Managing Mainland Salt Marshes for Breeding Birds

Interactions with Plants, Food and Predation

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Contents

Summary

The Wadden Sea region is one of the most important breeding areas in Western Europe for coastal breeding bird species. Salt marshes at the Wadden Sea are crucial for reproduction of many bird species. These salt marshes are protected under the European Habitat Directive and by national nature conservation acts. Nevertheless, many breeding bird species show declining trends in numbers of breeding pairs in this habitat. It is expected that management of salt marshes is important for successful conservation of breeding bird populations but the impact of management, e.g. grazing or mowing, on the habitat quality for breeding birds is still not fully understood.

In this study the effects of management on the three crucial habitat characteristics for breeding birds were studied on mainland salt marshes: effects of management on vegetation structure, on predation risk and on foraging conditions for invertebrate feeding chicks. In addition the changes in flooding risk for nests due to climate change were assessed.

The structure of the vegetation is a key determinant for the habitat quality of salt marshes for breeding birds. Our data confirmed the strong impact of grazing and mowing on structural vegetation parameters, specifically canopy height and sward density. Changes in canopy height and sward density have strong impacts on food availability and have repercussions for nest predation rates through altered nest concealment.

On salt marshes, predation rates of ground nests were strongly influenced by vegetation structure and management. High nest survival went along with a tall canopy of the vegetation. Temporal effects were also important, as nest predation rates were highest during the peak of the breeding season. Common Redshank showed behavioural adaptation to high predation risk, with decreased nocturnal nest attendance on sites with high predation risk as compared to areas with low predation risk.

The food availability and forage quality were analysed using pitfall traps and measurements of the caloric content of the potential prey items. Based on this study we can show that the salt marshes provided high spatial heterogeneity in the availability of total energy and quality of prey. At different sites and vegetation types, we found large deviations in the composition of the invertebrate communities, from those rich in insects and spiders to those dominated by amphipods. Food availability strongly depended on the invertebrate communities on salt marshes, whereas the quality of food was negatively correlated with the quantity. In other words: either high abundances of low-quality prey or low abundances of high-quality prey were available on the salt marshes we studied. The shift from low to high abundances of potential prey items was caused by the increased abundance of amphipods in late successional stages of the vegetation.

Most of the mainland salt marshes are man-made, which implies that an artificial drainage system alters the morphology of the marsh. Due to drainage, a rapid succession towards the climax of salt marsh succession takes place, especially under high sedimentation rates and at sites where natural dynamics are missing and no management in form of grazing of mowing takes place. The rapid development towards climax stages of salt marsh succession results in high proportion of tall and dense vegetation. Within such a vegetation structure hidden nests can profit by well concealment of nests and lower predation rates. But, within this tall and dense vegetation the quality of invertebrate prey is low and the accessibility of prey for foraging birds is reduced. In addition, these tall and dense vegetation stands are not suitable for breeding birds with open nests. Grazing or mowing of salt marshes, but also rewetting by removal of the artificial drainage system is expected to slow down the succession and provide a higher heterogeneity of habitats for breeding birds.

This study entangles the complex impacts of management on the habitat quality of salt marshes for breeding birds to improve the understanding of interactions between management, abiotic environment, vegetation and fauna on mainland salt marshes. This can support science-based management decisions on mainland salt marshes.

Chapter 1

General Introduction

Background of the project

The intensification of agriculture during the second half of the 20th century caused a substantial loss and degradation of habitats suitable for birds that breed in grasslands throughout Northwestern Europe (SUTHERLAND 1996; VICKERY et al. 2001; ROBINSON & SUTHERLAND 2002). Through drainage and conversion of grasslands into croplands, open habitats like wet grasslands, moorlands and low-yielding grasslands have disappeared. Intensification led to earlier mowing dates threatening nests of ground breeders (NEWTON 2004; SCHEKKERMAN et al. 2009; SCHROEDER et al. 2012). These changes caused by intensification resulted in a loss of suitable breeding and rearing habitats for a large number of bird species ranging from waders to songbirds (WILSON et al. 2005; ROODBERGEN et al. 2012). Most ground-nesting birds, i.e. waders that breed mainly on wet grasslands have declined rapidly over the last decades (BURFIELD & VAN BOMMEL 2004; VAN TURNHOUT et al. 2010).

While inland breeding populations of waders have declined significantly with the intensification of agricultural land use (ROODBERGEN et al. 2012), the salt marshes of the Wadden Sea provided relatively reliable breeding sites. In difference to inland grasslands, agricultural intensification of the salt marshes was prevented. Therefore, the salt marshes gained in importance since the loss of open habitats at inland sites. The breeding populations of some species on coastal salt marshes have remained stable or were even increasing, in contrast to the overall negative trend of meadow birds (HÖTKER et al. 2007). This development has significantly increased the importance of salt marshes for breeding populations of some coastal bird species (EXO 2008; THYEN et al. 2008).

The Wadden Sea is used by almost one million ground-breeding birds spread over 31 species, for many species including substantial parts of the flyway population (KOFFIJBERG et al. 2006). In Western Europe the Wadden Sea region is one of the most important breeding areas for breeding bird species connected to coastal areas such as beaches, salt marshes and polder areas, (WOLFF et al. 2010). Salt marshes within the Wadden Sea are of importance for many of the breeding bird species. An example of the importance of salt marsh habitats is provided by the breeding population of Common Redshank *Tringa totanus* (hereafter Redshank). The estimated number of breeding pairs in Germany is 14,500 whereof almost 50 % of the pairs breed in salt marshes at the mainland coast of the Wadden Sea (HÖTKER et al. 2007). Populations of Redshanks declined across Central and Northwest Europe in the second half of the 20th century (BURFIELD & VAN BOMMEL 2004). In contrast, on Wadden Sea salt marshes Redshank populations remained stable on a relatively high level for a long time and even increased slightly in some areas at the end of the 20th century. In recent years, however, the coastal Redshank population is in decline (KOFFIJBERG et al. 2009).

Due to the importance of the Wadden Sea region for breeding bird species it is crucial to ensure the reproduction of coastal birds in this region. For the conservation of biodiversity, the protection of sites is a widely accepted and generally successful means (LOVEJOY 2006). Protected sites can act as retreat areas in a landscape with intensive agricultural land use. The Wadden Sea is protected under the European Habitats Directive (92/43/EEC) and most parts also under national nature conservation acts (CWSS 2008). In the German part of the Wadden Sea three national parks were founded in the mid to late 1980s to secure the conservation of this coastal region. The objectives of the national parks focus on natural process and minimize human activities and interventions (CWSS 2008). Three decades of strict protection should result in a reasonable protection of breeding birds. But although the Wadden Sea habitats are well protected since more than 30 years, a moderate decline of breeding bird numbers takes place. Salt marshes have the highest proportion of declining species, among all breeding habitats of the Wadden Sea (KOFFIJBERG et al. in prep.; Fig. 1-1).

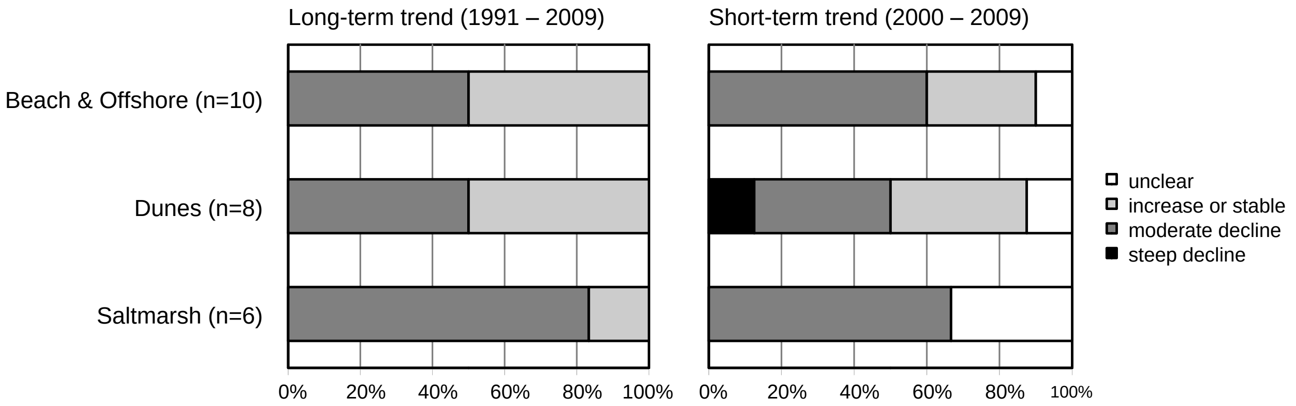

Figure 1-1 Overview of trend status of breeding birds dependent on the three main habitats in the Wadden Sea (according to KOFFIJBERG et al. in prep.)

