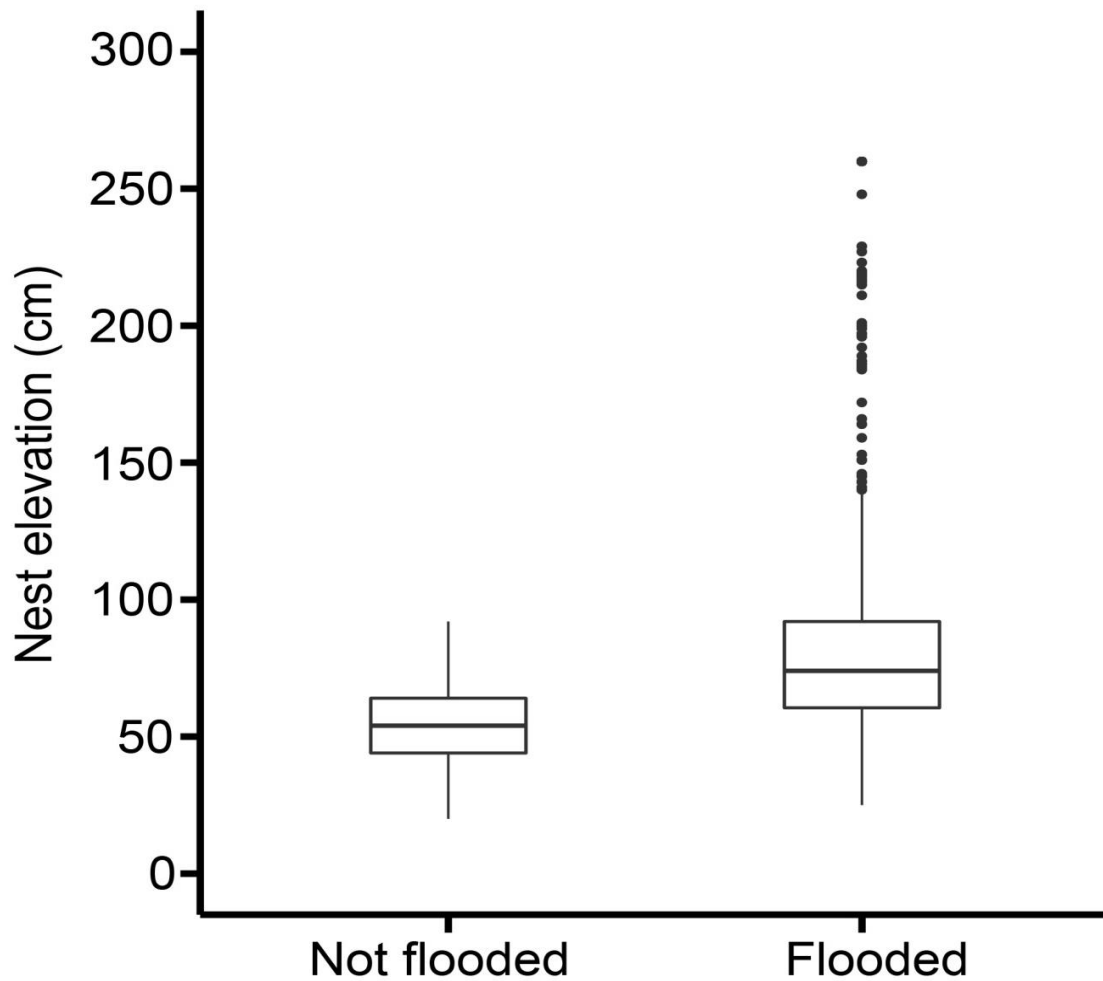


Figure S6: Nest elevation (cm above 1971 mean tide) of *Haematopus ostralegus* nests that experienced a flood and those that were never flooded. Analysis conducted using 1,508 nests from 297 males.

Appendix B: Analysis of fecundity selection landscape in *Haematopus ostralegus*

To analyse the fecundity selection landscape in *Haematopus ostralegus* we tested the relationship between nest elevation and annual fledgling production. *H. ostralegus* territories can vary considerably in their environmental conditions. We mean centred nest elevation within territories to account for these differences. Therefore, our analysis considered the impact of *relative* changes in nest elevation, within a territory, on *H. ostralegus* fledgling production.

Fledgling production is also known to vary considerably with social status (i.e. whether an individual has access to the coast). We included this categorical term in our model to account for these potential differences. Social status is only weakly correlated with nest elevation (Fig S7). Additionally, we predicted that the fledgling production of a territory might vary with the mean elevation of the territory, as higher elevation territories will have lower flooding risk. We included the mean territory elevation as a further term in our model. We also included an interaction between nest elevation and territory elevation to account for the possibility that the strength of directional selection may vary as flooding risk changes.

We predicted that nest elevation in *H. ostralegus* could be under either directional selection (as originally hypothesised) or stabilising selection. Therefore, we fitted models including both a linear and quadratic term for nest elevation. All models were fitted using a generalised linear mixed effects model with a poisson distribution and log link. Nest elevation data was log transformed to allow for model convergence. All models were compared using AICc.

Table S11: Model coefficients for generalised linear mixed models (poisson with log link) investigating the impact of nest elevation on reproductive success in *Haematopus ostralegus* (fledgling output $\pm$ SE). Models includes a fixed effects term for territory status (Status; coastal or non-coastal territory), with non-coastal territories as the reference group. Additionally, an interaction between nest elevation and mean territory elevation (Territory) is included to account for the fact that individuals in higher territories safe from flooding may show a different relationship between elevation and fledgling output than those in low elevation territories. A random intercept term for year and terms for both random slopes and intercepts in territory identity were also included.

Intercept	Elevation (cm)	Elevation ²	Status	Territory	Elevation * Territory	Δ AICc	w_i	k
-4.02 ($\pm$ 0.38)	-0.14 ($\pm$ 0.65)	-5.30 ($\pm$ 2.85)	1.34 ($\pm$ 0.28)	0.04 ($\pm$ 0.11)	-	0.00	0.88	5
-4.14 ($\pm$ 0.39)	-	-	1.33 ($\pm$ 0.28)	-0.01 ($\pm$ 0.10)	-	5.31	0.06	3
-4.14 ($\pm$ 0.40)	-0.43 ($\pm$ 0.36)	-	1.34 ($\pm$ 0.28)	0.02 ($\pm$ 0.10)	-	6.10	0.04	4
-4.14 ($\pm$ 0.39)	-0.27 ($\pm$ 0.46)	-	1.34 ($\pm$ 0.28)	0.02 ($\pm$ 0.10)	-0.14 ($\pm$ 0.25)	7.83	0.02	5

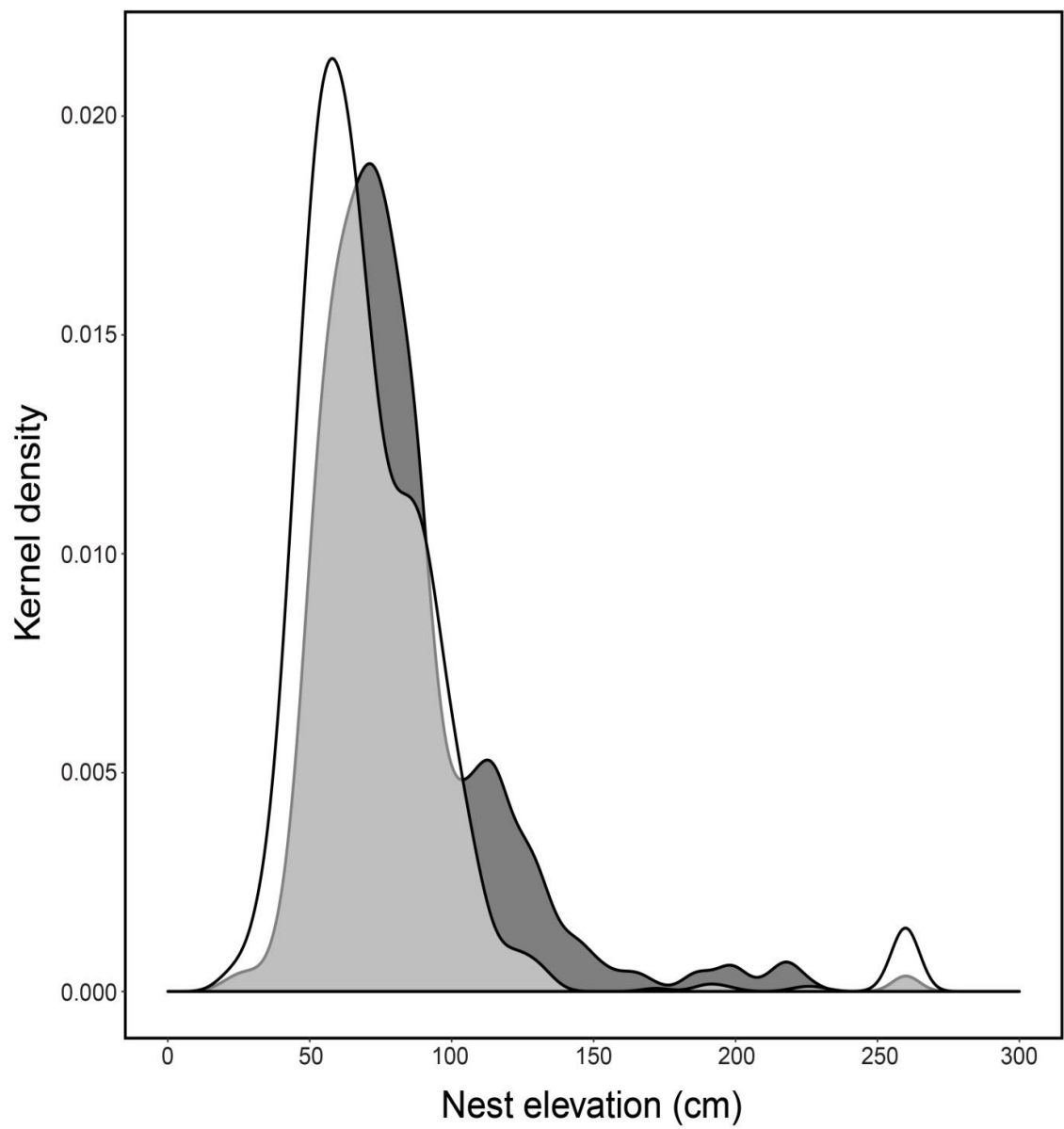


Figure S7: Kernel density plot of *Haematopus ostralegus* nest elevation (cm above 1971 mean high tide) for birds in coastal territories (white) and non-coastal territories (grey).

Appendix C: Analysis of vegetation height choice in *Haematopus ostralegus*

Haematopus ostralegus is generally considered to have a preference for low vegetation nest sites [1], potentially as a means of reducing adult predation [2,3]. We tested for this preference using our long-term dataset of *Haematopus ostralegus* on the Dutch barrier island of Schiermonikoog (53.4833° N, 6.1667° E). Below we outline the methods and present and discuss the results.

Methods

Nesting activity was monitored from April to August, with most nests laid between May and June. Nests were located through systematic searching in the field every 2-3 days, while also revisiting active nests to determine nest fate. Vegetation height data was recorded in 2008 and 2013 at nest sites and at random points within a pair's territory. Measurements were conducted as soon as possible after a nest was found to ensure that vegetation characteristics measured were as similar as possible to those present when breeding pairs made their nest site choice.

To estimate average vegetation conditions around the nest, vegetation height was measured 10 cm away from each nest at the four cardinal points using a graduated survey rod with a 30 cm disc attached. The attached disc was lowered down the survey rod until it came to a stop. Vegetation height, either living or dead, was recorded at the point at which the disc stopped. If no vegetation was present a vegetation height of 0 cm was recorded. To estimate average vegetation conditions within the territory, vegetation height was measured at four random locations within each territory. Random measurement sites were located along a transect running from each focal nest and heading away from the coastline. Four random numbers between 0 and 100 were selected to determine the number of steps along this transect at which each measurement would be collected. Measurement methods were the same as those around the nest. In total, we measured vegetation conditions for 206 different *H. ostralegus* nests (63 in 2008 and 143 in 2013).

To test for vegetation choice, we analysed the relationship between vegetation height in a territory and vegetation height at the nest. If *H. ostralegus* do not consider vegetation height during nest site choice we would expect a direct (1 to 1) relationship between vegetation height in the territory and at the nest as vegetation height at the nest should be driven exclusively by territory conditions. However, if vegetation height is considered we would expect the relationship between territory and nest vegetation to show a shallower slope, as pairs would seek to lay at their preferred vegetation height regardless of the surrounding

territory conditions. Linear models with a Gaussian distribution were used to test the effects of territory vegetation on nest vegetation, using the base function *lm* in R [4]. We considered a continuous term for territory vegetation (VegHeight) and a fixed term for year (Year), plus an interaction between the two. Model comparison was conducted using Akaike Information Criteria with the R package *MuMIn* [5,6].

Results

The relationship between vegetation height in the territory and at the nest was significantly shallower than the 1 to 1 relationship expected if vegetation height is not considered during nest site choice (Fig. S6; Table S9; $\beta_{\text{veg}} = 0.21$; 95%CI = 0.13 – 0.30). There was no discernible difference in this relationship between years (Table S9; $\beta_{2013 \times \text{veg}} = -0.10$, 95%CI = -0.09 – 0.28). Mean nest vegetation height across both years was 12.5 cm.

Discussion

As predicted, our results suggest that *H. ostralegus* considers vegetation height when making nest site choices. From our analysis, we would expect *H. ostralegus* to choose nest sites with a vegetation height of around 12.5 cm. The limited effect of year in our models suggests that this choice is fairly consistent over time.

Our results comply with the general expectation for *H. ostralegus* nest site selection [1]. The use of relatively low vegetation nest sites is likely to be a strategy to help reduce adult predation in this long-lived species [3], potentially even at the cost of higher nest predation [2].

Table S12: Models investigating the relationship between vegetation height at *Haematopus ostralegus* nests and within *H. ostralegus* territories (cm $\pm$ SE). Models include terms for territory vegetation height (VegHeight) and a categorical term for year (Year). 2008 is used as the reference category. *k* denotes the number of parameters estimated in each model. *w_i* denotes AICc model weights.

ΔAICc	<i>w_i</i>	<i>k</i>	Intercept	VegHeight (cm)	Year	VegHeight * Year
0.00	0.73	2	9.81 ($\pm$ 0.69)	-0.22 ($\pm$ 0.04)	-	-
1.99	0.27	4	11.47 ($\pm$ 1.32)	1.15 ($\pm$ 0.07)	-2.25 ($\pm$ 1.55)	0.10 ($\pm$ 0.09)

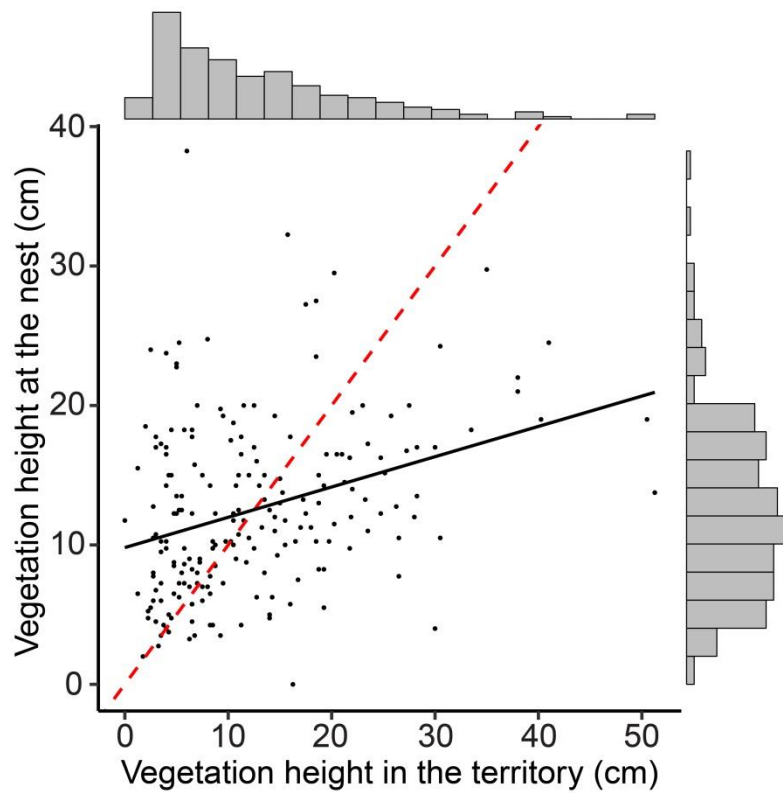


Figure S8: Relationship between the vegetation height of *Haematopus ostralegus* territories and vegetation height around *H. ostralegus* nests. Data collected from 204 nests in 2008 (62 nests) and 2013 (142 nests).

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Chapter 4

Changing habitat selection of a long-lived shorebird in response to extreme climatic events

This chapter is a manuscript currently under preparation for submission.