Causes for the declines among breeding birds within the Wadden Sea are not known yet, but it is expected that the declines are linked to human disturbance, lack of habitat dynamics, mussel- and cockle-fisheries, habitat degradation in the dunes and increased predation risk (KOFFIJBERG et al. 2006). These changes result in less favourable food availability, increased predation, disturbance through recreational activities and thus poor breeding performance. The regular Wadden Sea wide breeding bird censuses make the trends in breeding bird numbers visible, but are unable to reveal the ecological causes (KOFFIJBERG et al. 2006). In order to unravel causal links, species specific and detailed studies are necessary in addition to the regular breeding bird census. Only these additional studies will finally allow an assessment of the impact of salt marsh management on breeding birds (KOFFIJBERG et al. 2006).

ROODBERGEN et al. (2012) found that decreased reproductive performance is a steering factor for the general decline of European meadow bird species. Studies in the Wadden Sea of Lower Saxony indicate that for Redshanks current reproduction figures on mainland salt marshes are below maintenance levels of the breeding population (THYEN et al. 2008). This suggests that low reproduction could also be the main reason for the declines of breeding bird populations on salt marshes. It is crucial to visualize abiotic and biotic processes on salt marshes in order to understand declines in breeding bird populations. The geomorphology, tidal regime, wind-wave patterns and sedimentation are the abiotic factors influencing the properties of salt marshes (BAKKER et al. 2005). In salt marshes elevation influences the flooding frequency and in consequence the salinity of a site. Based on this environmental stress gradient a specific vegetation is formed (MINDEN et al. 2012) along with a highly specialized invertebrate fauna (FINCH et al. 2007). Flooding risk, plant community composition and vegetation structure along with the invertebrate fauna as potential food and predator occurrence form key determinants of the habitat suitability of a salt marsh for breeding birds.

It is known, that additional conservation actions targeted towards specific threats are beneficial in supporting the conservation aims for protected areas (WILSON et al. 2007). Site management plays here a governing role and impacts the habitat quality of salt marshes for breeding birds in various ways. Successful conservation can only be reached through effective management of protected sites (COOK et al. 2010). For the Wadden Sea, the impact of changes in salt marsh management on breeding birds and the effect on breeding bird numbers is yet largely unknown (WOLFF et al. 2010). Changes in management with the foundation of the German Wadden Sea national parks in the late 1980s went along with severe changes in the vegetation. This resulted in a decrease of the pioneer zone and an extension of late successional and climax stages in many salt marshes (WOLFF et al. 2010). In Lower Saxony the surface area of intensively grazed salt marshes declined from 23 % in the 1980s to 11 % in 1999. The cessation of intensive grazing on salt marshes is still going on: in 2003 70 % of the salt marshes were without agricultural usage, 18 % had moderate grazing, 8 % were mown regularly and just 4 % had intensive grazing (KOFFIJBERG et al. 2006). These changes in management with resulting changes in vegetation impact the habitat quality of salt marshes for breeding birds. The impact of salt marsh management works through on the biological processes mainly by removal of biomass by mowing or livestock grazing. But also the physical processes are changed in conjunction with management due to the drainage of salt marshes leading e.g. to altered sedimentation rates (TEMMERMAN et al. 2003). How physical processes, vegetation, invertebrate fauna and occurrence of predators are linked with management is not well understood and not always obvious. But only through an integrated approach of these driving factors for habitat quality for birds, it will be possible to evaluate the effects of salt marsh management on breeding bird trends. This thesis provides a first step towards this integrated approach.

Thesis outline

Within this project I aim to assess the impact of different types of salt marsh management on habitat properties for breeding birds and thereby at unravelling possible causes for declining breeding pair numbers on salt marshes. Fig. 1-2 provides a schematic overview of the complex interactions of factors influencing habitat quality for breeding birds.

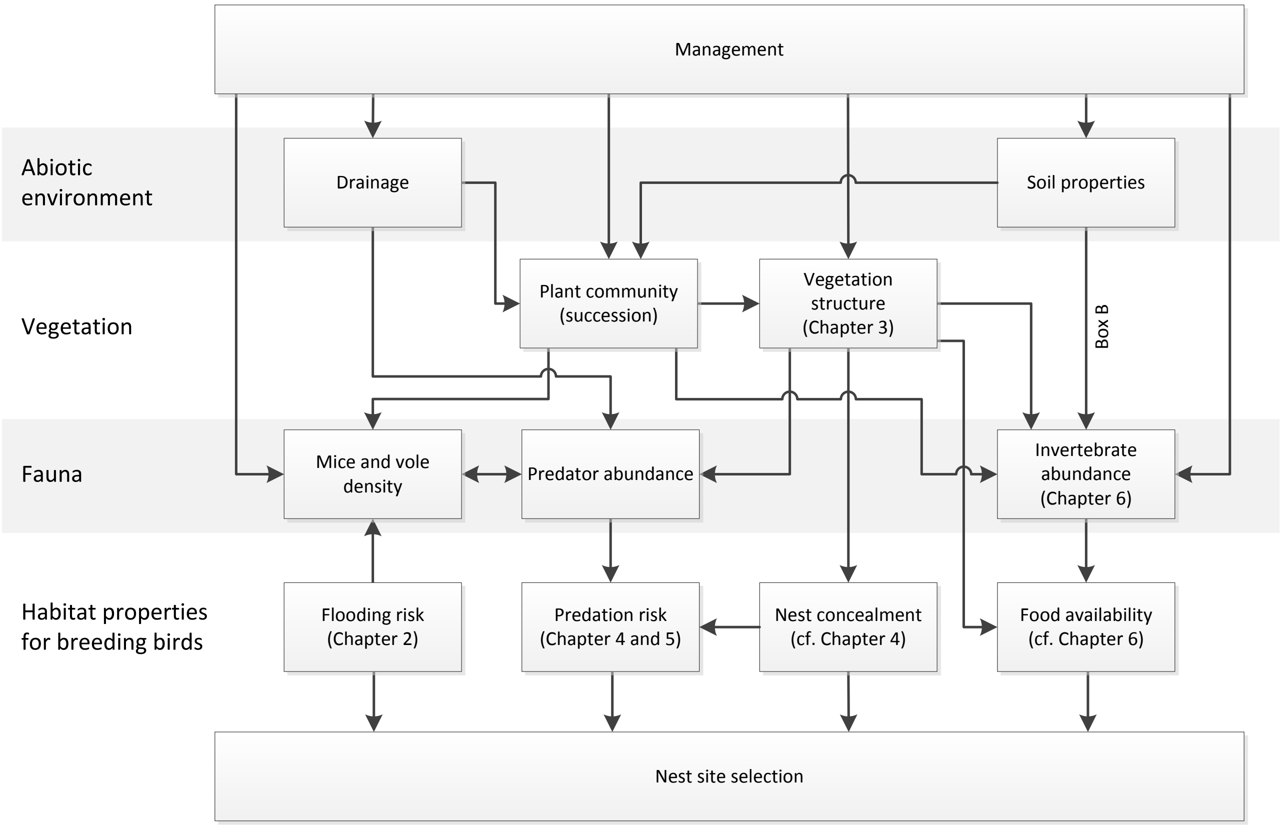

Figure 1-2 Conceptual model of management effects on habitat properties for breeding birds on salt marshes