Changing habitat selection of a long-lived shorebird in response to extreme climatic events

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Abstract

1. Changes in the frequency of extreme climatic events (ECEs), driven by anthropogenic climate change, are likely to have profound impacts on individual fitness, both degrading habitat quality and reducing temporal auto-correlation. Organisms may respond to changes in ECEs by adjusting habitat selection behaviour; however, documenting such changes in the wild can be difficult.
2. We collected data on territory settlement patterns of a long-lived shorebird (*Haematopus ostralegus*) over a 32 year period to determine whether habitat preference for elevation has changed in response to more frequent flooding events. We compared various habitat selection strategies (e.g., conspecific attraction, public information) to understand what information *H. ostralegus* use during habitat settlement.
3. Mean nest elevation of *H. ostralegus* increased over time as flooding events have become more frequent. This was driven by a reduced preference for low elevation habitat by settling birds in the later years of our study. *H. ostralegus* settlement was strongly correlated with conspecific density.
4. *H. ostralegus* exhibits phenotypic plasticity in habitat preference, providing evidence that organisms may be capable of responding to increased frequencies of ECEs. This result may be driven by individuals changing their habitat selection strategy in direct response to increased flooding frequency (i.e. altered elevation preference) or may be explained by the use of other correlated environmental cues during habitat selection that have changed over the study period (e.g. conspecific density). Disentangling these two possibilities may require more direct experimentation on *H. ostralegus* habitat preference.
5. Increased flooding frequency is likely to be a common threat among coastal organisms. This study provides some of the first evidence that vulnerable coastal species may be capable of responding to flooding events; however, the effectiveness of such responses to fully alleviate flooding impacts will depend on both the mechanisms and magnitude of the response.

Introduction

Habitat quality can vary widely across space and time (Orians & Wittenberger 1991), making habitat selection a key driver of reproductive success, survival and fitness (Ens *et al.* 1992; Tupper & Boutilier 1995; Wilson 1998; Kolbe & Janzen 2001; Silberbush & Blaustein 2011). Anthropogenic climate change will cause many organisms to experience rapidly changing patterns of habitat quality, with previously suitable habitat becoming degraded (Davies *et al.* 2006; Pike & Stiner 2007; Grémillet & Boulinier 2009). When these changes lead to an uncoupling of the relationship between habitat cues and true habitat quality, organisms can be ecologically ‘trapped’ using behaviours that are now maladaptive (Robertson & Hutto 2006). For example, increased sea surface temperature has driven changes in the abundance and distribution of fish populations, causing a mismatch between seabird foraging sites and food resources (Grémillet *et al.* 2008).

In addition to changes in mean climate, anthropogenic climate change is likely to increase the frequency of extreme climatic events (IPCC 2013; Coumou & Rahmstorf 2012).

Individual ECEs can have large impacts on population numbers through reduced recruitment (Tryjanowski *et al.* 2009) and increased mortality (Garrahou *et al.* 2009; McKechnie & Wolf 2009). As populations decline, the quantity of information available to make habitat selection decisions is also likely to decline (Schmidt *et al.* 2015). For example, at low densities individuals will have fewer neighbours to observe as a means of assessing patch quality. In particularly small populations this may produce an Allee effect, with the quantity of information being so low that individuals make uninformed and ultimately maladaptive decisions (Schmidt *et al.* 2015; Kokko & Sutherland 2001; Fletcher *et al.* 2012).

In addition, ECEs can also reduce the temporal autocorrelation of environmental conditions. Theoretical modelling suggests that reduced temporal autocorrelation will undermine the effectiveness of strategies that rely on information from previous breeding seasons, such as prior reproductive success. When auto-correlation is extremely low, strategies that require no prior information may even be favoured (Schmidt *et al.* 2015; Boulinier & Danchin 1997; Doligez *et al.* 2003; Bocedi *et al.* 2012). Therefore, both the frequency at which ECEs occur and the impacts of ECEs on habitat quality and population size may have substantial consequences on habitat selection behaviour.

Species may respond to ECE driven changes in habitat quality through phenotypic plasticity or inter-generational micro-evolutionary change driven by natural selection (Schlaepfer *et al.* 2002); however, the effectiveness of these responses will depend greatly on the species or population in question. Rapid habitat degradation will exclude the use of micro-evolutionary responses in species with long generation times (Kokko & Sutherland 2001). Even in short-lived species, it will be necessary for populations to possess high levels of diversity in habitat selection behaviour and/or variation in the transmission of habitat selection strategies between individuals (i.e. genetic heritability or social transmission) for successful micro-evolutionary responses to occur (Kokko & Sutherland 2001; Fletcher *et al.* 2012). Alternatively, organisms may exhibit learning in habitat preference, using both their own reproductive experiences (personal information) and observing the reproductive experiences of others (Danchin *et al.* 2004; Valone 2007). Use of public information is considered a particularly effective habitat selection strategy through which individuals can track environmental change (Kokko & Sutherland 2001; Ponchon *et al.* 2015). It is able to integrate a broad range of biotic and abiotic factors (Valone 2007; Pärt & Doligez 2003) and

removes the need for individuals to sample all habitats, which can be particularly costly (Danchin *et al.* 2004; Valone 2007).

Our current understanding of habitat selection responses to environmental change, as discussed above, is mostly derived from simulation studies (Schmidt *et al.* 2015; Kokko & Sutherland 2001; Fletcher *et al.* 2012; Boulinier & Danchin 1997; Bocedi *et al.* 2012; Ponchon *et al.* 2015). While these studies provide us with an important theoretical background, the amount of work that empirically tests habitat selection changes in response to anthropogenic climate change has been fairly limited (Davies *et al.* 2006). Testing these concepts in the field requires large amounts of detailed, long-term behavioural data, making such work practically challenging (Ponchon *et al.* 2015). This is even more so for studies of ECEs, which will ideally encompass multiple ECE occurrences to avoid being anecdotal (Bailey & van de Pol 2016; Chapter 1).

In this study, we examine changes in habitat selection using a 32 year individual-based dataset of a long-lived shorebird, the Eurasian oystercatcher (*Haematopus ostralegus*). Over the course of the study, rising sea levels and changing wind and storm patterns have led to a rapid increase in the frequency of extreme flooding events, from once every 7.0 years, between 1971 and 1991, to once every 2.7 years since 1991 (van de Pol *et al.* 2010). More frequent flooding events and consequent nest failures have reduced the quality of low elevation habitats, potentially compromising the viability of the population; however, changing nest elevation provides an effective mechanism by which *H. ostralegus* can mediate flooding risk (van de Pol *et al.* 2010).

To alter nest elevation *H. ostralegus* may adjust nest-site selection, which occurs frequently (1 – 2 times a year) at a small spatial scale (within a territory), and territory selection,

occurring infrequently (1-2 times in a lifetime) at a broad spatial scale (across a population). Previous work on the same study population showed that plasticity in nest-site selection had a limited impact on nest elevation (Chapter 3). This may be because nest flooding risk is too difficult to predict at such a fine scale, precluding the development of any sophisticated nest-site selection behaviour in response to flooding events (Orians & Wittenberger 1991; Bayard & Elphick 2011). This study instead focusses on the impacts of broader scale territory selection on nest elevation, focussing on patterns of *H. ostralegus* territory settlement. As territory settlement decisions are made infrequently, territory selection changes will primarily be detected by comparison between individuals, representing slow inter-generational change. If *H. ostralegus* show a response to extreme flooding events through territory selection we would expect to observe increased settlement in high elevation territories as flooding frequency increases.

To investigate changes in territory settlement (hereafter simply ‘habitat selection’) we considered three questions. First, has mean nest elevation of *H. ostralegus* increased over time? We consider time as a surrogate for ECE frequency as extreme flooding frequency has increased steadily over the course of our study. If habitat selection has changed to favour higher sites, we would expect to find an increase in mean nest elevation over time.

Second, can changes in habitat selection explain population trends? As our previous work showed generally weak nest-site selection effects, we would predict that between-individual changes are the key driver of population trends. However, changes in adult mortality (i.e. increased mortality in low elevation territories) may also lead to increasing territory elevation. Therefore, we considered elevation dependency in both adult settlement and mortality.

Finally, what cues do individuals use to make habitat selection decisions? Although *H. ostralegus* may show a preference for high elevation territories they may not directly use elevation information to inform habitat selection, instead using other correlated cues. We predicted that conspecific attraction (Greene *et al.* 2016; Szymkowiak *et al.* 2016) would play a role in habitat selection decisions as it is known to co-exist with other habitat selection strategies (Doligez *et al.* 2003). Individuals may also use environmental cues (e.g., territory elevation) or public information (Boulinier *et al.* 2008) to inform habitat selection; however, the efficacy of these cues can be difficult to predict and may even change over time (Schmidt *et al.* 2015). We tested how these different sources of information inform *H. ostralegus* settlement patterns.

In combination, answering these three questions will provide us with an insight into the effectiveness of habitat selection as a mechanism for individuals to respond to changing patterns of ECEs in future climates.

Methods

Study system

H. ostralegus is a widespread ground nesting Eurasian shorebird that regularly breeds on saltmarshes and beaches, close to the intertidal mudflats on which they feed. They are a long-lived species (generation time 13 years), and form stable, long-term pair bonds (van de Pol *et al.* 2006b). Breeding pairs show strong territory fidelity, generally returning to the same breeding territory each year, which they defend from both other breeding birds and intrusive non-breeders (van de Pol *et al.* 2006a; Ens *et al.* 2014). Within their territories, *H. ostralegus* lay eggs in shallow nest scrapes, dug by the breeding male (del Hoyo *et al.* 1992).

As they do not construct nest mounds and use limited nesting material, *H. ostralegus* nest elevation will be strongly constrained by the elevation of potential nest sites within their territory. Territory numbers are limited, and those individuals that fail to establish a territory end up as non-breeders (Heg *et al.* 2000; van de Pol *et al.* 2007).

Territory quality varies widely across the study area, due to both flooding risk (van de Pol *et al.* 2010) and distance to intertidal feeding sites (Ens *et al.* 1992). Breeding pairs residing in territories adjacent to the intertidal mudflats can take their chicks to the feeding ground and provision them there, while pairs in territories further inland must collect food from the intertidal mudflats and bring each food item back to their chicks in the nesting territory (Ens *et al.* 1992). The cost of provisioning for inland territories will increase steadily with distance from the shoreline due to travel time associated with each foraging trip.

This study was conducted on a population of *H. ostralegus* breeding on the Dutch barrier island of Schiermonnikoog (53.4833° N, 6.1667° E). Over 90% of *H. ostralegus* individuals breeding within the study area have been individually colour banded, allowing their behaviour to be followed over multiple years. The population has been monitored consistently since 1983 (Ens *et al.* 1992), during which time *H. ostralegus* numbers have declined strongly both within our study population and across the region (van Roomen *et al.* 2012; van de Pol *et al.* 2014). As a result of these declines, the area of the study has been expanded over time in an attempt to sample a similar number of breeding pairs each year.

Data collection

We monitored nesting activity of *H. ostralegus* annually from April to August, with most nesting occurring between May and June. Nests were located through systematic searching

every 2-3 days, and nest parents were identified by their colour bands. From 1984, the identity of all breeding pairs and the approximate location of their breeding territories were recorded on an accurate coastal map. From 1986, all nests found were recorded in the same way. From 2000, the GPS coordinates of all nests were also recorded.

We measured the elevation of *H. ostralegus* nests over a 20 year period (1995 – 2014; no data in 1997 - 1999) in centimetres (± 0.1 cm) above a reference point, here chosen as mean high tide in 1971 (here after MHT; source www.live.waterbase.nl). We collected nest elevation data from 2,912 nests of which 2,122 had at least one banded parent. In total, we had nest elevation data from 374 banded males and 404 banded females. The methods used to measure nest elevation varied between years. In eight years (1995, 1996, 2008, & 2010-2014) we measured nest elevation directly in the field. Elevation was determined in-situ using a water level device (1995 – 1996); laser machine control device (2008); and a differential GPS (2010 – 2014; ProMark 800 GNSS). All in-situ methods provide measurement accuracy to within 2cm, confirmed using existing calibration sites established by Rijkswaterstaat (Dutch Ministry for Infrastructure and Environment). For all other nests, we determined elevation by overlaying GPS coordinates of nests on a LiDAR digital elevation map (measured 2008; cell size 0.5 m x 0.5 m; <http://www.ahn.nl/index.html>). This ex-situ method was used to collect data between 2000 – 2007 and 2009, as well as supplementing data in predominantly in-situ measured years.

We used information on the known location of individual pairs (GPS nest coordinates in combination with georeferenced territory and nest maps) to generate territory polygons from 1984 to 2016 using a Voronoi equation (Aurenhammer 1991). This method is known to provide a reasonable estimate of territory characteristics and has been used previously to

capture important biological insights (Grabowska-Zhang *et al.* 2012; Schlicht *et al.* 2014). The median area of territory polygons was 2,551 m² (range 2 – 97,760 m²), although territory area has increased over time (Fig. S1). Territory polygons were overlaid on the LiDAR digital elevation map, from which we calculated median territory elevation (cm above MHT). As we have no record of *H. ostralegus* nests less than 20 cm above MHT all points below 20 cm were considered unviable nesting locations and were excluded from our elevation calculations. In total, we estimated the elevation of 3,423 different territories over 32 years. As saltmarsh elevation is strongly correlated with vegetation type and height (Olf *et al.* 1997; Bockelmann *et al.* 2002), our measure of median territory elevation should account for differences in elevation and vegetation between territories.

To investigate patterns of territory density and settlement we divided our study site into a 100 m x 100 m (1 ha) grid. For each grid cell, we determined the median elevation (using our LiDAR map) and distance to the coast. For territory density analysis, we compared the difference in the number of territory centre points in each grid square between 1999 and 2016. The largest flood on record occurred during the breeding season of 1998 (Fig. S2); therefore, we expected that changes in nest density driven by flooding would be most likely to occur after this event. For settlement analysis, we determined the centre point of all territories where a new banded male was first recorded breeding between the years 1985 to 2016. We considered male rather than female mortality for all our analyses, as male identity has been shown to have a stronger influence on nest elevation than female identity (Chapter 3). We calculated a binary variable to specify whether a grid square was settled during a given year. If more than one settlement occurred within the same grid square in the same year multiple records were created for the given grid square. These repeated grid

records constituted only 1% of our data (31). In total we obtained data on settlement patterns in 2,576 grid squares, with 266 settlement events observed over the 32 year period of our study.

To study adult mortality, we calculated a binary variable to specify whether or not mortality occurred within a territory in a given year. For all territory polygons with a known (colour banded) male we determined whether the male returned to the territory in the following year (survived; 0) or failed to return (died; 1). Unbanded males were excluded from the analysis as it was impossible to determine whether or not they returned to their territory each year. Our mortality data included 3,116 territories from 465 banded males. Data on individual males covered an average of 7 years. Over the 32 year period of our study we d 357 separate mortality events.

Data analysis

All analyses were conducted using R (R Core Team 2016). We used Akaike's Information Criterion with a correction for small sample size (AICc) to compare models (Anderson & Burnham 2002), taking care to avoid the addition of 'uninformative variables' (Arnold 2010). We carried out model selection using the package *MuMIn* (Bartoń 2016). We compared the strength of models using Akaike model weights (w_i), which provides a measure of the likelihood that a given model is the 'best' model within a set (Anderson & Burnham 2002). Conditional R^2 measurements were calculated for all models using methods from Nakagawa and Schielzeth (2013). To obtain a best estimate of the relationship between our predictor variables and habitat selection behaviour we model averaged parameter estimates (with separate model averaging for models with and without an interaction). To visualise these

data, we generated predictions using model averaging and calculated unconditional standard errors.

To analyse change in mean nest elevation over time, we use mixed effects models with a Gaussian distribution in the package *nlme* (Pinheiro *et al.* 2016). We fitted random intercepts for male identity and sub-area, based on previous modelling of the same dataset (Chapter 3), and considered the change in nest elevation over time using a continuous variable Year. We fitted our model error terms as a function of 'Method' to account for differences in precision between in-situ and ex-situ measured nests (see above). We then separated out within- and between-individual effects of Year using male identity (van de Pol & Wright 2009). We split between-individual effects further still to consider selective appearance and disappearance, by determining the relationship between the mean elevation of a given individual and the first and last years that it was observed in the population (van de Pol & Wright 2009). This allows us to estimate the relative importance of settlement (selective appearance) compared to adult mortality, pair divorce and active territory abandonment (selective disappearance).

To understand the relationship between median elevation and changes in territory density we fitted non-mixed linear models with a Gaussian distribution. We considered a logarithmic effect of elevation on territory density. Territory density data showed an outlier in residuals ($> 3\sigma$ from the mean). We ran the best model with and without this outlier and compared the results.

Settlement and mortality analysis were conducted using generalised linear mixed effects models with a logistic distribution with the package *lme4* (Bates *et al.* 2014). All models considered a logarithmic term for median elevation and distance to the coastline, plus a

measure of time, and a random intercept of sub-area. Time was fitted as a categorical variable to consider two separate time periods: early years (1984 - 1998) and late years (1999 - 2016). We also included an interaction between time period and elevation. Mortality analyses included a further term for status (i.e. inland territories compared to territories adjacent to intertidal mudflats) and a random intercept for male identity. A term to account for distance to the nearest gully, which can act as an alternative foraging site, was included in settlement analysis. This same term was used in mortality analysis, but was found to be an uninformative variable and so was removed (Arnold 2010). Settlement analysis included a term that accounted for differences in available habitat between grid squares (i.e. area within each grid square greater than 20cm above MHT). As we were interested in describing the effect of median elevation in both analyses the elevation term was included in all potential models.

To understand the drivers of settlement patterns we fitted new generalised linear mixed effects models, with logistic distribution and identical random effects structure as above. All models contained the same categorical time period variable. We fitted models to test three potential hypotheses: 1) use of purely environmental information (logarithmic elevation and coastal distance terms), 2) conspecific attraction (logarithmic territory density term), and 3) use of public information (relative fledgling production of the surrounding 100 m x 100 m (1 ha) grid cell). We also considered the possibility that *H. ostralegus* territory settlement uses no cues, which may equate to random habitat selection. As *H. ostralegus* make habitat selection decisions before breeding begins, we assumed that individuals would use territory density and public information from the preceding year to make habitat selection decisions. As the quality of social information can be degraded as populations decline (Schmidt *et al.*

2015), we also fitted models with an interaction between time period and both public information and territory density.

All results show the parameter estimates plus the 95% confidence intervals.

Results

Changes in nest elevation

H. ostralegus nest elevation increased strongly over time (Fig. 1; $\beta = 0.39$ cm/year [0.17 – 0.62]). Model comparison using AICc showed strong support for a model containing the continuous Year term (Table 1; $w_i = 0.97$). Within-group centring showed that this trend included a strong positive between-individual increase in nest elevation (Table 2; $\beta = 0.47$ cm/year [0.15 – 0.80]), meaning that individuals in later years were occupying higher elevation territories than those in earlier years. This between-individual effect could be seen clearly in patterns of territory density, with *H. ostralegus* territory density decreasing strongly over time at lower elevations (Fig. 2; $\beta_{\text{ELEVATION}} = 1.35$ territories/ha [0.24 – 2.46]; removing outliers $\beta_{\text{ELEVATION}} = 1.11$ territories/ha [0.07 – 2.15]).

Drivers of nest elevation change

Changes in nest elevation were explained well by habitat settlement patterns.

Decomposition of the data showed that the appearance of new individuals (i.e. settlement) was a much stronger driver of between-individual effects than the disappearance of previously settled individuals (e.g. adult mortality; Table 2; $\beta_{\text{SETTLEMENT}} = 0.76$ cm [0.34 – 1.18], $\beta_{\text{MORTALITY}} = -0.11$ cm [-0.45 – 0.23]).

Settlement probability was affected by elevation, and this relationship changed over the period of the study (Table 3; Fig. 3a; $\beta_{\text{TIME} \times \text{ELEVATION}} = 1.11 [0.12 - 2.10]$). *H. ostralegus* showed a negative relationship between elevation and settlement in early years (Table 3; $\beta = -0.32 [-1.23 - 0.58]$) but a positive relationship in later years (Table 3; $\beta = 0.78 [-0.03 - 1.54]$).

The probability of adult mortality also depended on territory elevation and varied over the period of the study (Table 4; Fig. 3b; $\beta_{\text{MORTALITY} \times \text{TIME}} = -0.84 [-1.53 - -0.15]$). In early years, there was a positive relationship between elevation and mortality (Table 4; $\beta = 0.53 [0.06 - 1.01]$), but a weak negative relationship in later years (Table 4; $\beta = -0.31 [-0.81 - 0.20]$).

There was a considerable difference in the magnitude of settlement and mortality changes. In the lowest elevation areas the probability of adult mortality increased by approximately 1.75 times from early to late years, while settlement probability decreased more than 6-fold over the same time. Low elevation territories that had a 28% chance of being settled before 1999 had only a 4% chance of settlement from 1999 onwards.

Drivers of settlement

H. ostralegus settlement was best explained by differences in conspecific density (Table 5). Settlement was shown to be more likely in areas of higher density (Table 5; $\beta = 1.41 [0.92 - 1.90]$), a relationship that became slightly stronger over time (Table 5; $\beta_{\text{DENSITY} \times \text{TIME}} = 0.49 [-0.13 - 1.01]$).

Discussion

We used extensive longitudinal data on *H. ostralegus*, collected over 32 years, to investigate changes in habitat selection as a response to increasingly frequent extreme climatic events (ECEs). The level of detail provided by our long-term dataset allowed us to accurately quantify the settlement patterns of *H. ostralegus* individuals as a measure of habitat selection behaviour. The strong competition for territory sites and large spatial variation in territory quality means that habitat selection in *H. ostralegus* is likely to have substantial reproductive consequences, making it an ideal system for this type of study (Ens *et al.* 1992; Kokko 1999; Doligez *et al.* 2002). We documented a clear increase in mean nest elevation of *H. ostralegus* as flooding events have become more frequent, with birds in later years occupying territories at a higher elevation than those in earlier years. *H. ostralegus* settlement behaviour was the major driver of changes in territory usage, with adult mortality providing little explanation for nest elevation variation. As *H. ostralegus* is a long-lived species, the changes we observe in nest elevation and territory usage are most likely an example of phenotypic plasticity rather than intra-generational micro-evolutionary change. Without the ability to adapt through micro-evolution, long-lived species will face a substantial challenge from changing ECE patterns; however, our results provide evidence that phenotypic plasticity in habitat selection can provide a mechanism for long-lived species to respond.

Habitat selection cues

To understand *H. ostralegus* settlement patterns we must consider the cues that individuals use when making habitat selection decisions. One possibility is that *H. ostralegus* may directly utilise territory elevation to inform habitat selection. In this scenario, the trends we

see in *H. ostralegus* settlement patterns likely represent a shift in habitat selection strategies. Individuals that once preferred low elevation areas may have altered their habitat selection strategy to avoid, or at least no longer preference, low elevation sites that have become more vulnerable to flooding. The ability for individuals to shift their habitat selection strategy in direct response to flooding patterns may exist as a useful behavioural mechanism to cope with cyclical changes in flooding frequency, such as the lunar nodal cycle (Chapter 3).

Alternatively, however, *H. ostralegus* may not directly utilise elevation information during habitat selection, but may instead use other environmental or social cues that correlate with elevation. Our comparison of different habitat selection strategies suggests that *H. ostralegus* use conspecific density as a key cue during territory settlement. In this case, it is unlikely that *H. ostralegus* have changed their habitat selection strategy, but rather that the information used by individuals has changed. We observed a decline in the range of conspecific densities over our study period, such that the difference between high and low density areas has more than halved between early and late years (Fig. 4; Early years: 0 – 16 territories/ha; Late years: 0 – 7 territories/ha; see Fig. S3 for animation of territory declines). These conspecific density changes will reduce the ability for settling individuals to discern differences between territories, representing a decline in information quality. Population declines are likely to be the key driver of reduced conspecific density. If *H. ostralegus* population declines do not abate, the quality of information available to settling individuals may become so low that it will be difficult for new settlers to make informed habitat selection decisions (Bocedi *et al.* 2012), perhaps leading to uninformed (random) habitat selection decisions.

Conspecific attraction

Conspecific attraction is expected to be particularly common in systems that show strong spatial auto-correlation in habitat quality (Schmidt *et al.* 2015). This is likely to be the case in *H. ostralegus* salt-marsh systems as the quality of territories will be spatially correlated with coastal distance (Ens *et al.* 1992). However, for conspecific attraction to function effectively during *H. ostralegus* habitat selection existing breeding pairs must possess a cue that encourages the aggregation of conspecifics in high quality areas (Doligez *et al.* 2003). Knowing this, it is likely that other habitat selection strategies are also in play within our system that we did not directly detect.

One possibility may be that the conspecific density term in our model simply provides a good integrator of a number of different sources of information. Individual settlers may in fact be using an array of different correlated information sources when making habitat selection decisions. Correlation between conspecific density and both median elevation and fledgling production of neighbours (i.e. public information) in our data was not particularly high (Pearson's correlation: Density ~ Elevation = 0.24; Density ~ Fledgling = 0.23), suggesting that these variables are unlikely to be integrated within our conspecific density term. Philopatry has also previously been discounted as a driver of natal settlement in *H. ostralegus* (van de Pol *et al.* 2006a). However, we cannot rule out the existence of other factors that may drive *H. ostralegus* settlement.

Vegetation characteristics may be one such unmeasured factor that could play an important role in *H. ostralegus* settlement decisions. The species and height of vegetation present in a territory can influence the concealment and camouflage of nests and is likely to be a particularly important component of nest site selection (Troscianko *et al.* 2016). Although

we expected our measure of median territory elevation to be broadly correlated with vegetation characteristics (Olf *et al.* 1997; Bockelmann *et al.* 2002), variation in plant communities at smaller scales will also be influenced by geomorphological variation (e.g. creek drainage systems) and local wind patterns that would not be directly accounted for by using median territory elevation (Bockelmann *et al.* 2002). Finer scale variation in vegetation communities within a territory may provide appropriate nesting opportunities for breeding birds that would not be detected by our coarse scale measure of median territory elevation. Vegetation composition may also change over time as flooding patterns shift (Olf *et al.* 1997), and so properly understanding the role of vegetation in territory settlement could also be important for predicting patterns of *H. ostralegus* into the future. Use of fine scale vegetation maps would be necessary to investigate this possibility further. Experimental tests on *H. ostralegus* habitat selection using vegetation manipulation would also allow for a more detailed understanding of the different sources of information used by *H. ostralegus* during habitat settlement.

Effectiveness of nest elevation responses

Long-term monitoring of *H. ostralegus* has allowed us to document phenotypic plasticity in nest elevation that will help reduce the impacts of increased flooding frequency. This provides encouraging evidence that organisms can show responses to long-term ECE changes over a relatively short period of time through phenotypic plasticity, a topic that is not often considered (Moreno & Møller 2011). These results further suggest that changes in flooding patterns have not produced an ‘ecological trap’ in *H. ostralegus*, as individuals have shown movement away from sites where quality has declined. However, the strength of observed nest elevation change appears insufficient to keep pace with increases in

maximum high tides (0.39cm/year nest elevation change vs. 0.8cm/year change in maximum high tide; Chapter 3).

Even if *H. ostralegus* showed a stronger nest elevation increase, the mechanism behind nest elevation change is unlikely to provide an effective response to increased flooding frequency over an extended period. Importantly, *H. ostralegus* will be limited in the availability of viable high elevation sites for territory establishment. In the saltmarsh which they inhabit, higher elevation sites will often be unsuitable for breeding due to high, thick vegetation (del Hoyo *et al.* 1992; Götmark *et al.* 1995), potentially acting as a hard barrier beyond which *H. ostralegus* cannot move and limiting the extent to which *H. ostralegus* can increase the elevation of their territories. With an upper limit on territory elevation, reduced utilisation of low elevation territories will only provide a temporary buffer against continued flooding changes. Eventually, all low elevation territories will be unused, at which point further benefits of habitat selection change will be limited.

Changes in other reproductive characteristics, in combination with increased nest elevation, will likely be required for *H. ostralegus* to more effectively respond to changing flooding patterns. For example, advancing laying date and reducing the length of the incubation and the early chick phase will provide alternative mechanisms by which breeding individuals can reduce their flooding risk (van de Pol *et al.* 2010). The combined use of multiple behavioural pathways in response to more frequent flooding will likely be a common situation throughout many coastal nesting species. For example, species of saltmarsh sparrow can reduce flooding risk by adjusting nest elevation (Bayard & Elphick 2011), timing of nesting (Shriver *et al.* 2007) and also nest structure (Humphreys *et al.* 2007). Similarly, beach nesting sea turtles can adjust the location, timing, and depth of their nests to reduce

flooding risk (Pike & Stiner 2007). Future research should attempt to consider a range of behavioural characteristics in conjunction to better understand responses of organism to ECEs and anthropogenic climate change more generally.

Conclusions

In conjunction with our previous work we have been able to show distinctly different habitat selection responses occurring at different spatial and temporal scales, a phenomenon that has previously been documented in other species (Orians & Wittenberger 1991). *H. ostralegus* showed limited evidence for fine scale changes in nest-site selection (Chapter 3), yet we found strong evidence that broad between-individual changes in territory settlement are occurring in the same population. This provides some of the first evidence to document phenotypic plasticity in response to changing patterns of ECEs. However, while these results are theoretically interesting, we expect that both the rate of the response and the mechanism behind the response will be insufficient to cope with predicted changes in flooding frequency. This raises concerns for the long-term viability of our study population (van de Pol *et al.* 2010), and will be an important consideration for other coastal species, many of which are experiencing marked declines (van Roomen *et al.* 2012; Correll *et al.* 2016; Field *et al.* 2016; Valdes *et al.* 2016).

Our results highlight the importance of studying ecological trends at both a phenomenological and mechanistic levels to understand both the responses and the resilience of wild populations to anthropogenic climate change. Changes in the frequency and magnitude of ECEs are likely to pose a serious challenge for the conservation of populations, especially where the species in question possesses little ability to effectively respond. This may be particularly important for long-lived species where the rate of micro-

evolutionary change is limited. While we have shown the potential for phenotypic plasticity in the face of increased ECEs, our results do not provide a positive picture for the future of our study population. Greater understanding of the impacts of ECEs and responses to such events will be necessary to determine whether our conclusions can be applied more generally across wild populations.

Table 1: Models investigating the change in *Haematopus ostralegus* nest elevation (cm above mean high tide in 1971 $\pm$ SE). Models include a continuous time variable (Year). k denotes the number of parameters estimated in each model. w_i denotes AICc model weights.

ΔAICc	w_i	k	Intercept	Year
0.00	0.97	2	76.02 ($\pm$ 4.30)	0.39 ($\pm$ 0.11)
7.19	0.03	1	79.52 ($\pm$ 4.38)	-

Table 2: Changes in *Haematopus ostralegus* nest elevation (cm above mean high tide in 1971 $\pm$ SE), decomposed to consider between-individual change (Between), within-individual change (Within), selective appearance (Settlement) and selective disappearance (Mortality).

Intercept	Between	Within	Settlement	Mortality
75.30 ($\pm$ 4.42)	0.47 ($\pm$ 0.17)	0.32 ($\pm$ 0.16)	-	-
75.53 ($\pm$ 4.34)	-	0.33 ($\pm$ 0.16)	0.76 ($\pm$ 0.21)	-0.11 ($\pm$ 0.17)

Table 3: Conditional model averaging showing the effect of salt marsh elevation on *Haematopus ostralegus* territory settlement odds ($\pm$ SE). All models include a logarithmic effect of territory elevation (Elev; cm above mean high tide in 1971), a measure of available area for territory settlement (Area; m²), a categorical variable for time (Time; Early [1984 - 1999] and Late [1999 - 2016]), and an interaction between Time and Elev, plus random intercepts for study sub-area. Additionally, some models also included a logarithmic effect of distance between a territory and the coastline (Coast; m) and distance to the nearest gully (Gully; m). Early years were used as the reference category. For full model selection results see Table S1.

Intercept	Elev	Time	Elev*Time	Coast	Gully	Area
-0.16 ($\pm$ 0.45)	-0.32 ($\pm$ 0.46)	-2.29 ($\pm$ 0.47)	1.11 ($\pm$ 0.50)	-1.78 ($\pm$ 0.37)	-0.55 ($\pm$ 0.28)	0.02 ($\pm$ 0.08)

Table 4: Conditional model averaging showing the effect of *Haematopus ostralegus* territory elevation on the odds of adult mortality ($\pm$ SE). All models include a logarithmic effect of territory elevation (Elev; cm above mean high tide in 1971), a categorical variable for time (Time; Early [1984 - 1999] and Late [1999 - 2016]), and an interaction between Time and Elev, plus random intercepts for male identity and study sub-area. Additionally, some models also included a logarithmic effect of distance between a territory and the coastline (Coast; m) and social status (Status; mudflat or non-mudflat territories). Non-mudflat territories in early years were used as the reference category. For full model selection results see Table S2.

Intercept	Elev	Time	Elev*Time	Coast	Status
-2.32 ($\pm$ 0.19)	0.53 ($\pm$ 0.24)	0.40 ($\pm$ 0.26)	-0.84 ($\pm$ 0.35)	0.31 ($\pm$ 0.14)	-0.13 ($\pm$ 0.15)

Table 5: Models investigating the support for different habitat selection strategies on *Haematopus ostralegus* territory settlement odds ($\pm$ SE). All models include a categorical factor for time (Time; Early [pre-1999] and Late [1999 onwards]), a measure of available area for territory settlement (Area; m²), conspecific density (Density; territories/ha), and random intercepts for study sub-area. Additionally, models include an interaction between Density and Time. Early years were used as the reference category. All models within the 95% confidence set are displayed, see Table S3 for full model comparison table. k denotes the number of parameters estimated in each model. w_i denotes AICc model weights.