For nest site selection on salt marshes, four factors are of crucial importance: flooding risk, possibilities for nest concealment, predation risk and food availability. Although flooding risk is not altered by management, there is a human dimension to flooding risk mediated by climate change. An increase in flooding risk would lead to reduced breeding success as flooding can cause a total loss of nests, if the flooding occurs during the nesting phase. The effect of climate change on flooding risks of nests during the breeding season is evaluated in chapter 2 of this thesis. The impact of management on vegetation structure and a characterisation of vegetation structure within different types of salt marsh vegetation, are presented in chapter 3 backed by a methodological dissemination of field techniques to assess vegetation structure. The vegetation structure is a key factor for breeding birds which has impacts both on forage conditions and predation risks. Vegetation structure defines the quality of foraging habitats, as the accessibility of invertebrate prey is driven by this factor. But vegetation structure also determines the concealment of nests and can therefore influence predation risk for breeding birds. The predation pressure on artificial nests is assessed in chapter 4, and predator induced changes in nesting behaviour of Redshanks in chapter 5. In chapter 6 the food availability on salt marshes is assessed, as this is an important factor for breeding success especially for precocial chicks of waders and for songbirds foraging on salt marshes invertebrates. In chapter 7 the interaction of management and habitat quality for breeding birds is elaborated.

This thesis is a compilation of my research over the last years, consisting of data collection in the field, processing and analysing of data and writing of manuscripts. Chapter 2, 3, 4, 5 and 6 were prepared together with co-authors acknowledged in the respective chapters. Main author of chapter 2 was Martijn v.d. Pol. The information on Redshank nest locations for that study was gathered during my field work. For chapter 5 temperature data logger information and nest controls from *Beckmannsfeld* were gathered during my field work for this project and the data preparation for analyses were done together with Anja Cervencl, the main author of chapter 5.

Species in focus and study sites

Redshank, a typical salt marsh breeding bird species, is in the focus of this study. Redshanks are ground breeders that nest preferably in high and dense vegetation stands (THYEN & EXO 2005). The nests are concealed in the vegetation, and therefore high vegetation coverage is a key habitat parameter for this species (KOFFIJBERG et al. 2006). However, within this study I look at general patterns on salt marshes, and therefore data gathered will be applicable for other breeding bird species with comparable habitat choice profiles (e.g. Black-tailed Godwit *Limosa limosa* and Meadow Pipit *Anthus pratensis*).

In an international context, the Wadden Sea is a core breeding area for Redshank. Large numbers of breeding pairs are found along the coastline of sheltered bays. *Jadebusen* is the most important breeding region within the Wadden Sea with more than 2,000 breeding pairs (KOFFIJBERG et al. 2006). Other important breeding regions are the *Leybucht* and the *Dollard* region. This project took place in the *Jadebusen*, *Norderland* and *Leybucht*. The study sites are spread along a coastline of approx. 140 km at the mainland coast of Lower Saxony from the mouth of Weser River to the mouth of Ems River, including important breeding regions for Redshank and other wader species (Fig. 1-3).

The management of the study sites is constant on the long-term (no changes for at least 20 years). In the *Jadebusen* salt marshes were traditionally mown and are so partly today, whereas on the salt marshes at *Norderland* and *Leybucht* the salt marshes were traditionally grazed by livestock, and are so today. In *Norderland* a comparison of different livestock stocking densities is possible as there are different stocking densities on adjacent sites. Besides the traditional management fallow sites are included in this study for each of the study regions. All salt marshes of the study sites are man-made, with groyne fields and a dense drainage network. The vegetation of the study sites was representative of mainland salt marshes, spanning the whole elevational gradient from lower to upper salt marsh. The upper salt marsh was mainly dominated by *Elymus spp.* (*Elymus athericus* and *Elymus repens*). The lower salt marsh was covered with the

Puccinellietum maritimae and the *Halimionetum portulacoidis* associations (for details see MINDEN et al. 2012).

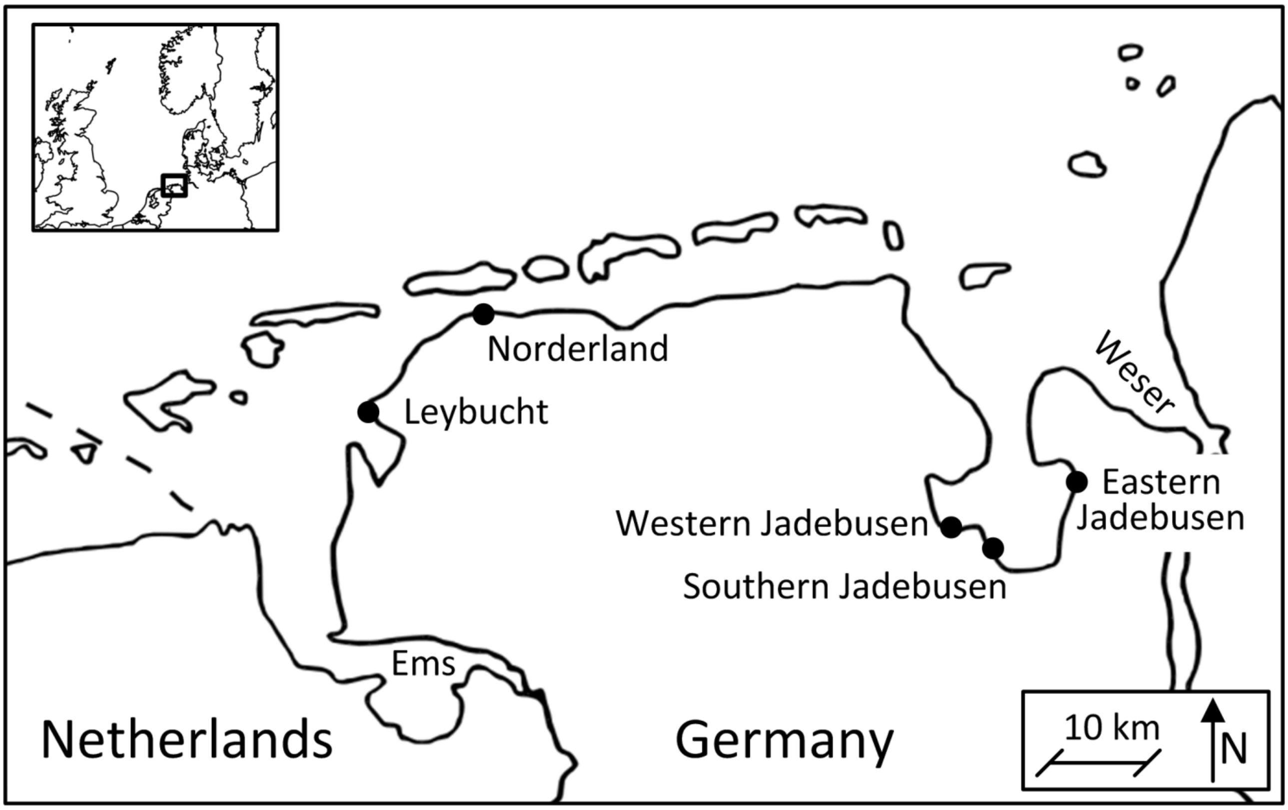

Figure 1-3 Study sites along the mainland coast of Lower Saxony, Germany

Chapter 2

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

MARTIJN VAN DE POL, BRUNO J. ENS, DIK HEG, LYANNE BROUWER, JOHAN KROL, MARTIN MAIER, KLAUS-MICHAEL EXO, KEES OOSTERBEEK, TAMAR LOK, CORINE M. EISING & KEES KOFFIJBERG