Δ AICc	w_i	k	Intercept	Density	Time	Density * Time	Area
0.00	0.54	5	-2.43 ($\pm$ 0.27)	1.41 ($\pm$ 0.21)	-1.22 ($\pm$ 0.31)	0.49 ($\pm$ 0.32)	-0.03 ($\pm$ 0.07)
0.34	0.46	4	-2.65 ($\pm$ 0.23)	1.62 ($\pm$ 0.16)	-0.82 ($\pm$ 0.17)	-	-0.02 ($\pm$ 0.07)

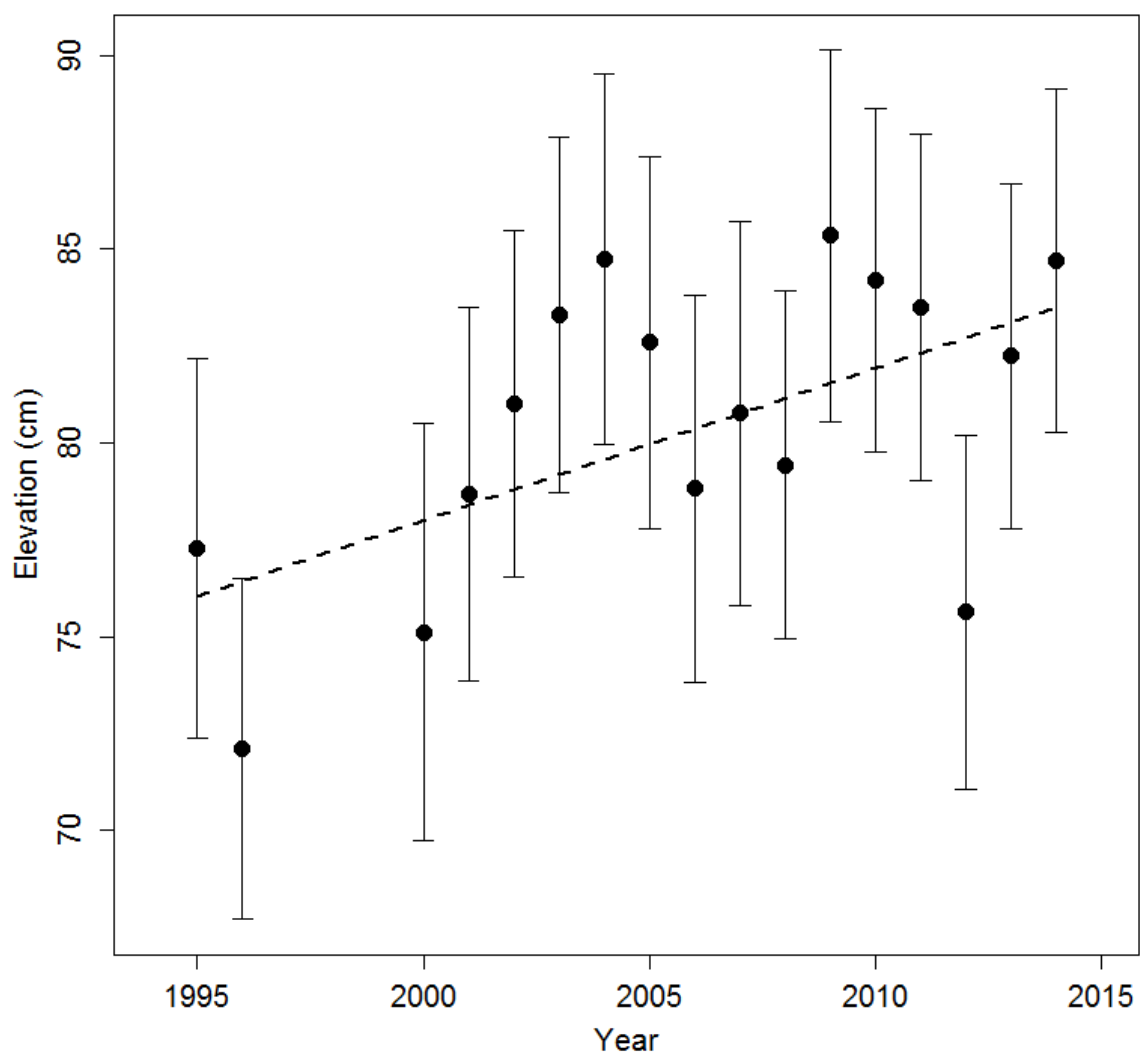


Figure 1: Change in *Haematopus ostralegus* nest elevation (cm above mean high tide in 1971 $\pm$ SE) over time.

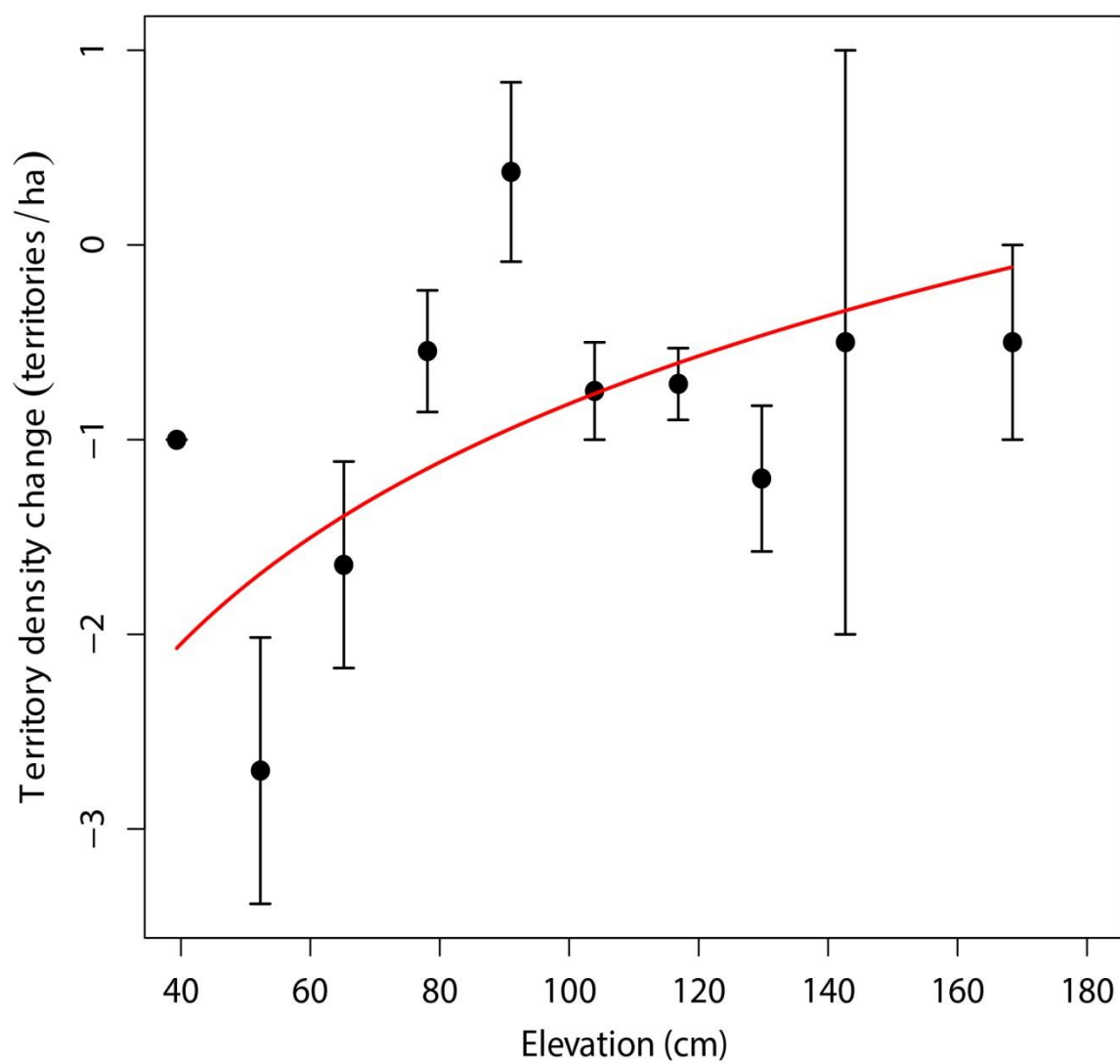


Figure 2: Change in *Haematopus ostralegus* territory density (territories/ha $\pm$ SE) between 1999 and 2016 at different territory elevations (cm above 1971 mean high tide). Model predictions (red line) show the logarithmic effect of elevation on territory density change.

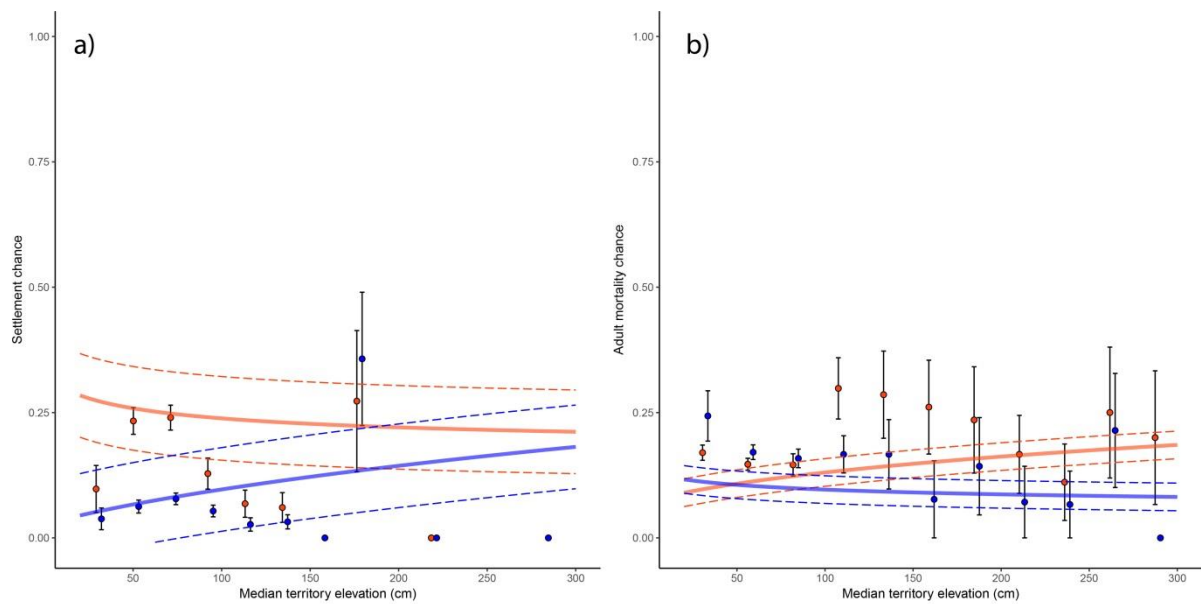


Figure 3: a) Effect of median elevation (cm above 1971 high tide) on the odds of male *Haematopus ostralegus* settlement in a given area ($\pm$ SE) in early years (1984-1998; black) and late years (1999-2016; blue). Lines show model averaged predictions from all fitted models ($\pm$ SE). b) Effect of median elevation (cm above 1971 high tide) on the odds of male *H. ostralegus* mortality in early years (1984-1998; black) and late years (1999-2016; blue).

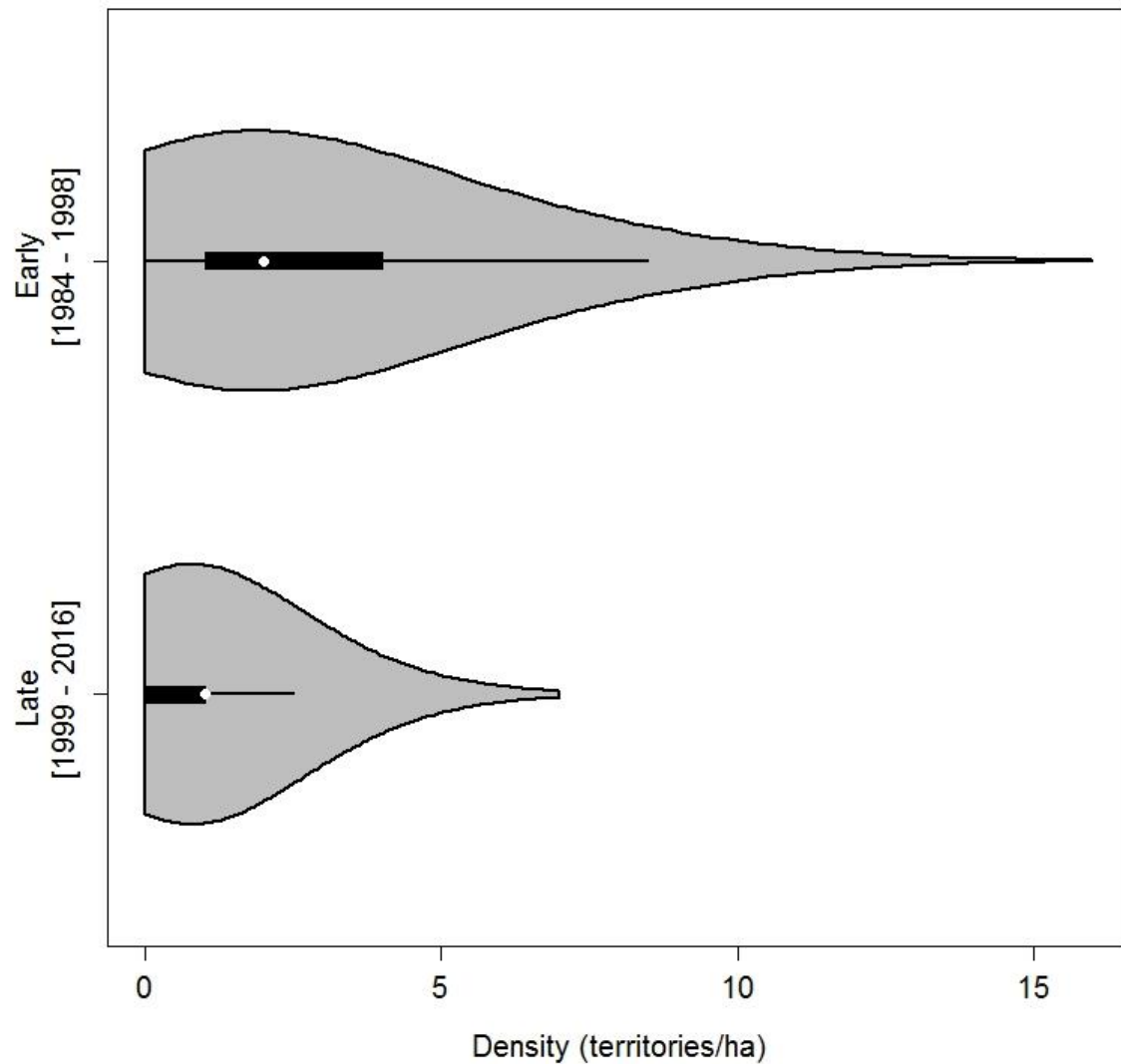


Figure 4: Violin plot of *Haematopus ostralegus* territory densities (territories/ha) in early years (1984 – 1998) and late years (1999 – 2016). Black box and lines show a boxplot of the data. Grey shaded regions represent kernel density plots of the data.

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Table S1: Models investigating the effect of saltmarsh elevation on territory settlement odds ($\pm$ SE). All models include a logarithmic effect of territory elevation (Elev; cm above mean high tide in 1971) and a measure of available area for territory settlement (Area; m²) and a random intercept term for sub-area. Some models also include a logarithmic effect of distance between a territory and the coastline (Coast; m), a logarithmic effect of distance to the nearest gully (Gully; m), a categorical factor for time (Time; Early [1984-1998] and Late [1999-2016]), and an interaction between Time and Elev. k denotes the number of parameters estimated in each model. w_i denotes AICc model weights. Conditional R² values provided for all models based on methods from Nakagawa and Schielzeth (2013).

Δ AICc	w_i	k	Intercept	Elev	Coast	Time	Gully	Elev*Time	Area	R ²
0.00	0.58	7	-0.13 ($\pm$ 0.45)	-0.28 ($\pm$ 0.46)	-1.83 ($\pm$ 0.36)	-2.31 ($\pm$ 0.47)	-0.55 ($\pm$ 0.28)	1.13 ($\pm$ 0.51)	0.01 ($\pm$ 0.08)	0.26
1.95	0.22	6	-0.23 ($\pm$ 0.44)	-0.44 ($\pm$ 0.45)	-1.65 ($\pm$ 0.35)	-2.22 ($\pm$ 0.46)	-	1.04 ($\pm$ 0.50)	0.03 ($\pm$ 0.08)	0.27
3.00	0.13	6	-0.80 ($\pm$ 0.33)	0.43 ($\pm$ 0.32)	-1.73 ($\pm$ 0.36)	-1.32 ($\pm$ 0.16)	-	-	-0.01 ($\pm$ 0.08)	0.26
4.29	0.07	5	-0.84 ($\pm$ 0.32)	0.22 ($\pm$ 0.30)	-1.57 ($\pm$ 0.36)	-1.32 ($\pm$ 0.16)	-	-	0.01 ($\pm$ 0.07)	0.26
31.44	0.00	5	-0.68 ($\pm$ 0.43)	-0.61 ($\pm$ 0.44)	-	-2.16 ($\pm$ 0.46)	-	0.85 ($\pm$ 0.50)	-0.08 ($\pm$ 0.07)	0.14
32.35	0.00	4	-1.13 ($\pm$ 0.34)	-0.08 ($\pm$ 0.31)	-	-1.42 ($\pm$ 0.15)	-	-	-0.10 ($\pm$ 0.07)	0.13
33.45	0.00	6	-0.68 ($\pm$ 0.43)	-0.61 ($\pm$ 0.45)	-	-2.16 ($\pm$ 0.46)	-0.01 ($\pm$ 0.28)	0.86 ($\pm$ 0.51)	-0.08 ($\pm$ 0.08)	0.14
34.34	0.00	5	-1.13 ($\pm$ 0.34)	-0.09 ($\pm$ 0.32)	-	-1.42 ($\pm$ 0.15)	0.04 ($\pm$ 0.27)	-	-0.10 ($\pm$ 0.07)	0.13
75.17	0.00	5	-1.74 ($\pm$ 0.26)	0.41 ($\pm$ 0.30)	-1.89 ($\pm$ 0.28)	-	-0.40 ($\pm$ 0.23)	-	0.01 ($\pm$ 0.07)	0.17
76.26	0.00	4	-1.76 ($\pm$ 0.27)	0.21 ($\pm$ 0.28)	-1.74 ($\pm$ 0.28)	-	-	-	0.03 ($\pm$ 0.07)	0.18
114.03	0.00	3	-2.31 ($\pm$ 0.34)	-0.02 ($\pm$ 0.30)	-	-	-	-	-0.09 ($\pm$ 0.07)	0.10
115.95	0.00	4	-2.31 ($\pm$ 0.34)	-0.05 ($\pm$ 0.31)	-	-	0.09 ($\pm$ 0.30)	-	-0.09 ($\pm$ 0.07)	0.09

Table S2: Models investigating the effect of *Haematopus ostralegus* territory elevation on adult mortality odds ($\pm$ SE). All models include a logarithmic effect of territory elevation (Elev; cm above mean high tide in 1971). Additionally, some models also include a categorical factor for time (Time; Early [1984-1998] and Late [1999-2016]), logarithmic effect of distance between a territory and the coastline (Coast; m) and social status (Status; mudflat or non-mudflat territories). Models also consider an interaction between Elev and Time. Non-mudflat territories in early years were used as the reference category. k denotes the number of parameters estimated in each model. w_i denotes AICc model weights. Conditional R^2 values provided for all models based on methods from Nakagawa and Schielzeth (2013).