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Summary

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

Introduction

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

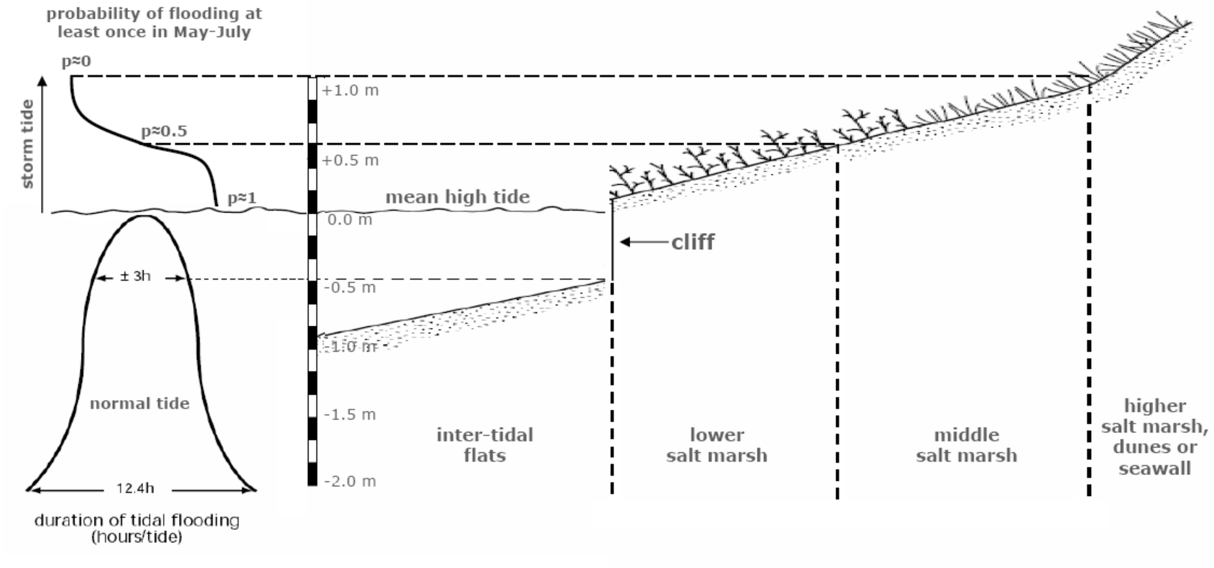


Figure 2-1 Zonation of an inter-tidal salt marsh in relation to the normal tidal dynamics and summer storm tide flooding probabilities. The elevation of a cliff can vary due to the fact that a cliff moves landwards resulting from erosion by waves. When a cliff has not formed, a gradual slope with pioneer vegetation is present instead. Birds typically nest on the salt marsh and feed on the inter-tidal flats

The shores of estuaries, such as salt marshes, are subject to strong environmental variability caused by the tidal cycle. Salt marshes are situated above mean high tide, but flood occasionally during stormy weather (Fig. 2-1). In summer, salt marshes are important breeding areas for many bird species (orders *Charadriiformes*, *Ciconiiformes*, *Anseriformes*, *Passeriformes*) in all hemispheres of the world (e.g. BILDSTEIN et al. 1991; KOFFIJBERG et al. 2006). Flooding is rare in any given breeding season; nevertheless their effects can be catastrophic: eggs wash away and chicks die. Thus, more frequent flooding events could impact estuarine ecosystems globally and quantifying and predicting their impact will be crucial to manage the biodiversity of estuaries (BILDSTEIN et al. 1991; ERWIN et al. 2006). Flooding events also provide a unique opportunity to gain insights in the impact of extreme climatic events on populations, because (*i*) the impact of flooding events is directly quantifiable by comparing a storm tide's height with the elevation of nesting sites, (*ii*) many tidal gauge stations have long historical records, and (*iii*) climate change and sea-level rise (SLR) are predicted to alter the frequency and magnitude of flooding events (IPCC 2007).

The Wadden Sea is Europe's largest wetland (Fig. 2-2) and the core breeding area in Western Europe for dozens of coastal bird species (KOFFIJBERG et al. 2006). In this estuary mean sea levels have been rising with 0.1cm/year over the last centuries (OLFF et al. 1997), but in the second half of the 20th century this rate has increased to 0.3cm/year (ESSELINK et al. 1998) and is expected to increase even further (potentially up to 1.2cm/year in 2100; VAN DORLAND et al. 2009). The recent increase in SLR is mainly attributed to global warming causing seawater to expand (IPCC 2007), but some land subsidence due to post-glacial rebound and local gas-extraction also occurs in this estuary (MARQUENIE & DE VLAS 2005).

Salt marshes naturally compensate for relative SLR, as higher flooding frequencies result in increased sedimentation and thereby land accretion. Notwithstanding, discussion exists as to whether salt marshes worldwide can keep up with the current high rate of climate change. Some modelling studies have argued that sedimentation can fully compensate for increasing rates of SLR (e.g. TEMMERMAN et al. 2004; HUGHES & PARAMOR 2004), while others have argued marshes will eventually drown (e.g. ERWIN et al. 2006; GOODMAN et al. 2007). The outcome may well vary within and among estuaries due to differences in geomorphology. Using both model and empirical data, VAN WIJNEN & BAKKER (2001) suggested that island salt marshes in the Wadden Sea estuary are already unable to keep up with current rates of SLR and will drown over the next centuries if no action is taken. In addition, lateral erosion of salt-marsh cliffs (Fig. 2-1) due to wave action has become common, resulting in inland movement of salt marshes (WOLTERS et al. 2005). New marshes can develop at higher sites, but often these higher sites are unavailable due to inland boundaries such as seawalls (i.e. coastal squeeze).

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

In this study we develop a general framework to perform a risk assessment for coastal-nesting bird populations to changes in the frequency, magnitude and timing of extreme climatic events. We first quantify changes in the means and extremes of summer tidal data over the past four decades at 27 stations in the Wadden Sea. Second, we evaluate to what extent island salt marshes compensate for SLR by land accretion, now and in the near future. Third, we combine data on nest elevations, the timing of egg-laying and the duration eggs and chicks are at risk, to quantify the flooding risk of six salt-marsh nesting bird species: common terns *Sterna hirundo*, pied avocet *Recuvirostra avocetta*, common redshanks *Tringa totanus*, black-headed gulls *Larus ridibundus*, Eurasian oystercatchers *Haematopus ostralegus* and Eurasian spoonbills *Platalea leucorodia*. Fourthly, we combine these previous steps to quantify historical, current and future flooding risks for these species. Fifth, we assess how flooding events have affected the viability of an oystercatcher population for which 26 years of reproductive data and a population model was available. Finally, we discuss the various mechanisms by which birds can adapt to increased flooding risk and explore the possibility that lower parts of salt marshes become an ecological trap (DWERNYCHUK & BOAG 1972).

Materials and methods

Tidal and weather data

To estimate flooding risks, we collated daily high-tide data from 27 stations across the Wadden Sea (Fig. 2-2; see Appendix Fig. 8-1 for location names). We used data from 1971-2008, as these 38 years comprise two complete lunar nodal periods of ~19 years each, which cyclically affect tidal patterns (ROSSITER 1972). The rate of SLR —with reference to the peak of the breeding season— was defined as the annual increase in mean high tide (MHT) as estimated by the linear regression coefficient of MHT in May-July against year (1971-2008). We also estimated the annual increase in maximum high tide (XHT) in May-July using linear regression over the same period.

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

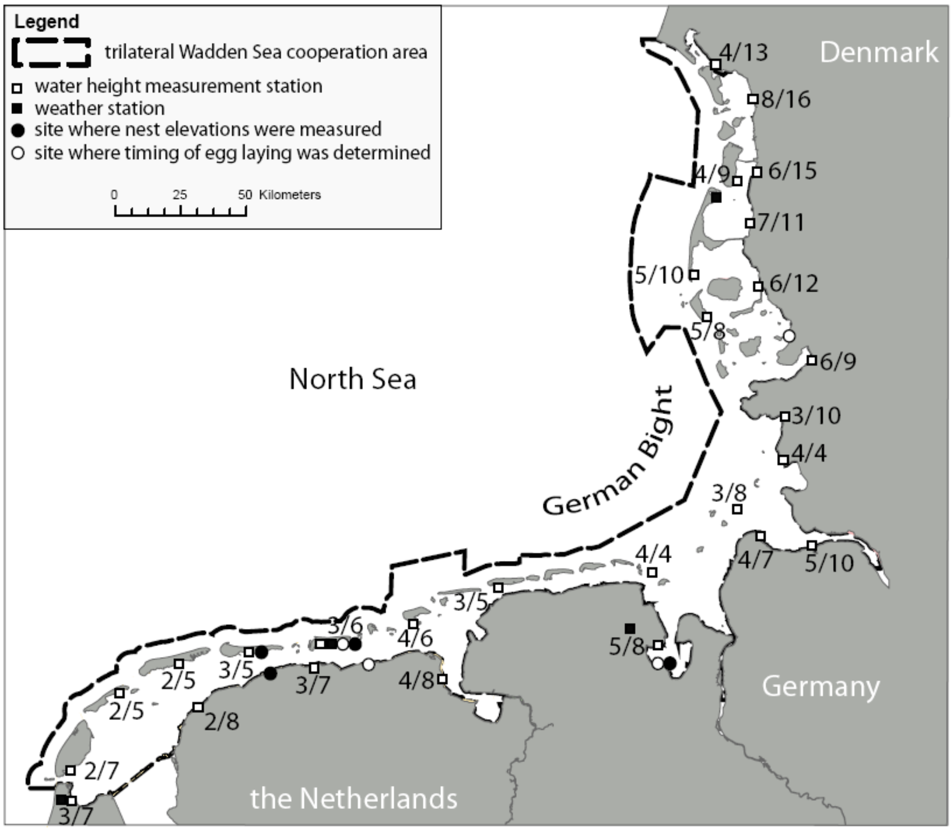


Figure 2-2 Map of the Wadden Sea estuary. Island salt marshes are located on the landward side of the barrier islands, and mainland salt marshes are located along parts of the mainland's coastline. For each of the 27 tidal measurement stations the annual increase in mean high tide (1st number) and maximum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

Island salt marshes' response to sea-level rise

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

$$E_{t+1} - E_t = A_t - S_t \tag{1}$$

with

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

and

$$S_t = C_t \times a + b \tag{3}$$

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

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

Flooding risk of nests

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

$$q = 1 - \prod_{t=s}^{t=s+d} \left(1 - p(e,t)\right) \tag{4}$$

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

Species' characteristics

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

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

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

Historical, current and future impact on species

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

Daily flooding probabilities (*p(e,t)*, eqn. 4) were based on tidal data from the 10 stations closest to where nest elevations were measured (Fig. 2-2), as changes in tidal patterns varied geographically (see Results). Current risks were calculated using tidal gauge data from the last 19 years (1990-2008). Historical (1971-1989) flooding risks were calculated using tidal gauge data from the years 1971-1989, while accounting for changes in salt-marsh elevation over time due to compensatory land accretion (using accretion rates of a 50-year old island salt marsh; VAN WIJNEN & BAKKER 2001). Similarly, future (2009-2017) flooding risks were projected using tidal gauge data from the years 1990-2008 adjusted for future mean SLR of 0.41 cm/year (see Results), while accounting for land accretion. For both historical and future projections we assumed that birds used the same nesting locations as in the current period and did not change their timing of egg-laying (see Discussion). Using a null model of no change in *e* and *s* allows us to calculate changing flooding risks under a scenario of no adaptation or alternatively predict how much birds need to adapt their timing and nest site selection to climate change to experience a constant, stable flooding risk over time.

Flooding risk, nesting success and population viability: a case study

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

Results

Changes in frequency, magnitude and timing of flooding events

Flooding events have increased both in frequency and in magnitude. MHT in May-July has increased at an average rate of 0.41cm/year over the last four decades at 27 Wadden Sea sites. Rates of SLR varied strongly among sites (0.21-0.77 cm/year), with smallest increases in the western (Dutch) and largest increases in the northern (Danish) Wadden Sea (Fig. 2-2). Over the same period, XHT increased twice as much (0.83cm/year) compared to MHT averaged across sites. Rates of change in XHT also varied strongly among sites (0.39-1.59 cm/year), again with smallest increases in western and largest increases in northern parts (Fig. 2-2).

The daily probability of an extreme high tide (>50cm +MHT; which floods at least the entire lower salt marsh) changes dramatically during the breeding season: it is high at the beginning of April, decreases fourfold to a low in May, after which it increases gradually over the course of June, July and August (Fig. 2-3; see Appendix Fig. 8-2 for patterns at individual sites). The timing of flooding events also changed when comparing the periods 1971-1989 and 1990-2008: averaged across all stations extreme tides have become more common over most of the breeding season and especially in the second half of June and first half of July (Fig. 2-3), when the eggs of most species just hatched.

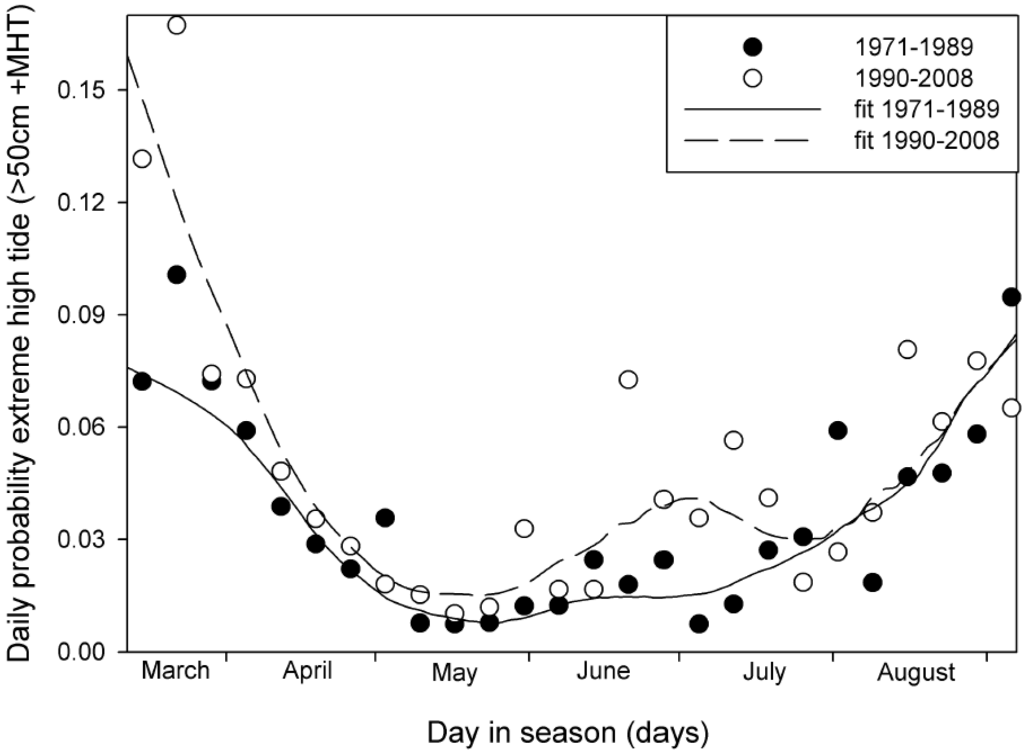


Figure 2-3 Seasonal changes in the daily probability that the lower salt marsh (0-50cm above Mean High Tide) floods, averaged over all 27 stations in the Wadden Sea for the periods 1971-1989 and 1990-2008. Dots represent averages per week; lines are fitted on raw daily data using a negative exponential smoothing function. The x-axis runs from the first date (March 11th) to the last date (to September 7th) that any nest was at risk from flooding. See Appendix Fig. 8-2 for patterns at each site

Extreme summer tides generally coincided with spring tides and strong westerly winds. Higher than normal tides (30-50cm +MHT) and extreme tides (>50cm +MHT) were respectively 50% and 20% more likely to occur around a spring tide (±2 day period) than during other days in May-July. Furthermore, higher than normal and extreme tides were associated with stronger winds (6.8±1.0 and 8.5±1.2m/s, respectively) than during the rest of May-July (5.1±0.6m/s) and were always associated with a specific range of south-western to north-western winds (mean 270°, 90%-percentiles 224°-315°), untypical for that period of the year. This pattern did not differ between island and mainland sites (Appendix Fig. 8-3), suggesting that their opposite landward and seaward salt-marsh orientation does not further influence flooding risks (i.e. western winds cause summer flooding events by pushing water from the North Sea into the Wadden Sea, not by blowing water from the Wadden Sea onto salt marshes). Due to the geographical bend in the Wadden Sea (Fig. 2-2), marshes north of the German Bight flood during south-western winds, while marshes west of the German Bight flood during north-western winds (Appendix Fig. 8-3).