$\Delta AICc$	w_i	k	Intercept	Elev	Coast	Time	Status	Elev*Time	R^2
0.00	0.41	5	-2.36 (± 0.17)	0.54 (± 0.24)	0.32 (± 0.13)	0.40 (± 0.26)	-	-0.86 (± 0.35)	0.07
1.67	0.18	6	-2.31 (± 0.19)	0.53 (± 0.24)	0.27 (± 0.15)	0.41 (± 0.27)	0.08 (± 0.14)	-0.85 (± 0.35)	0.07
2.73	0.11	5	-2.21 (± 0.18)	0.53 (± 0.24)	-	0.41 (± 0.26)	-0.22 (± 0.12)	-0.76 (± 0.34)	0.08
4.10	0.05	4	-2.09 (± 0.13)	0.09 (± 0.18)	0.30 (± 0.12)	-0.18 (± 0.12)	-	-	0.07
4.26	0.05	4	-2.24 (± 0.22)	0.53 (± 0.25)	-	0.38 (± 0.27)	-	-0.81 (± 0.35)	0.08
4.29	0.05	3	-2.13 (± 0.13)	0.02 (± 0.17)	0.26 (± 0.12)	-	-	-	0.07
4.32	0.05	3	-2.00 (± 0.14)	0.08 (± 0.17)	-	-	-0.24 (± 0.11)	-	0.08
4.96	0.03	4	-2.04 (± 0.15)	0.03 (± 0.17)	0.17 (± 0.14)	-	-0.16 (± 0.13)	-	0.07
5.46	0.03	5	-2.04 (± 0.15)	0.09 (± 0.18)	0.23 (± 0.15)	-0.15 (± 0.13)	-0.11 (± 0.14)	-	0.07
5.63	0.03	4	-1.97 (± 0.14)	0.12 (± 0.17)	-	-1.00 (± 0.12)	-0.23 (± 0.11)	-	0.08
6.73	0.01	2	-2.11 (± 0.13)	0.09 (± 1.63)	-	-	-	-	0.08
7.53	0.01	3	-2.07 (± 0.13)	0.15 (± 0.17)	-	-0.13 (± 0.12)	-	-	0.08

1 **Table S3:** Models investigating the support for different habitat selection strategies on *Haematopus ostralegus* territory settlement odds ($\pm$ SE). All models
2 include a categorical factor for time (Time; Early [1984-1998] and Late [1999-2016]), a measure of area available for territory settlement (Area; m²), and
3 random intercepts for study sub-area. Models also include a logarithmic effect of conspecific density (Density; territories/ha), a logarithmic effect of
4 territory elevation (Elev; cm above mean high tide in 1971), a relative fledgling success of neighbouring pairs (Fledge), a logarithmic effect of distance
5 between a territory and the coastline (Coast; m), plus an interaction between the Time and each of Density, Elev and Fledge. Early years were used as the
6 reference category. k denotes the number of parameters estimated in each model. w_i denotes AICc model weights. Conditional R^2 values provided for all
7 models based on methods from Nakagawa and Schielzeth (2013).

$\Delta AICc$	w_i	k	Intercept	Density	Elev	Coast	Fledge	Time	Density *	Elev *	Fledge *	Area	R^2
0.00	0.54	5	-2.43 (± 0.26)	1.41 (± 0.21)	-	-	-	-1.22 (± 0.31)	0.49 (± 0.32)	-	-	-0.03 (± 0.07)	0.25
0.34	0.46	4	-2.65 (± 0.23)	1.62 (± 0.16)	-	-	-	-0.82 (± 0.17)	-	-	-	-0.02 (± 0.07)	0.22
78.27	0.00	6	-0.38 (± 0.45)	-	-0.35 (± 0.44)	-1.74 (± 0.36)	-	-2.08 (± 0.47)	-	0.94 (± 0.50)	-	-0.03 (± 0.08)	0.29
98.87	0.00	4	-1.32 (± 0.21)	-	-	-	0.16 (± 0.05)	-1.35 (± 0.15)	-	-	-	-0.07 (± 0.07)	0.15
100.82	0.00	5	-1.32 (± 0.21)	-	-	-	0.14 (± 0.07)	-1.36 (± 0.16)	-	-	0.03 (± 0.10)	-0.07 (± 0.07)	0.15
105.01	0.00	3	-1.33 (± 0.21)	-	-	-	-	-1.33 (± 0.15)	-	-	-	-0.10 (± 0.07)	0.14

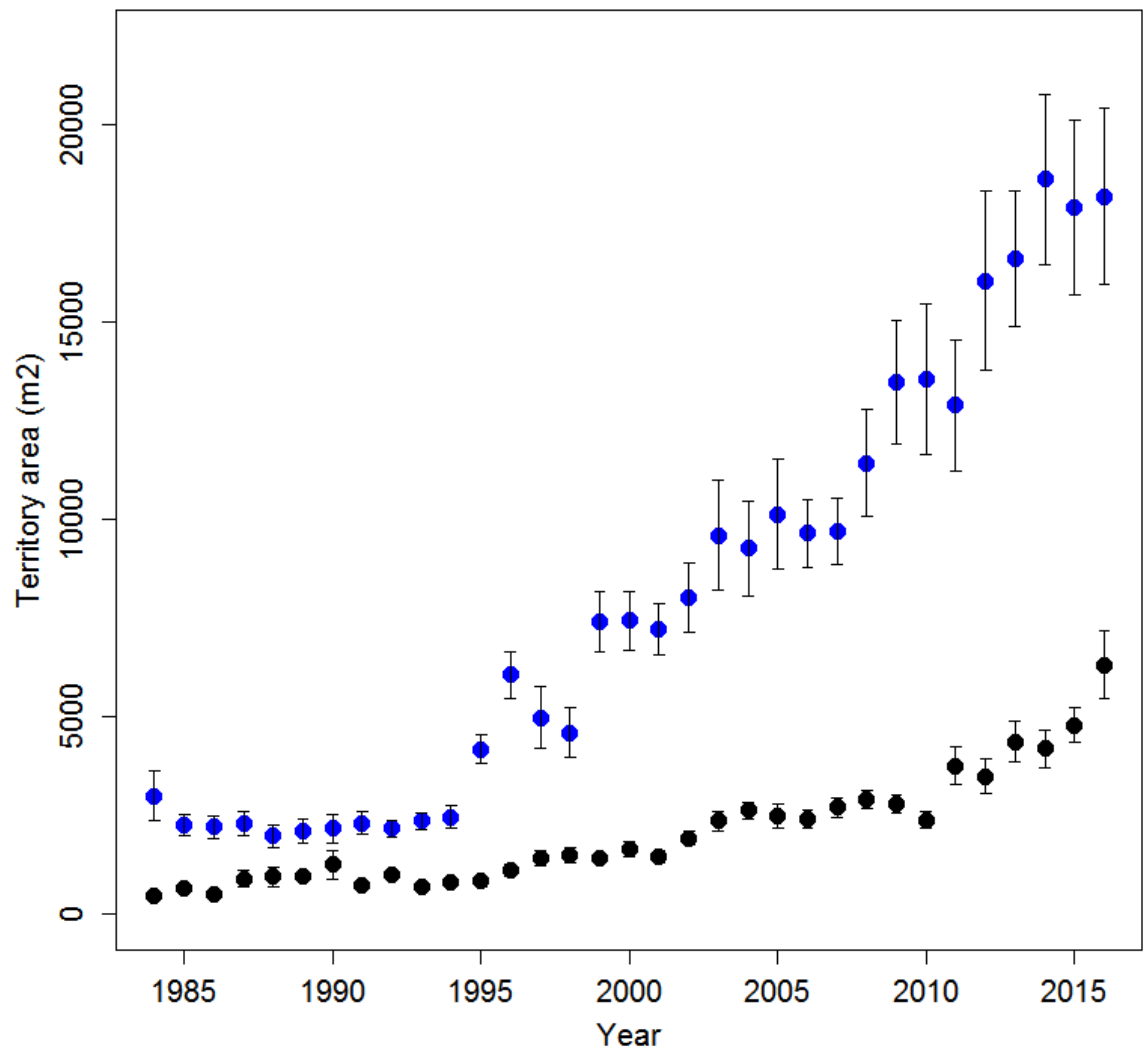


Figure S1: Change in *Haematopus ostralegus* territory area ($\text{m}^2 \pm \text{SE}$) over time in birds with direct access to the mudflat feeding area (black) and those without mudflat access (blue; see Ens et al. 1992 for details).

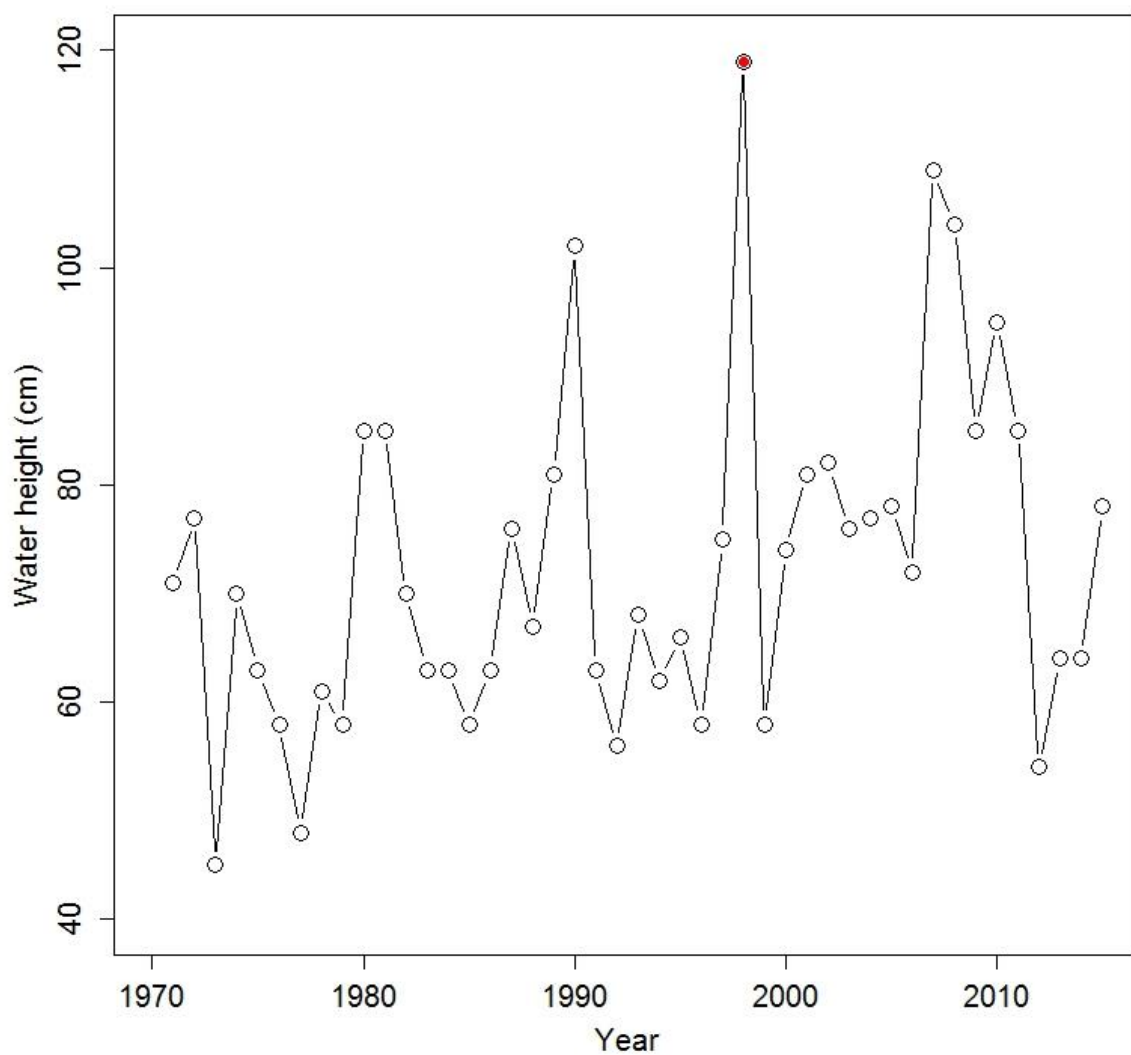


Figure S2: Maximum high tide on the Dutch Wadden Island of Schiermonnikoog during the breeding season of *Haematopus ostralegus* (May – July; cm above mean high tide in 1971). The red point shows the highest tide on record (199 cm), which occurred during the breeding season of 1998.

Figure S3: Animated GIF of *Haematopus ostralegus* territory boundaries on the Dutch Island of Schiermonnikoog between 1984 and 2016. Animated file can be accessed at <https://osf.io/5k3rx/>.

Chapter 5

Negative density-dependent nest predation in threatened a mobbing bird species

This chapter is a manuscript currently under preparation for
submission.

Negative density-dependent nest predation in a threatened mobbing bird species

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Abstract

1. Individuals often face a trade-off between the benefits (e.g. predator vigilance) and costs (e.g. disease transmission) of increased conspecific density. Density-dependent predation is one potential factor that may influence whether or not individuals choose to aggregate or remain solitary.
2. Birds are often expected to experience positive density-dependent nest predation (i.e. high nest predation at high densities), as nest predators will learn to identify and exploit high density areas. However, many studies have focused on predation of artificial nests, thus failing to consider the impact of parent behaviour on nest predation. As such, it is not clear whether our current understanding of density-dependent nest predation will apply generally when parental behaviour is taken into account.
3. We tested for density-dependent nest predation in a mobbing species, the Eurasian oystercatcher (*Haematopus ostralegus*), using both artificial and natural nests. We tested the effects of both density and nearest neighbour distance of natural nests with actively defending parents.
4. Our analysis showed a strong *negative* density dependent result for both artificial and natural nests, with nest predation declining at higher densities. Analysis of nearest neighbour distances showed a similar benefit of associating with conspecifics. This effect is likely driven by more effective mobbing at higher densities. Therefore, assumptions of positive density-dependent nest predation may not hold true for mobbing species.
5. Our results suggest that the behaviour of nesting parents can drive density-dependent nest predation. Anti-predator behaviour will vary considerably between species; therefore, future studies should consider the density of natural nests to achieve a more realistic understanding of nest predation patterns. Understanding the prevalence of negative density-dependent predation will be an important conservation challenge as declining populations may experience increasing nest predation. We predict this to be the case in *H. ostralegus*.

Introduction

Animals are often observed grouping together with conspecifics, which is known to provide a range of benefits to individuals through improved hunting success (Creel & Creel 1995; MacNulty *et al.* 2011), lower predation risk (Roberts 1996; Fairbanks & Dobson 2007; Cresswell & Quinn 2011), and reduced chance of brood parasitism (Zimmerman 1983; Stokke *et al.* 2007; Feeney *et al.* 2013). However, living at high densities doesn't come without costs. Aside from the increased competition for resources and reproductive opportunities that individuals will often experience (Skogland 1985; Coltman *et al.* 1999), high conspecific density has also been linked to increased disease transmission (Langwig *et al.* 2012) and increased rates of nest predation (Martin 1988; Gunnarsson & Elmberg 2008). Therefore, individuals will need to consider a trade-off between the costs and benefits of group living.

Density-dependent nest predation is one area of research that has received considerable attention over a long period of time, with a particular focus in birds (Göransson *et al.* 1975; Martin 1988; Schmidt & Whelan 1999; Gunnarsson & Elmberg 2008; Carpio *et al.* 2016). In colonial species where nest densities are particularly high, such as seen in the family Laridae (Wittenberger & Hunt 1985; Groom 1992; Oro *et al.* 2006), increased density will often reduce predation rates (Hamilton 1971; Young & Titman 1986; Groom 1992; Picman *et al.* 2002; Druzyaka 2016). This anti-predator behaviour is one factor often considered as a driver of coloniality (Schreiber & Burger 2001). However, in non-colonial species, such as water fowl, natural nesting densities are often much lower and density dependent effects are less clear. Previous density-dependent nest predation studies on non-colonial birds have shown mixed results, with nest predation showing both density-dependence (Page *et al.* 1983; Martin 1988; Larivière & Messier 1998; Gunnarsson & Elmberg 2008) and density-independence (Schmidt & Whelan 1998, 1999; Ackerman *et al.* 2004; Padyšáková *et al.* 2011). Yet, where density-dependent nest predation does occur in non-colonial study systems, the relationship between nest density and nest predation has generally been observed to be positive (Page *et al.* 1983; Larivière & Messier 1998), and it is therefore often assumed that a positive density-dependent nest predation relationship is most common (Gunnarsson & Elmberg 2008; Ringelman *et al.* 2012).

Documented positive density-dependent nest predation effects in non-colonial species are likely driven by predator behaviour, with predators learning to recognise and exploit higher nest densities (Larivière & Messier 1998). This is particularly likely in generalist predators with large foraging distances that are capable of assessing and rapidly adjusting their foraging behaviour to exploit variations in resource abundance (Schmidt & Whelan 1999). Additionally, when predators find a nest they may often exhibit ‘area restricted searching’, increasing the chance that any nearby nests are detected (Larivière & Messier 1998; Ringelman *et al.* 2014). However, some cases of negative density-dependent nest predation relationships (low nest predation at high densities) have also been documented, particularly in recent years (Andersson & Wiklund 1978; Ringelman *et al.* 2012, 2014; Carpio *et al.* 2016). Negative density-dependent nest predation results are often attributed to predator satiation at higher densities (Carpio *et al.* 2016), but may also be driven by anti-predator behaviour of nest parents (Andersson & Wiklund 1978; Wiklund & Andersson 1994; Oro *et al.* 2006).