Response of island salt marshes to sea-level rise

Under current rates of SLR, land rise can only keep up at the lowest parts of newly formed island salt marshes (<30cm +MHT, 0-year old; Fig. 2-4). Salt marshes of 50-100 year old –most common in the Wadden Sea— are much less resilient than new salt marshes (Fig. 2-4). Old salt marshes have built up thick clay layers and therefore shrink more (VAN WIJNEN & BAKKER 2001). When modelling how a new salt marsh develops over time, it can be seen that eventually all parts develop an elevation deficit as they age, causing them to drown (Fig. 2-4).

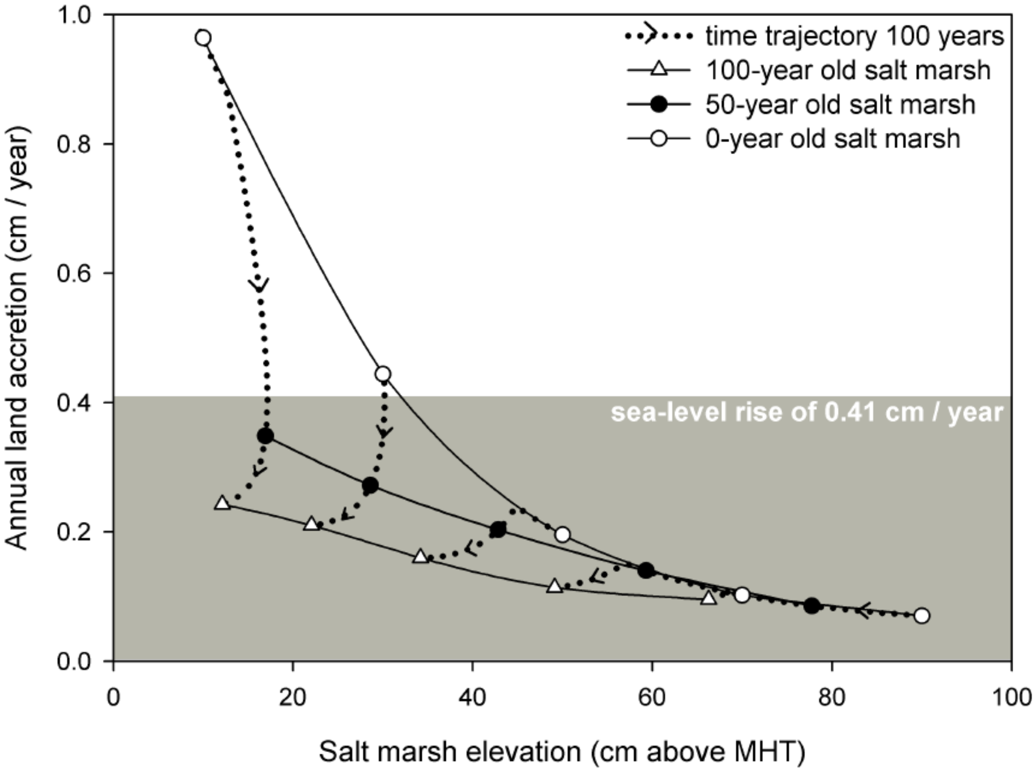


Figure 2-4 Predicted annual rate of vertical land accretion of island salt marshes according to the model of VAN WIJNEN & BAKKER (2001). At current rates of sea-level rise, new salt marshes (0-year old) have accretion surpluses (accretion > sea-level rise) at low elevations, but as they age (see time-trajectories) salt marshes rapidly develop deficits at all elevations. Note that when following time-trajectories the elevation of a site is relative to the Mean High Tide in a given year

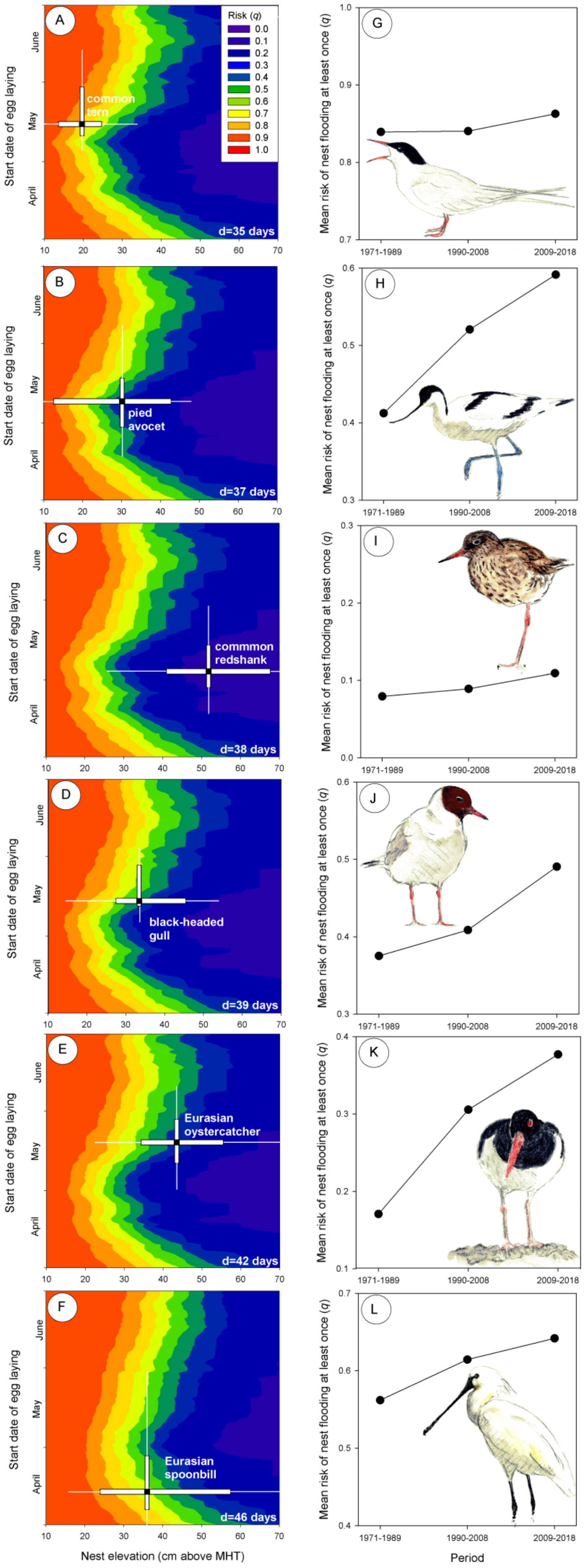
Current flooding risks of nests

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

Changes in flooding risks

When comparing historical, current and future flooding risks, all six species are predicted to have experienced increased risks and this is expected to worsen in the near future, if birds do not adapt their nest-site selection (Fig. 2-5G-L). In absolute terms, the increase in risk over time was smallest in common terns, a species with already high overall flooding risks. Common redshanks were also predicted to experience only slight increases in absolute flooding risk ($\bar{q}_{1971\text{-}1989} = 0.08$, $\bar{q}_{2009\text{-}2017} = 0.11$), but this does imply that the expected flooding frequency increased from once every 13 years in 1971-1989 to once every 9 years in 2009-2017.

Figure 2-5
(A-F) The three characteristics that determine a nest's flooding risk for each of the bird species: the elevation of a nest site (*e; x*-axes), the start date of egg-laying (*s; y*-axes) and the duration a nest is at risk (*d;* top through bottom panels). Bi-directional box-plots cross at the medians, with boxes representing quartiles and error bars representing 5%/95% percentiles of each species distribution of *e* and *s*. Also shown is each species risk of a nest flooding at least once (*q*) as a function of *e*, *s* and *d*, with different colours representing different degrees of risk (data 1990-2008).
(G-L) Historical (1971-1989), current (1990-2008) and future (2009-2017) flooding risks averaged over the entire distribution of *e, s & d* for each bird species (assuming birds use the same nesting locations in all periods). Note that *y*-axes in the right panels differ in range



Selection for adaptations to flooding risks

Sensitivity analyses of flooding risk showed that all species would benefit most from selecting higher nest sites, as *q* was typically more sensitive to a 1cm change in nest elevation than to a 1 day change in the timing of egg-laying (i.e. delay or advancement towards a period with lower flooding risks) or to a 1 day reduction of the duration a nest is at risk (Table 2-1). This conclusion is reinforced if we assume that it is less costly or easier to increase the nest elevation with 1cm than changing the start of egg laying or reducing the period nests are at risk with 1 day. In addition, when looking at sensitivities of *q* to changes of *e*, *s* & *d* in units of standard deviations, this also suggests that birds would benefit most from adjusting their nest elevation (Table 2-1).

Table 2-1 Predicted changes in a nests flooding risk (q) to adaptations (i.e. small changes) in nest elevation (e), start date of egg-laying (s) and the duration nests are at risk (d) evaluated for a typical nest for each species (i.e. at each species median values e*, s*, d*, see Fig. 2-5A-F) using tidal data from 1990-2008. Sensitivity values reflect how much q is expected to change in response to a 1cm increase in nest elevation, a 1 day later start of egg-laying or a 1 day longer duration nests are at risk. Note that a change in the opposite direction only changes the sign of the sensitivity-values (e.g. spoonbills would reduce q by delaying the start of egg laying s, while common terns would reduce q by laying earlier). Values between parentheses reflect how much q is expected to change in response to an increase in e, s, or d of one standard deviation of the population distribution

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

The benefit of selecting higher sites is huge, as a 10cm higher nest site than typical for a species would reduce the flooding risk with 0.07 in common redshanks up to 0.28 in common terns. Eurasian spoonbills would typically benefit from delaying egg laying, while common terns, black-headed gulls and Eurasian oystercatchers would gain from laying earlier. On average pied avocets and common redshanks would gain little by adjusting their timing of egg-laying, since sensitivities were close to zero (Table 2-1; Fig. 2-5B,C). The common redshank, the species with the lowest flooding risk (Fig. 2-5I), is likely to gain least from reducing their duration that nests are at risk (Table 2-1).

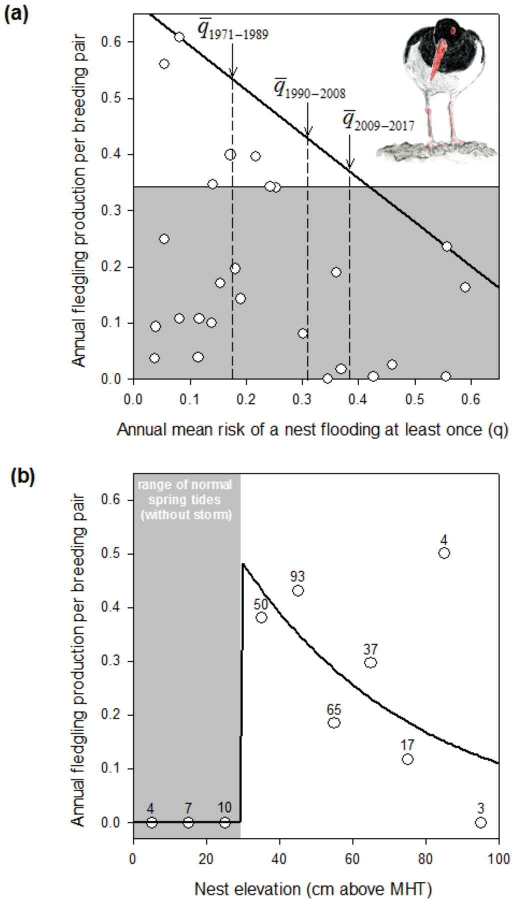
Flooding risk, nesting success and population viability: the Eurasian oystercatcher

As expected, annual mean flooding risk $\bar{q}$ was not a simple linear predictor of annual fledgling production. Flooding risk primarily appears to impose a ceiling to productivity of Eurasian oystercatchers (Fig. 2-6a). When in a given year the mean flooding risk was high, then reproduction was low. However, when the flooding risk was low, then fledgling production could be either high or low (likely depending on other determinants of nesting success such as predation and food abundance; Ens et al. 1992; van de Pol et al. 2010). Most importantly, Fig. 2-6a shows that the predicted increases in flooding risk $\bar{q}$ for oystercatchers (Fig. 2-5K) are expected to severely limit this population’s potential to reach an annual fledgling production high enough to sustain a stable and viable population.

Figure 2-6

(a) The relationship between the annual mean risk of nests flooding and the annual fledgling production per Eurasian oystercatcher pair on the island of Schiermonnikoog (1984-2009). The solid line depicts the quantile regression of the 95th percentile (t_1=3.1, P=0.005, n=26 years), suggesting that flooding events impose on upper limit on fledgling production. The grey area indicates values of fledgling production too low for a stable population size (VAN DE POL et al. 2010). The dashed lines depict estimated historical, current and future flooding risks (Fig. 2-5K)

(b) The relationship between nest elevation and oystercatcher's fledgling production in a year with no catastrophic flooding event ($\bar{q}_{1996} = 0.14$). The line is a spline function fitted by Poisson regression (P<0.001); numbers above dots refer to sample sizes (no. of pairs). Note that nests below 30cm above Mean High Tide (grey area) never produce any fledglings because their nests flood during normal spring tides (~fortnightly) even when these spring tides do not coincide with stormy weather



The response of annual productivity to flooding risk is further shaped by the fact that oystercatchers' nests with the highest flooding risk also have the highest potential value. In a year without extreme flooding events, low nests closest to the inter-tidal flats (with direct access to food; ENS et al. 1992) produce much more offspring than high nests further inland (Fig. 2-6b; but a threshold nest elevation above the normal range of spring tides is required for success). Thus, even a small increase in flooding risk at 30-50cm above MHT is expected to disproportionally reduce mean productivity and thereby oystercatchers' population viability.

Discussion

Climate change and flooding risks

We have shown that a rare extreme climatic event – a summer flooding – has become less rare and more extreme, especially during the period when the eggs of most species have just hatched (Figs. 2-2 & 2-3). Land rise of island salt marshes is insufficient to keep pace (Fig. 2-4), and consequently the changes in the frequency, magnitude and timing of catastrophic flooding events likely reduced the nesting habitat quality of six bird species (Fig. 2-5). Our study also shows for the first time that changing flooding risks decreased the population viability locally for at least one species (Fig. 2-6).

In the Wadden Sea area 45% of Eurasian spoonbills, 72% of pied avocets, 81% of Eurasian oystercatchers, 83% of common redshanks, 83% of black-headed gulls, and 96% of common terns nest in areas that are potentially at risk from tidal flooding (KOFFIJBERG et al. 2006), suggesting their entire meta-populations could be heavily impacted. Moreover, changing tidal patterns likely affect various other salt-marsh nesting species (wader-, gull-, duck- and songbird-species) and potentially beach-nesting species too (tern- and plover-species). Alarmingly many bird species have declined over the last two decades in the Wadden Sea estuary (including 4, possibly 5 of our 6 study species; KOFFIJBERG et al. 2010). Although we do not claim that increased flooding risks have been the main driver behind these declines, flooding events can severely limit productivity in some years. We therefore think that changes in extreme flooding events form a dangerous cocktail in combination with other threats (agriculture, fisheries, recreation, eutrophication, predation; KOFFIJBERG et al. 2006) and future research should specifically consider their combined interactive effects.