Experimental studies of density-dependent nest predation (both positive and negative) have often utilised artificial nests as a tool to determine rates of nest predation (Major & Kendal 1996; Gunnarsson & Elmberg 2008). Practically, artificial nests can be extremely useful in bird systems where natural nests are difficult and time consuming to find and will allow for the direct manipulation of nesting conditions (e.g., habitat type, vegetation cover; Jokimäki & Huhta 2000; Gunnarsson & Elmberg 2008; Carpio *et al.* 2016). Most importantly, experiments using artificial nests can help disentangle confounding effects of habitat density and habitat/individual quality (Larivière & Messier 1998). High density locations may correspond to areas containing high quality nesting sites (e.g. greater nest concealment) and/or high quality individuals (e.g. parents that build less conspicuous nests). This may lead to ‘concealed density dependence’, where individual or site quality at high densities masks a positive density-dependent nest predation effect (Ringelman *et al.* 2012), or produce an apparent negative density-dependent nest predation effect.

However, an issue with artificial nests is that they lack active parents, providing one potential explanation for the discrepancy in predation rates seen between natural and artificial nests (Haskell 1995a). Parental activity may increase nest predation by alerting predators to the locations of nests (Forbes *et al.* 1994; Martin & Ghalambor

1999) or reduce nest predation through nest defence (Andersson & Wiklund 1978; Pavey & Smyth 1998). Many previous studies have only considered the effect of artificial nest density on the predation rates of artificial nests, such that all surrounding nests are completely unguarded (Andersson & Wiklund 1978; Page *et al.* 1983; Wiklund & Andersson 1994; Larivière & Messier 1998; Ackerman *et al.* 2004; Gunnarsson & Elmberg 2008; Ringelman *et al.* 2012; Carpio *et al.* 2016). Hence, many previous density-dependent nest predation studies are effectively a test of predator foraging behaviour with no consideration of anti-predator defences by the prey species.

Parental anti-predator defences may reduce nest predation rates through nest camouflage (Forbes *et al.* 1994; Troscianko *et al.* 2016), predator distraction (Lord *et al.* 2001; Fisher *et al.* 2004), and predator mobbing (Pavey & Smyth 1998; Carrillo & Aparicio 2001; Krams *et al.* 2008; Krams *et al.* 2010). The effectiveness of these defences is likely to be affected by conspecific density. Vigilance will increase at higher densities (Fairbanks & Dobson 2007), allowing for parents to more easily detect approaching predators and show early responses, such as quietly leaving the nest to prevent nest detection or sitting tight to avoid egg snatching (Brunton 1990; Yorio & Quintana 1997). In those species that exhibit mobbing, increased nest density may also increase the size and intensity of mobbing groups (Robinson 1985; Wiklund & Andersson 1994; Krams *et al.* 2009) and thus the effectiveness of mobbing behaviour (Pavey & Smyth 1998; Schreiber & Burger 2001). Therefore, parental anti-predator behaviour may reduce or even reverse any density-dependent nest predation relationship that would be detected when using exclusively artificial nests. While studies have shown evidence for a relationship between density and mobbing effectiveness in colonial species (Andersson & Wiklund 1978; Wiklund & Andersson 1994; Oro *et al.* 2006), the potential importance of parental behaviour is still often overlooked in the density-dependent nest predation literature for other species.

We considered density-dependent nest predation in a non-colonial mobbing shorebird, the Eurasian oystercatcher (*Haematopus ostralegus*). Gulls (*Larus* sp.) and carrion crows (*Corvus corone*) are two of the major nest predators in this species (personal observation), and previous research would suggest that such wide ranging generalist nest predators will learn to recognise and exploit high nest densities, driving a positive

relationship between nest density and nest predation (Schmidt & Whelan 1999). However, *H. ostralegus* is also known to exhibit intensive group mobbing (Gochfeld 1984), which could instead lead to a negative relationship between nest density and nest predation. Finally, if both predator and mobbing behaviour impact nest predation equally, these two drivers may cancel one another out, leading to density-independent nest predation. These three possibilities make *H. ostralegus* an ideal species in which to test density-dependent nest predation relationships.

To investigate density-dependent nest predation in *H. ostralegus* we considered two questions, using both experiments with artificial nests and observations of natural nest predation patterns. First, is the daily chance of artificial nest predation impacted by the density and nearest neighbour distance of active *H. ostralegus* nests and at what distance is the density effect strongest? Second, is the daily chance of natural *H. ostralegus* nest predation impacted by conspecific nest density and nearest neighbour distance?

Testing for the existence of negative density-dependent nest predation in mobbing species is not only interesting theoretically but has important conservation implications in light of the rapid population declines observed globally across many taxa and occurring particularly strongly in shorebirds (Alford *et al.* 2001; Craigie *et al.* 2010; van Roomen *et al.* 2012). *H. ostralegus* is no exception to such conservation concerns, with the species outlook recently changed from ‘Least Concern’ to ‘Near Threatened’ on the IUCN red list (BirdLife International 2015). If the occurrence of positive density-dependent nest predation is as common as often assumed, population declines may actually alleviate predation pressure (Sherley *et al.* 2014); however, where a negative density-dependent nest predation relationship occurs, population declines may be compounded by increasing nest predation rates, potentially representing an example of an Allee effect (Courchamp *et al.* 1999). Investigating the potential occurrence of negative density-dependent nest predation relationships will therefore be important to help understand the impacts of future population declines and potentially alter the focus of conservation strategies.

Methods

Study system

H. ostralegus is a ground nesting shorebird occurring across Europe and Asia that regularly breeds on saltmarshes and beaches near the intertidal mudflats on which they feed. A key aspect of *H. ostralegus* ecology is their territoriality; pairs will establish a breeding territory that they defend from both other breeding birds and intrusive non-breeders (van de Pol *et al.* 2006a; Ens *et al.* 2014).

During the breeding season, *H. ostralegus* males dig a number of shallow nest scrapes in which eggs are laid (del Hoyo *et al.* 1992). Following clutch completion (3 eggs on average), bi-parental incubation lasts for an average of 28 days. The saltmarsh habitat in which *H. ostralegus* reside is dominated by grasses (Olf *et al.* 1997; Bockelmann *et al.* 2002). With limited use of nesting material, grass height around *H. ostralegus* nests provides the major source of nest concealment (Götmark *et al.* 1995).

This study was conducted on a population of *H. ostralegus* breeding on the Dutch island of Schiermonnikoog (53.4833° N, 6.1667° E). Territory density at this site has been known to vary from as little as 1 territory/ha to as much as 16 territories/ha (Chapter 4), driven in part by substantial spatial heterogeneity in habitat quality (Ens *et al.* 1992; van de Pol *et al.* 2006a). The population has been monitored consistently since 1983, with a well-established protocol for nest searching and monitoring (Ens *et al.* 1992). Over 90% of *H. ostralegus* individuals breeding within the study area have been individually colour banded, allowing us to account for individual differences in behaviour. Over the course of the long-term study, *H. ostralegus* numbers have undergone strong declines both on Schiermonnikoog and across the region (van Roomen *et al.* 2012; van de Pol *et al.* 2014), with corresponding declines in territory density (Chapter 4).

H. ostralegus is an aggressive mobbing species (Gochfeld 1984), with multiple breeding individuals observed chasing avian nest predators throughout the incubation and chick rearing phase. Gulls (*Larus* sp.), carrion crows (*Corvus corone*) and Western marsh harriers (*Circus aeruginosus*) have all been observed preying on *H. ostralegus* nests. Feral cats (*Felis* sp.), rats (*Rattus* sp.) and hedgehogs (*Erinaceus europaeus*) may also

act as nest predators at our study site (van der Ende 2015); however, records of nest predation by mammals are exceedingly rare and tend to be anecdotal.

Natural nests

In 2014 and 2015, we monitored nesting activity of *H. ostralegus* from April to August, with most nesting occurring between May and June. GPS coordinates of all nests were recorded, and a small pole was placed 3 meters north of the nest to allow nests to be relocated. New nests were located through systematic searching every 2-3 days and nest parents were identified by their colour bands, with known nests also checked during this time to determine nest fate. Our nest checking and marking method has little effect on the predation rate of *H. ostralegus* nests (Verboven *et al.* 2001), allowing us to gain a reliable measure of natural predation rates. Nests were continually checked until all eggs were missing. *H. ostralegus* chicks are semi-precocial and leave the nest within days of hatching. Therefore, nests were excluded from analyses following hatching as we could not accurately determine chick survival and location.

H. ostralegus nests can experience a range of fates. In addition to nest predation, nests may fail due to tidal flooding (van de Pol *et al.* 2010) and trampling by cows (Mandema *et al.* 2013). Flooding was easily noticeable in the field as the saltmarsh is inundated during such events. We checked known nests following flooding events and classified nests as flooded when all eggs were missing and the nest cup was wet. We determined the potential for cow trampling based on the state of eggs (cracked or crushed) and any surrounding evidence of cow activity. Nest loss due to cow activity was rare (3% of artificial nests). Nest abandonment is also possible in *H. ostralegus*; however, this occurs infrequently and will often be indistinguishable from nest predation as abandoned nests are likely to have higher predation rates than active nests (see Results). Therefore, nest abandonment was not considered in our analyses. Finally, natural nests may be empty due to hatching. Nests that were close to hatching were checked daily, providing us with an accurate measure of hatching success. The date of nest fate was considered the mid-point between the ultimate and penultimate nest check.

Artificial nests

To account for potential correlation between nest density and site/individual quality, we set up 100 artificial nests across a range of *H. ostralegus* nest densities during the 2015 breeding season. Artificial nests consisted of three medium sized painted chicken eggs placed in a small divot to mimic *H. ostralegus* nest scrapes (Fig. 1). A small pole was placed 3 meters north of the nest to facilitate relocation. Inappropriate egg size has been one of the key criticisms behind artificial nest use, with eggs that fail to mimic oystercatcher egg size potentially deterring nest predators (Haskell 1995b). Eggs used for artificial nests in this study were slightly wider and heavier than natural oystercatcher eggs (mean chicken egg: 55.5 mm x 42.23 mm, 58 g; mean oystercatcher egg: 55.43 mm x 39.4 mm, 45 g; United Nations 2010); however, we observed similar avian predators at both natural and artificial nests (personal observation). It should be noted that we do not expect artificial nests to estimate biologically realistic predation rates, but rather consider them a method to determine *relative* nest predation at varying densities of natural nests.

Artificial nest were set up across the study area beginning on May 7th. Initial artificial nest locations were selected to encompass the full range of potential nest densities present across the study area (0 – 7 nests/ha). All artificial nests were placed at least 200 m away from any other artificial nest to reduce dependence between samples that may arise due to area restricted searching by predators (Larivière & Messier 1998; Ringelman *et al.* 2014). When an artificial nest was depredated a new artificial nest was set up in the same area; however, specific artificial nest sites were never re-used. We continued to set up artificial nests throughout the breeding season (May 7th - July 1st), allowing us to account for potential changes in predation behaviour that may occur over the course of the breeding season (Schmidt & Whelan 1999).

Artificial nests were monitored daily to determine nest fate. Nest flooding was determined with the same method as natural nests (see above). To determine whether an artificial nest was trampled a small clay disc (6 cm) was buried slightly below each artificial nest. If eggs were missing or crushed and the clay disc was broken we considered this to be a trampling event. An artificial nest was considered depredated when all eggs in the nest were missing. Although partial predation is common in our study system (23% of artificial nests), there was a concern that individual partial

predation events may not be independent of one another. Artificial nests survived an average of 3 days on the saltmarsh.

Statistical analysis

All analyses were conducted in R (R Core Team 2016). We determined daily chance of nest predation for both artificial and natural nests. For every given nest on a given day we determined the density and the nearest neighbour distance of active *H. ostralegus* nests. Natural nests were a median 46 m from their nearest neighbouring nest (Fig. S1a; range: 3 m – 1,643 m). The scale at which density is measured can impact the outcome of analyses (Ringelman *et al.* 2014); therefore, we tested density over a range of distances. For artificial nest analysis we considered the number of active *H. ostralegus* nests within 50, 100, 150, and 200 m of the artificial nest. For natural nests, we considered only *H. ostralegus* density within 50 m as this showed the strongest relationship in artificial nests (see Results).

To analyse daily chance of nest predation for artificial and natural nests we fitted generalised linear mixed effects models with a binomial distribution in the package lme4 (Bates *et al.* 2014). All models were fitted with a random intercept term for nest identity, to account for pseudo-replication. Different areas within our study site may have consistently different predation levels; therefore, we also included a random intercept term for study sub-area. The predation of natural nests will likely depend on both the activity of neighbours and the activity of nest parents. As we collected data on multiple nests from the same parents over 2014 and 2015, we included a random intercept term for male parent identity in our analysis of natural nests.

Both models included a continuous effect of nest start date (days since March 1st) to account for variation in predation rates across the breeding season. As mobbing intensity is observed to differ between incubating and non-incubating nests we considered both the density effect of all active nests (nests with any number of eggs) and the percentage of active nests that were complete clutches. As predation pressure may vary between years (Schmidt & Whelan 1999) we included a categorical Year term in our analysis of real nests to account for these potential differences.

Natural nests active at the start and end of breeding season often had no nearest neighbours (i.e. they were the only nest recorded in the study area; <1% of total

nests). Therefore, nearest neighbour analysis was conducted separately on a subset of the data where nearest neighbour distances could be calculated. Effect of nearest neighbour distance was investigated for both artificial and natural nests. Model structure was identical to that outlined above, with terms for nest density and full clutch percentage replaced by a logarithmic term for nearest neighbour distance (m).

All results show parameter estimates and 95% confidence intervals. Density and nearest neighbour terms were standardised (mean: 0, standard deviation: 1) to allow for easy comparison.

Results

Artificial nests

We found evidence of negative density-dependent nest predation in artificial nests at all measured distances, but the strongest effect was driven by the number of *H. ostralegus* nests within 50 m (Fig. 2). Predation chance of artificial nests decreased as the number of nests within 50 m increased (Fig. 3; Table 1). The number of surrounding nests that were incubated and the placement date of artificial nests had no discernible effect on predation chance (Table 1).

Daily chance of artificial nest predation was also positively influenced by nearest neighbour distance. Artificial nests with closer immediate neighbours had lower daily predation chance (Fig. 4; Table 2).

Natural nests

Negative density-dependent nest predation was also observed in natural *H. ostralegus* nests. Daily nest predation chance decreased with increasing number of conspecific nests within 50 m, although the effect was less strong than that observed in artificial nests (Fig. 3a; Table 1). The number of surrounding nests that were incubated had no discernible effect on predation, nor did the year of study or the nest start date (Table 1).

Daily chance of natural nest predation was also strongly impacted by the distance of the nearest neighbour. Nests with closer immediate neighbours had a lower predation

chance, although this effect was once again weaker than that observed for artificial nests (Fig. 4; Table 2).

Discussion

Using an artificial nest experiment in conjunction with observational data on natural nests we detected the presence of negative density-dependent nest predation in nests of the Eurasian oystercatcher. By using artificial nests we remove any effects of individual (parental) quality that may influence nest predation rates. Furthermore, by monitoring predation rates across a large temporal range (May 7th to July 1st) and spatial range (1.52 km²) and at varying nest densities we were able to account for effects of habitat quality and potential temporal variation in predator behaviour. . Testing density-dependent nest predation effects with natural nests allowed us to verify the results of our artificial nest experiment and estimate realistic predation rates in our focal species. In combination, analyses with both artificial and natural nests provide a thorough test of density-dependent nest predation relationships (Ackerman *et al.* 2004).

Our study adds to a number of previous studies that have reported negative density-dependent nest predation (Andersson & Wiklund 1978; Oro *et al.* 2006; Ringelman *et al.* 2012, 2014; Carpio *et al.* 2016), raising the possibility that positive density-dependent nest predation relationships may not be as widespread as is commonly considered. One major difference between our study and the majority of previous density-dependent nest predation research has been the consideration of real nest density rather than artificial nest density (Andersson & Wiklund 1978; Wiklund & Andersson 1994). Unlike most previous studies, therefore, our result is able to account for changes in both predator and nest parent behaviour as nest densities vary, making it a more biologically realistic test of density-dependent effects. It is possible that previous studies where positive density-dependent nest predation has been recorded may in fact show different results when parental behaviour is considered, particularly in species with aggressive anti-predator defences like small passerines, which are a common focus of density-dependent nest predation studies (Pavey & Smyth 1998; Krams *et al.* 2008; Krams *et al.* 2010).

Although the use of artificial nests may have important impacts on the estimation of density-dependent nest predation, the inconsistency between our results and those of previous studies could also be explained by differences in the study systems. *H. ostralegus* differs in a number of respects to the waterfowl and small passerine systems where positive density-dependent nest predation has previously been observed (Martin 1988; Schmidt & Whelan 1998, 1999; Gunnarsson & Elmberg 2008; Ringelman *et al.* 2012, 2014; Carpio *et al.* 2016), being larger than passerines and more aggressive nest defenders than waterfowl (Forbes *et al.* 1994). Smaller and less aggressive species may be ineffective mobbers and so will instead rely on concealment as an anti-predator defence, a strategy that is likely to be ineffective at high densities (Page *et al.* 1983; Larivière & Messier 1998; Ringelman *et al.* 2014). The size and/or aggression of nesting birds may therefore be important for predicting the direction of density-dependent nest predation in poorly studied natural systems, and may also help explain the inconsistencies observed between colonial and non-colonial species.

The effectiveness of mobbing as an anti-predator defence may also be highly dependent upon the local predator guild, regardless of the size or aggression of nesting species. Our study population experiences predominantly avian predation, noticeably different to many previous studies where mammalian predators dominate (Schmidt & Whelan 1999; Jokimäki & Huhta 2000; Carpio *et al.* 2016). Similarly, many colonial nesting species inhabit areas with limited predator access, such as seabirds nesting on oceanic islands (Oro *et al.* 2006). In fieldfares, the impacts of conspecific density varied considerably between populations depending on the predators in the area (Wiklund & Andersson 1994), raising the possibility that density-dependent nest predation effects may vary broadly between species and also between populations within a species. The relative importance of anti-predator behaviour and predator guild composition in driving density-dependent nest predation is therefore hard to discern and will require greater focus.

Negative density-dependent nest predation in natural nests may be driven by increased vigilance or increased mobbing effectiveness. As *H. ostralegus* is known to be an aggressive mobbing species, increased size and/or intensity of mobbing groups at higher densities is most likely to drive the negative density-dependent nest predation relationship we observe in this study (Robinson 1985; Wiklund & Andersson

1994; Krams *et al.* 2009). Increased mobbing intensity was also considered the driver of a similar trend seen in colonial fieldfares (Andersson & Wiklund 1978; Wiklund & Andersson 1994). The fact that both artificial and natural nests benefit from high nest densities suggests that the density-dependent trends we observe may be, at least partly, an incidental benefit of neighbour defence. Nesting *H. ostralegus* pairs will chase off avian predators that fly near their nest, creating a 'protective zone' which may incidentally safeguard neighbours.

Explaining why an individual should cooperate in a mobbing activity is a classic question in evolutionary and behavioural ecology (Wheatcroft & Price 2008). As nest predators are not known to predate on parents in *H. ostralegus*, the cost of contributing to mobbing is likely to be small; however, conspecific density may play an important role. Potential 'defector' behaviour may become more likely when conspecific density is high, as the benefit of participating in anti-predator behaviour will decline (Fig. 4). Previous work has suggested that defecting from mobbing will be costly, as neighbours may remember previous cases of defection and refuse to assist defectors in future predation incidents (Krams *et al.* 2008). In *H. ostralegus*, familiarity between neighbours is known to be important in *H. ostralegus* territory settlement (Bruinzeel & van de Pol 2004), and so may also be important in nest defence. However, *H. ostralegus* may be less capable of punishing defectors as this species exhibits anti-predator behaviour over a large area that will encompass multiple neighbouring nests (personal observation), making it difficult to reward specific neighbours and ignore others. Our current analysis provides no mechanism to consider the behaviour of individual pairs; however, future work on *H. ostralegus* anti-predator behaviour, including direct field observation and use of GPS loggers, may allow us to better understand the cooperation in predator defence between breeding *H. ostralegus* pairs.

In addition to providing a test of density-dependent nest predation, our analyses using natural *H. ostralegus* nests provides an insight into predation rates in *H. ostralegus* that are biologically realistic. Over the 28 days of incubation, differences in predation pressure between low and high density areas will have a substantial impact on individual reproductive success, with low density areas experiencing exceedingly high predation rates (Fig. 3b). Breeding pairs with 0 - 1 nearby neighbours had a greater than 50% chance of experiencing nest predation during the 28 day incubation period

(0.91 and 0.62 respectively). These values are likely to be a conservative estimate of density dependence in reproductive success as they do not consider the period between hatching and chick fledging, which might also show density-dependent patterns (Wiklund & Andersson 1994). Although densities of 0 – 1 within 50 m may seem particularly low, mean daily nest density during our two study years was close to these levels (Fig. S1b; 2014: 1.15; 2015: 0.88) and with numbers of *H. ostralegus* declining steadily both within our study site and across the wider region, it is possible that densities may decrease further (van Roomen *et al.* 2012; van de Pol *et al.* 2014).

While the results of this study paint a bleak picture for breeding *H. ostralegus*, it should be noted that the population of *H. ostralegus* on Schiermonnikoog is still relatively dense compared to inland populations (Kamplicher *et al.* 2013). Despite their low densities, these inland populations showed substantial population increases across much of the 20th century (van de Pol *et al.* 2014). It is possible, therefore, that negative density-dependent nest predation effects may be weaker or even non-existent in other populations. As discussed above, differences in predator guilds may be an important mediator of density-dependent nest predation (Wiklund & Andersson 1994) and may trigger inter-population differences in density-dependent effects within *H. ostralegus*. Predator guilds differ markedly between island populations where avian predation dominates (e.g., this study; Schwemmer & Garthe 2011), and inland populations where mammalian predators like red foxes (*Vulpes vulpes*) have become more common (van de Pol *et al.* 2014). Replicated density-dependent nest predation studies across a range of island and inland populations of *H. ostralegus* will be necessary to identify and explain any differences in density-dependent effects.

With the incidence of negative density-dependent nest predation, continued density declines raise a concern for the viability of our study population. However, it is not clear whether changes in nest predation will drive declines at the population level, representing an Allee effect. This relationship should not be assumed, as previous research has shown the impacts of environmental change at the individual level will not always translate to the population level (McLean *et al.* 2016). Population modelling in *H. ostralegus* will be required to properly understand how density-dependent nest predation will impact population viability by accounting for potential changes in adult and nestling survival that may also vary with density (Wiklund & Andersson 1994).

Modelling work should also consider the role of heterospecifics in *H. ostralegus* nest predation. While this study focusses exclusively on *H. ostralegus* nest density, heterospecifics breeding in the study area are also likely to assist in predator mobbing and may impact nest predation rates (Pavey & Smyth 1998; Göransson *et al.* 1975). Many shorebird species that might assist in predator mobbing, such as godwits (*Limosa* sp.) and lapwing (*Vanellus vanellus*), have also declined within our study region (van Roomen *et al.* 2012), and this should be accounted for when estimating reproductive success and population viability of *H. ostralegus*. Furthermore, modelling should account for both temporal and spatial synchronisation in *H. ostralegus* nesting. While the current study considers spatial variation in nesting, individuals may also alter their laying date to coincide with neighbours and increase nest density. Laying date of birds may change over time due to both demographic (van de Pol *et al.* 2006b) and climatic shifts (Visser & Both 2005), and these changes should be incorporated into population models. Understanding the prevalence of negative density-dependent nest predation in natural systems and the potential consequences for population viability using population modelling presents a pressing future research avenue which will provide us with a more complete picture of future population trajectories.

Table 1: Relationship between daily nest predation chance and *H. ostralegus* nest density (Density) in both artificial and natural *Haematopus ostralegus* nests ($\pm$ SE). In artificial nest analysis, nest density was tested at 50, 100, 150, and 200 m. Analysis with natural *H. ostralegus* nests was conducted at 50 m. All density terms were scaled into z-scores (mean of zero, standard deviation of one) to allow for effective comparison between models. Logistic regression models include the percentage of nests with complete clutches (Full_clutch) and a continuous measure of placement date (Start_Date; days after March 1st). All models also included a random intercept term for nest identity and study sub-area. The natural nest model included an additional categorical term to account for differences between years (Year; 2014 and 2015) and a random intercept term for male parent identity. 2014 is used as the reference category. Significant variables are presented in bold.

Response variable	Intercept	Density	Full_clutch	Year	Start_Date
Real nests (50 m)	-3.92 ($\pm$ 0.68)	-1.22 ($\pm$ 0.26)	0.13 ($\pm$ 0.28)	-0.29 ($\pm$ 0.19)	0.01 ($\pm$ 0.01)
Artificial nests (50 m)	-0.44 ($\pm$ 1.03)	-1.76 ($\pm$ 0.51)	0.71 ($\pm$ 0.59)	-	0.01 ($\pm$ 0.01)
Artificial nests (100 m)	-0.84 ($\pm$ 1.04)	-1.41 ($\pm$ 0.39)	0.28 ($\pm$ 0.53)	-	<0.01 ($\pm$ 0.01)
Artificial nests (150 m)	-0.80 ($\pm$ 1.07)	-1.20 ($\pm$ 0.35)	0.09 ($\pm$ 0.55)	-	<0.01 ($\pm$ 0.01)
Artificial nests (200 m)	-1.25 ($\pm$ 1.04)	-1.03 ($\pm$ 0.32)	-0.58 ($\pm$ 0.57)	-	0.01 ($\pm$ 0.01)

Table 2: Model outputs showing the logarithmic relationship between nearest neighbour distance (distance to the nearest *Haematopus ostralegus* nest) and daily nest predation chance of both artificial and natural nests ($\pm$ SE). Nearest neighbour distances were transformed into z-scores (mean of zero, standard deviation of one) to allow for effective comparison between models. Logistic regression models included a continuous variable for nest initiation date (Start_Date; days after March 1st). Models also included a random intercept term for nest identity and study sub-area. Analysis with natural nests also included a categorical term to account for differences between years (Year; 2014 and 2015) and a random intercept term for male parent identity. 2014 is used as the reference category. Significant variables are presented in bold.

Model	Intercept	Distance	Year	Start_Date
Artificial Nest	-2.56 ($\pm$ 1.15)	2.35 ($\pm$ 0.62)	-	0.02 ($\pm$ 0.01)
Natural Nest	-4.61 ($\pm$ 0.74)	1.38 ($\pm$ 0.23)	-0.18 ($\pm$ 0.20)	0.01 ($\pm$ 0.01)



Figure 1: a) Artificial nest made using medium sized painted chicken eggs. b) *Haematopus ostralegus* nest.

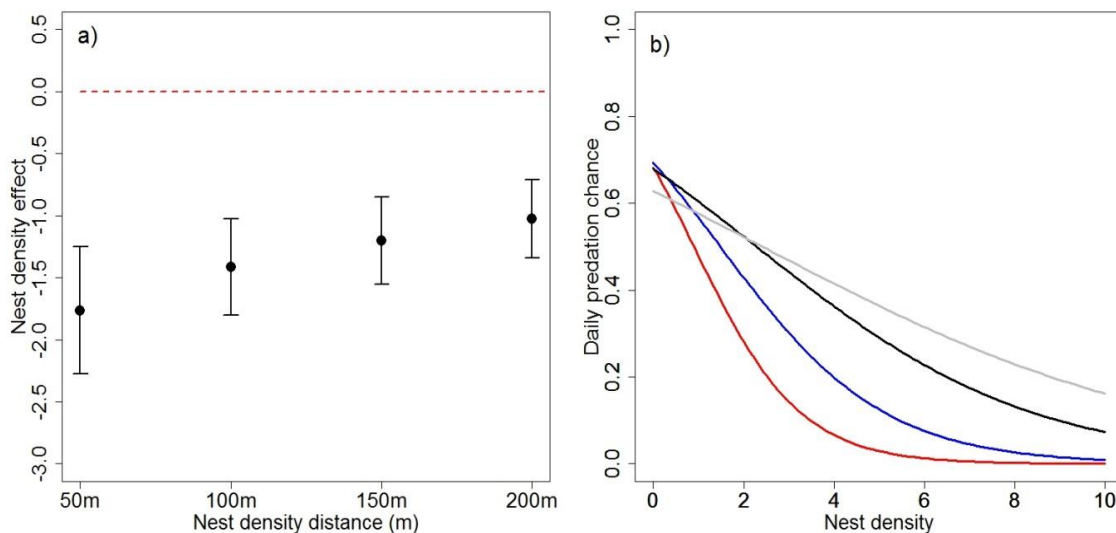


Figure 2: a) Standardised parameter estimates of models testing the impact of *Haematopus ostralegus* nest density at 50, 100, 150 and 200 m on the daily chance of artificial nest predation ($\pm$ SE). Dashed red line represents the point at which no density-dependent predation is occurring. Points below this line represent negative density-dependent predation. b) Model estimates showing the impact of *H. ostralegus* nest density within 50 m (red), 100 m (blue), 150 m (black), and 200 m (grey) on the daily chance of artificial nest predation.

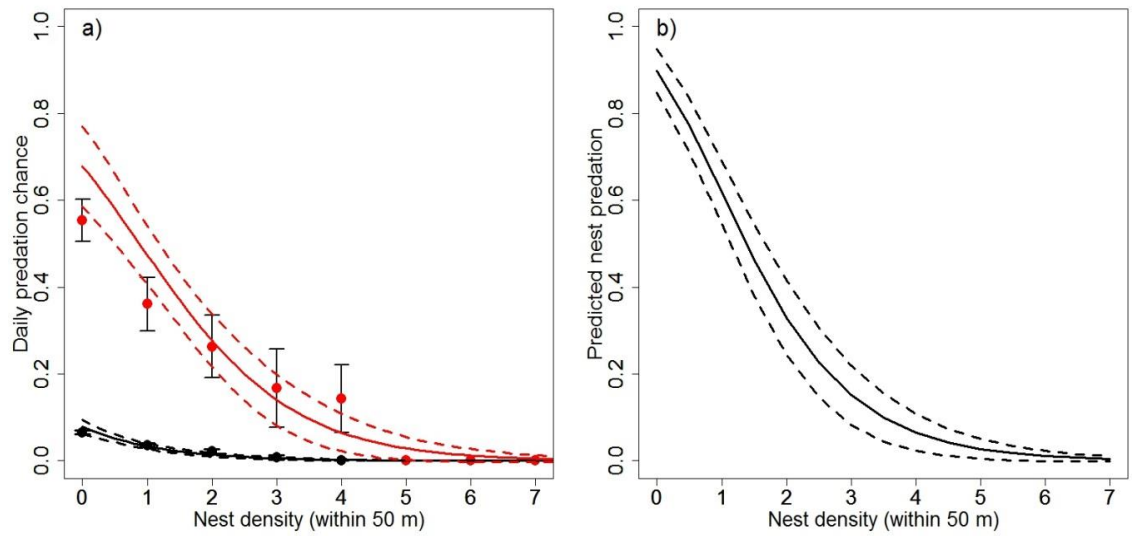


Figure 3: a) Daily chance of nest predation for artificial (red) and natural nests (black) at increasing *H. ostralegus* nest densities (number of nests within 50 m). b) Nest predation chance of *H. ostralegus* nests across the full length of incubation (28 days) at increasing *H. ostralegus* nest densities (number of nests within 50 m).

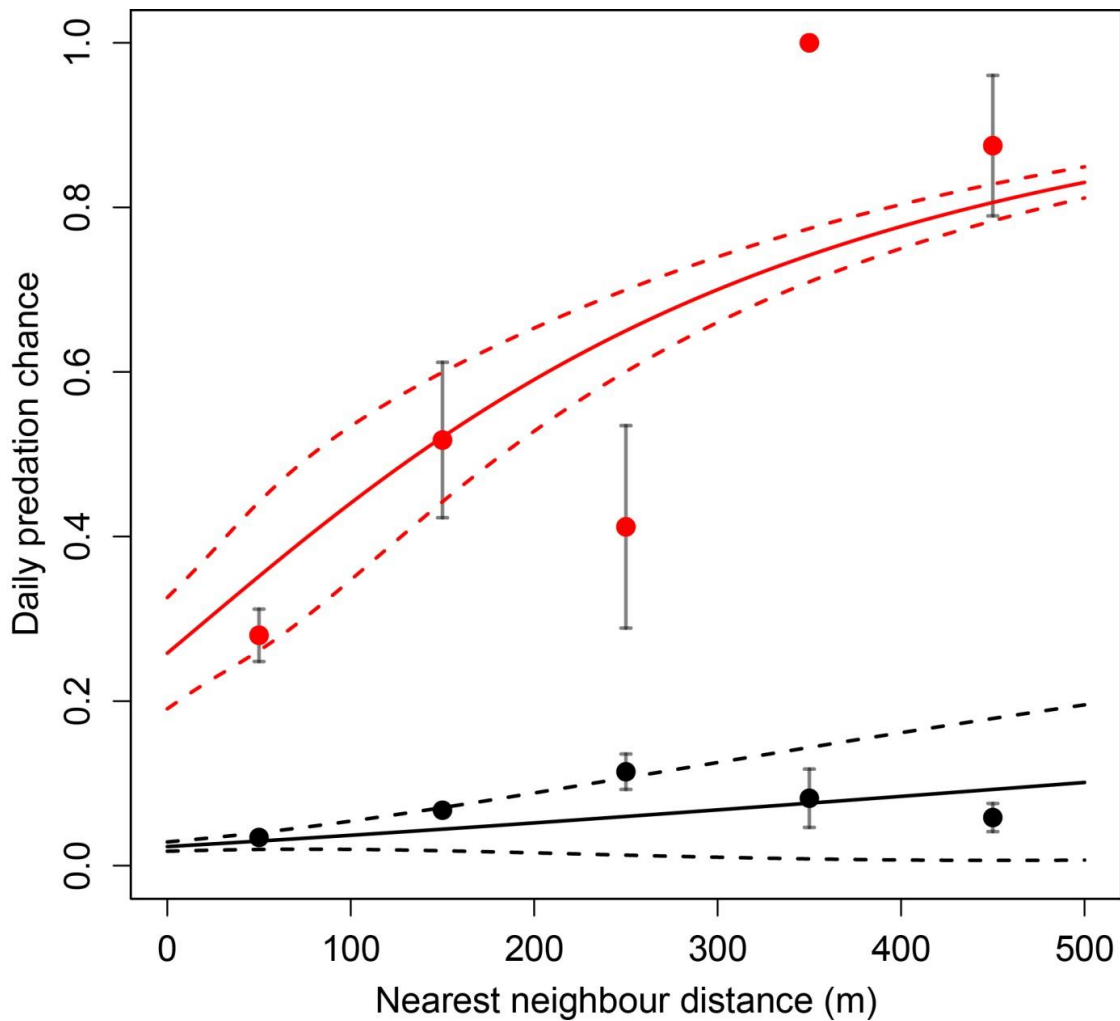


Figure 4: Daily chance of nest predation for artificial nests (red) and active *Haematopus ostralegus* nests (black) at varying nearest neighbour distances (distance to nearest active *H. ostralegus* nest; m). Data has been restricted to include only those nests with nearest neighbours between 0 and 500 m to illustrate the nearest neighbour relationship of the majority of nests (Fig. S1a). Data are grouped together in 100m blocks. Model predictions are estimated from a full dataset containing all data. A plot containing the full dataset is provided in Fig. S2. Effects of nearest neighbour distance are consistent when modelling when using the full dataset and the subset of data below 500 m.

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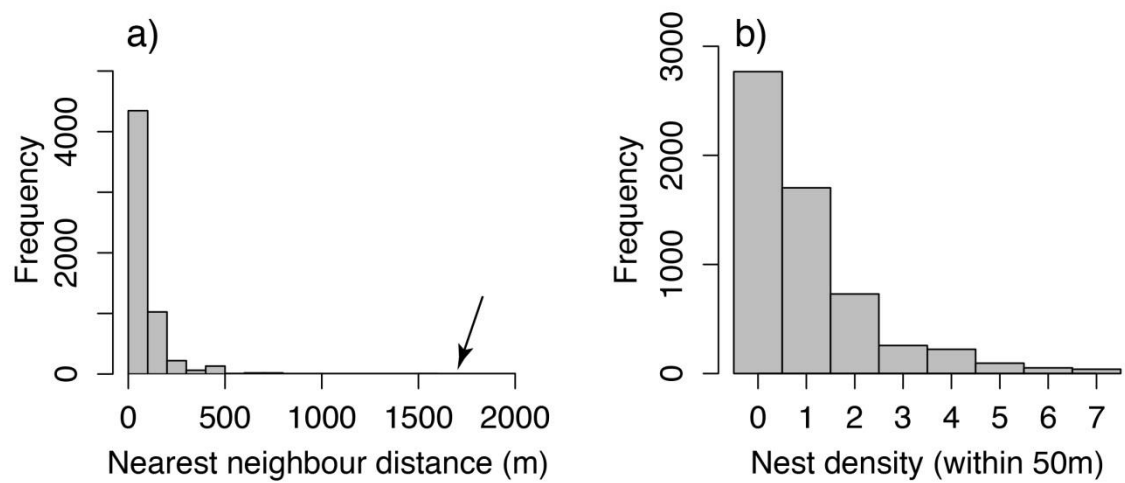


Figure S1: a) Frequency of nearest neighbour distances (m) in natural *Haematopus ostralegus* nests during 2014 and 2015. Black arrow marks the largest recorded nearest neighbour distance (1,643 m). b) Frequency of nest densities (nests within 50 m) in natural *Haematopus ostralegus* nests during 2014 and 2015.

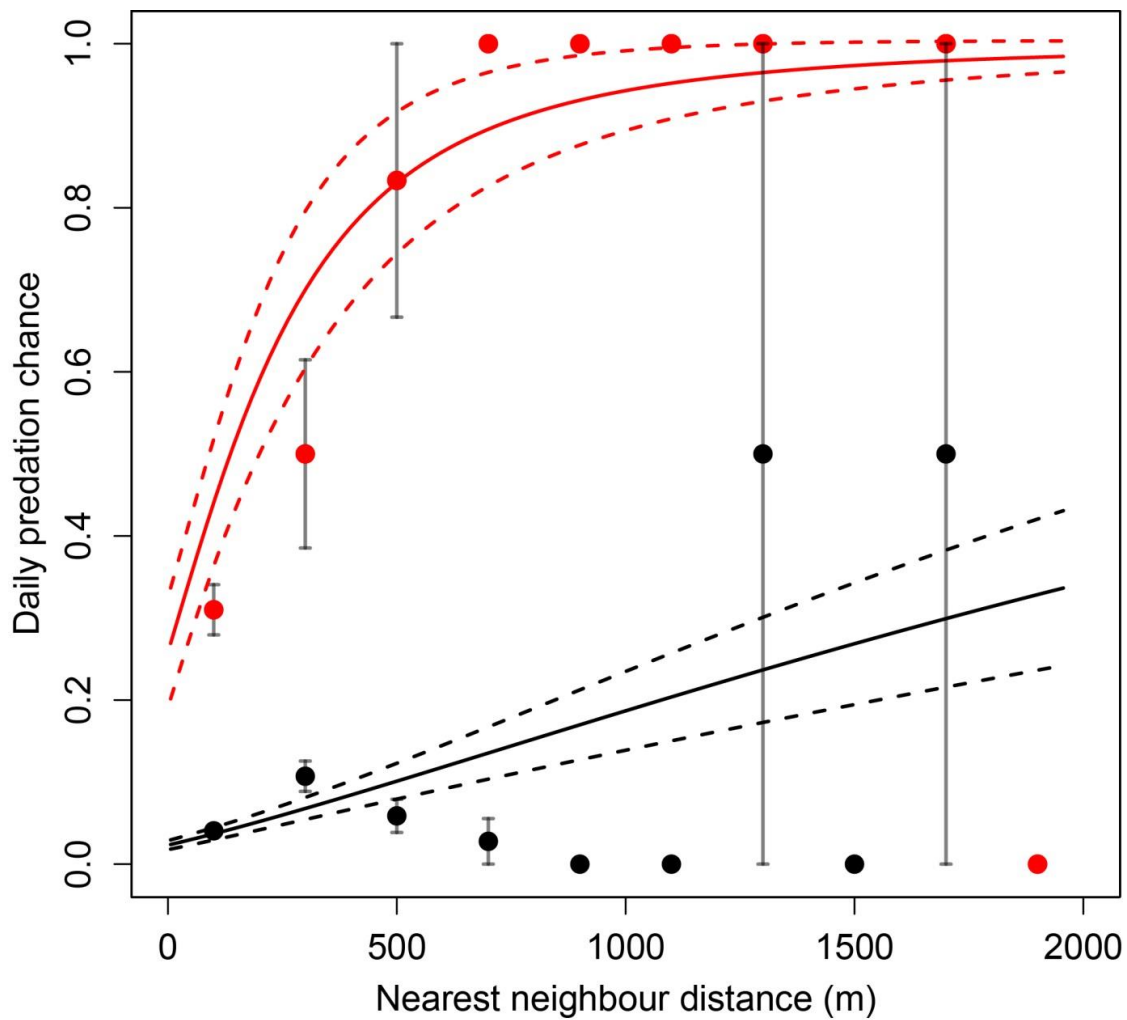


Figure S2: Daily chance of nest predation for artificial nests (red) and active *Haematopus ostralegus* nests (black) at varying nearest neighbour distances (distance to nearest active *H. ostralegus* nest; m). Points show the mean daily chance of nest predation grouped together in 200m blocks.

Synthesis & Conclusions

Over the past few decades, it has become increasingly clear that extreme climatic events (ECEs) can have important impacts on ecosystems, imposing strong selective pressure (Gibbs & Grant 1987; Brown & Brown 1998; Chevin *et al.* 2013) and increasing extinction risk (Kokko & Sutherland 2001; Schwager *et al.* 2006). In 2007, seminal work by Jentsch *et al.* argued for a shift in focus within climate change ecology, away from studies that consider trends in climatic means towards those that consider ECEs. Research interest in ECEs has increased considerably since the publication of Jentsch *et al.*'s work (Bailey & van de Pol 2016; Chapter 1). Yet our understanding of ECE impacts is still in its infancy. This thesis takes some steps towards addressing our knowledge gaps in this research area. Below, I will synthesise the results of the five presented chapters and discuss potential future work which may stem from these research projects.

Changing study design

Although the number of studies on ECEs has more than doubled since the turn of the millennia, much of the previous ECE work has been restricted to a small range of research questions. This limitation is largely driven by the choice of study system and the study design of previous research. Of particular concern is the common focus on single event studies (Bailey & van de Pol 2016; Chapter 1). Studies which encompass only a single ECE will be unable to account for the context dependent nature of ECE impacts, preventing general predictions of future ECE effects on the same or different systems. With single event studies, we also have no ability to consider micro-evolution or phenotypic plasticity as a response to ECEs. Furthermore, single event studies have no ability to consider impacts of changing ECE frequencies, which will be particularly important in the context of future climate change. To overcome these limitations, I recommend the combined use of experimental studies, theoretical modelling, and a greater focus on long-term observational work that encompasses the occurrence of multiple ECEs (Bailey & van de Pol 2016; Chapter 1). It may be possible to obtain appropriate multi-ECE data on natural systems using spatial replication, which has already seen some success (Phillimore *et al.* 2010; Oliver *et al.* 2013). Such multi-event studies will allow us to answer more complex and relevant ECE questions, such as the impacts of changing ECE frequencies and the potential role of phenotypic plasticity. While some long-term study systems of this nature do exist (Mooij *et al.* 2002;

Frederiksen *et al.* 2008; van de Pol *et al.* 2010), expanding the number of these studies should be an important goal when allocating limited resources. There is also the potential for future meta-analyses that can incorporate the variety of ECE studies produced over the past decades to provide a broad picture of ECE impacts. Yet, for meta-analyses of this type to be most effective, it is imperative that research is explicit about how ECEs are defined.

While it is important to focus the efforts of future ECE work on appropriate study systems, it is also imperative that we consider ECE impacts at an appropriate time of year, when biological systems will be most vulnerable to climatic perturbation. Without full knowledge of organismal climatic sensitivity, research may focus on the impacts of climatic conditions within a biologically inappropriate period, limiting the ability to make meaningful conclusions. In Chapter 2, I introduced a new statistical toolbox, *climwin*, designed to quantify climatic sensitivity within a year. *climwin* builds on previous climate sensitivity research (van de Pol & Cockburn 2011; Kruuk *et al.* 2015) to provide a standard and time efficient method for conducting such analyses.

With the public release of *climwin*, there is the potential to answer a range of outstanding questions in both climate change ecology generally and ECE research specifically. For one thing, *climwin* may be used to test for the prevalence of non-linear relationships (e.g. quadratic, logarithmic) between climate and biological variables. Such an analysis will give us an idea of the frequency with which threshold-like responses to climate occur in natural systems, which will have important implications for the way in which we define ECEs (Bailey & van de Pol 2016; Chapter 1). Furthermore, *climwin* may be used to understand the variability in climatic sensitivity between different species or populations of the same species. This may have particular importance in the context of spatial replication and space-for-time substitution discussed in Chapter 1. Limited consistency in climatic sensitivity between conspecific populations will undermine the effectiveness of spatially replicated datasets for use in climate change ecology. Future progress in *climwin* will incorporate a wider range of climate sensitivity methods (e.g., Teller *et al.* 2016), thus expanding the versatility of this toolbox for future users. This will also allow for an easy comparison of the performance of different climate sensitivity approaches, which will be a necessary next step to help improve the efficiency of these analyses.

Phenotypic plasticity in response to extreme events

Individuals faced with more frequent occurrences of ECEs may be capable of responding to such events through phenotypic plasticity, reducing the consequences of potential future ECEs. This will be particularly relevant in long-lived species where rates of micro-evolutionary change are low. If phenotypic plasticity is present, documented impacts of a single ECE at one point in time are likely to over-estimate the impacts of a similar ECE in the future, as responses of individuals to the same climatic conditions will have changed to incorporate previous ECE experience. Yet a consideration of phenotypic plasticity as a response to ECEs is still lacking (Bailey & van de Pol 2016; Chapter 1). Chapters 3 and 4 provided some of the first tests for phenotypic plasticity in response to increased ECE frequency in the Eurasian oystercatcher (*Haematopus ostralegus*). The focal population of *H. ostralegus* fits many of the characteristics of an ideal study system for consideration of ECEs (Bailey & van de Pol 2016; Chapter 1). Data has been collected over 32 years and ECEs (flooding events) have become more frequent over time, now occurring reasonably regularly. This system therefore provided an ideal opportunity to test outstanding questions concerning ECEs.

This thesis provided a thorough test of potential phenotypic plasticity in *H. ostralegus* by considering the role of both nest-site and territory selection as potential mechanisms of nest elevation change (Chapter 3 and 4). Considering phenotypic plasticity in this way is particularly relevant as changes in habitat selection behaviour may vary with the spatial and temporal scale at which decisions are made (Orians & Wittenberger 1991). Indeed, analysis of broad scale territory settlement patterns in *H. ostralegus* provided evidence of phenotypic plasticity, while a similar investigation at a finer scale, using nest-site selection, showed little evidence of phenotypic plasticity. Limited nest-site selection responses may be explained by the presence of counter-acting selective pressures that constrain the potential for phenotypic plasticity as a response to ECEs in *H. ostralegus*. Balancing responses to ECEs with other major selective forces (e.g. adult/nest predation, brood parasitism) may play a vital role in shaping species responses to climate change and ECEs. This thesis provides one of the first tests of phenotypic plasticity as a response to ECEs; however, conducting similar

investigations on a range of other species will be an important next step towards understanding the general applicability of these results. Different species may display markedly different rates of phenotypic plasticity in response to ECEs, perhaps linked to differences in life history characteristics. For example, it may be possible that long-lived species that show limited habitat fidelity will show much stronger responses to ECE frequency as individuals are more likely to switch habitats between years. Furthermore, it will be important to consider phenotypic plasticity in response to different types of ECEs (e.g. floods, heatwaves). In cases where organisms can respond to ECEs behaviourally, phenotypic plasticity may be common. Yet where responses in less labile traits such as morphology are required to alleviate ECE impacts, the occurrence of phenotypic plasticity may be more limited. Additionally, the speed with which ECEs occur will impact the viability of phenotypic plasticity, with rapid ECEs (e.g. flash flooding) providing little time for response between detection of environmental cues and the onset of extreme conditions (Bailey & van de Pol 2016; Chapter 1).

Failure to respond and potential consequences

Although *H. ostralegus* exhibited increased nest elevation, driven by changing territory settlement patterns, this increase is unlikely to provide an effective long-term response to continuing climatic change. Rates of nest elevation change will be insufficient to keep pace with flooding changes (0.4 cm/year nest elevation change vs. 0.8 cm/year change in maximum high tide; Chapter 3). Additionally, the benefits of changing territory settlement patterns will be limited as there will be a few high elevation territories viable for *H. ostralegus* nesting. Increased flooding frequency is therefore likely to drive greater rates of nest failure, limiting population recruitment (van de Pol *et al.* 2010) and potentially exacerbating current population declines (van Roomen *et al.* 2012; van de Pol *et al.* 2014). As wild populations like this continue to decline (Alford *et al.* 2001; Craigie *et al.* 2010; van Roomen *et al.* 2012) there is an urgent need to understand how density-dependent processes may either alleviate or exacerbate population viability. Some populations may experience improved outcomes at lower densities, as rates of predation and transmission of disease are reduced (Gunnarsson & Elmberg 2008; Langwig *et al.* 2012), while for others reduced conspecific density will worsen population viability, through reduced hunting success or increased brood parasitism (Creel & Creel 1995; Feeney *et al.* 2013). Analysis of nest

predation in *H. ostralegus* at varying density levels showed strong evidence for negative density-dependence, with increased nest predation at low densities, likely driven by reduced effectiveness of mobbing behaviour (Chapter 5). Not only does this paint a worrying picture for the viability of the focal population but it also raises the possibility that similar examples of elevated nest predation at low densities will be common among other mobbing bird species, a situation that is not well considered in the literature.

The results presented in this thesis paint a bleak picture for *H. ostralegus* in the face of climate change, but there is a need for further study before any definitive conclusions can be drawn. There is potential for breeding individuals to display responses to increased flooding frequency through alternative pathways. Advancing laying date and shortening the length of incubation and the early chick phase have been suggested as additional mechanisms by which flooding risk may be decreased (van de Pol *et al.* 2010). Additionally, changes in the flooding resilience of eggs (Ward & Burger 1980) may facilitate reduced impacts of extreme flooding, not by reducing the chance of a nest being flooded but minimising the chance that a flooded nest will subsequently fail. Furthermore, changes in nest structure may also be possible to reduce the chance of eggs being washed away (Humphreys *et al.* 2007). Although, *H. ostralegus* nests are rudimentary and offer little egg protection, changes in nest location which alter vegetation height or thickness, may serve a similar purpose by trapping eggs near the nest during flooding. Ideally, all these factors should be considered in population modelling, along with density-dependent effects, to gain a more effective indication of future population trajectories in *H. ostralegus*. If population predictions continue to show downwards trends when these additional factors are accounted for it may be necessary to consider active conservation strategies to insulate breeding populations of *H. ostralegus* against flooding and predation pressures. Vegetation management may deliver one potential solution by adjusting vegetation characteristics at high elevations (e.g. vegetation height, vegetation species) thus making high elevation areas more enticing for reproductive individuals. The addition of elevated nest plots may be another way to provide *H. ostralegus* with suitably elevated nesting sites within established territories, reducing the need for territory movement to facilitate elevation increase. However, a pilot experiment with small elevated plots (Width: 50

cm x Length: 50 cm x Height: 20 cm) showed mixed results on Schiermonnikoog (Bailey, unpublished data).

Conclusions

This thesis has expanded theoretical, methodological and empirical aspects of ECE research. This diverse body of work will lay the foundations for broader future ECE research that seeks to encompass multiple ECE occurrences and answer more complex scientific questions. As has now been well documented, changing patterns of ECE will be an important and distinct aspect of future anthropogenic climate change. Properly understanding the impacts of ECE patterns and organismal responses to such patterns will be integral to the documentation and prediction of population changes in the Anthropocene.

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