Substantial geographical differences nonetheless likely exist. We focussed on the dynamics of island salt marshes; while mainland salt marshes in the Wadden Sea estuary can have much higher accretion rates and thus might be more resilient (ESSELINK et al. 1998). Also, flooding of northern sites was caused by different winds than flooding of western sites (Appendix Fig. 8-3), suggesting sites might respond differentially to changing wind patterns (changes in maximum high tides were in fact strongest in Denmark; Fig. 2-2). Finally, birds may nest higher on the marsh in some areas than in others, potentially depending on predators and vegetation characteristics (grazing or mowing management). A better knowledge of what causes the abovementioned geographical differences will be crucial for accurately predicting the future impact of changes in flooding events on a larger scale and for different types of salt marshes.

Although it is well established that mean sea-level rise is mainly caused by climate change (IPCC 2007), current climate models are still insufficiently detailed to predict future changes in the magnitude and timing of flooding events in summer. Climate models predict that winter storminess and thereby tidal variability will increase in the Wadden Sea (OOST et al. 2005), but no studies have investigated summer storms. Irrespective whether the magnitude of summer storm tides will continue to increase and thereby further decrease habitat quality in the near future, in the long-term major habitat loss seems unavoidable as island salt marshes are already unable to keep up with the current rates of sea-level rise (VAN WIJNEN & BAKKER 2001), and this will only worsen as salt marshes age (Fig. 2-4) and sea-level rise continues to accelerate (VAN DORLAND et al. 2009).

Since global warming causes sea levels to rise (IPCC 2007), salt marshes around the world likely face similar problems (BILDSTEIN et al. 1991). At various sites along the Atlantic coast of North America sea levels are also rising faster than land accretion can keep up with, causing summer flooding to become more frequent. It is feared many North American coastal nesting species will suffer as a consequence (ERWIN et al. 2006). Global warming could even affect nesting areas which typically have not been subject to flooding. For example, in Arctic coastal nesting areas seas are mostly frozen, but this may change rapidly (IPCC 2007).

Mechanisms of adaptation

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

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

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

Adaptive response or ecological trap?

Instead of soliciting an adaptive response, rapid environmental change can also cause the formation of ecological traps (DWERNYCHUK & BOAG 1972). If either the habitat quality or the cue used in habitat selection changes so that one does not reliably indicate the other, organisms may be lured into, or remain in poor habitat. Our study shows that climate change decreases the habitat quality of low areas due to increased flooding risks, but the corresponding environmental cues are probably hard to track for most animal species, because flooding is a rare and unpredictable event. For a bird nesting at a specific elevation it will be extremely difficult and require many years to learn that the annual flooding risk has increased from 0.2 to 0.4 (a change in flooding frequency from once to twice in every five years), while this could mean the difference between a viable and non-viable population, as shown for Eurasian oystercatchers. Furthermore, other cues (e.g. proximity to food) might still suggest that low areas should be preferred over high areas. In theory, long-term fledgling productivity of conspecifics might be the most reliable and integrative cue to use; however in practice this cue is time-consuming to assess and constrained by sampling effort (DOLIGEZ et al. 2002).

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

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

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

Acknowledgments

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Chapter 3

Vegetation structure of TMAP vegetation types on mainland salt marshes

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Introduction

The structure of vegetation has a strong impact on habitat characteristics and ecological processes. BARKMAN (1979) specifies direct and indirect effects of vegetation structure, for example, influences on germination and establishment of plant species, as well as the creation of microhabitat differences in temperature, wind, precipitation, light and radiation. Vegetation structure modifies trophic interactions, most obviously on the level of plant-herbivore interactions. Arthropod diversity and abundance (DENNO & RODERICK 1991) and grazing preferences of herbivorous geese (VAN DER GRAAF et al. 2002; BOS et al. 2005b) depend on vegetation structure, but also perceived predation risks and habitat selection of breeding birds (WHITTINGHAM & EVANS 2004). THYEN & EXO (2005) and NORRIS et al. (1998) found a significant relationship between agricultural land use and breeding densities of redshanks *Tringa totanus* on salt marshes. This was mainly due to the strong effects of agricultural land use on the structure and zonation of vegetation. It is suggested that vegetation structure is an important factor for redshank reproduction through provisioning of suitable nesting localities (THYEN & EXO 2005).

The Trilateral Monitoring and Assessment Program (TMAP), implemented in 1997, is the most important monitoring system in the Wadden-Sea area. The aim is to provide a scientific assessment of the status and development of the Wadden-Sea ecosystem, and to assess the status of implementation of trilateral targets of the Wadden-Sea Plan. One important part of the TMAP is the monitoring of salt-marsh areas to provide a comprehensive inventory. To synchronise the vegetation mapping in the three countries involved (The Netherlands, Denmark, Germany), the TMAP vegetation types for salt marshes were defined by an expert panel and first published in the Quality Status Report 2004 (BAKKER et al. 2005). Nowadays virtually all vegetation maps of salt marshes in the TMAP region are based on this typology, however only little is known about the structural parameters of the TMAP vegetation types. The characterisation of the vegetation structure according to the different TMAP vegetation types will provide a tool for extracting information on vegetation structure from available TMAP vegetation maps with the potential of extrapolating data on vegetation structure for most of the international Wadden-Sea region.

The aim of this study is a comparison of different TMAP vegetation types in salt-marsh communities with respect to various parameters of vegetation structure. As previous studies on the vegetation structure of salt marshes identified human land use as a parameter with prime importance (ANDRESEN et al. 1990; BAKKER & DE VRIES 1992; KIEHL 1997), we compared the influence of different types of management (mown, grazed and fallow) on the vegetation structure of the TMAP vegetation types, and assessed the seasonal variation within one growing season. While the ecological importance of vegetation structure is widely acknowledged in literature, a variable use of definitions and the absence of measuring standards hamper the comparability of studies (cf. ZEHM 2006). In our approach, we apply different methods in the analysis of vegetation structure in order to ease the search for a standardised method.

Methods

Study area

The study was conducted on mainland salt marshes along the German Wadden-Sea coast of Lower Saxony (National Park *Niedersächsisches Wattenmeer*). All study sites fall within the TMAP area and are mapped regularly within the trilateral monitoring. Data for this study were gathered at three locations: *Jadebusen* with mown, fallow and grazed salt marshes (N 53° 24'; E 8° 8'), *Norderland* with grazed and fallow sites (N 53° 40'; E 7° 21') and *Leybucht* with grazed and fallow sites (N 53° 30'; E 7° 6'). Elevation of the study sites ranged from 1.10 m above sea level (ASL) up to 2.99 m. Grazing intensities are approx. 1 (head of) cattle per ha. Grazing takes place from end of April till mid-October. The mown areas are mown once a year after the 1st of July and fallow sites have remained without any agricultural land use for at least 20 years. Data were pooled for all sites as there were no significant differences in vegetation structure between the three locations.

Sampling design

We used random stratified sampling to generate measuring points within each study site (approx. 3 sample points per ha). Stratification was done according to the latest TMAP vegetation map available. The main measuring period was from end of June till the beginning of August 2007. To analyse seasonal changes additional measurements were done for part of the data set between mid-April and mid-May 2007.

Table 3-1 TMAP vegetation types analysed in this study

TMAP code	TMAP vegetation type
S 1.2	Pioneer zone, *Salicornia* type
S 2.1	Low marsh, *Puccinellia maritima* type
S 2.4	Low marsh, *Atriplex portolacoides* type
S 3.0	High marsh, unspecific
S 3.3	High marsh, *Festuca rubra* type
S 3.5	High marsh, *Artemisia maritima* type
S 3.7	High marsh, *Elymus* ssp. type
S 3.9	High marsh, *Atriplex* ssp. type

Vegetation data were collected at each plot in a percentage abundance scale. All plot data were classified according to TMAP vegetation types (BAKKER et al. 2005, Table 3-1). For the definition of vegetation structure we follow ZEHM et al. (2003) and distinguish vertical (elements in side view) and horizontal structure (i.e. light penetration). Vertical vegetation structure was analysed with a standardized photographic method. At 297 points, we took digital photographs of the vegetation as described in ZEHM et al. (2003). The software tool SIDELOOK (NOBIS 2005) calculates spatial parameters of the vegetation by analysing the 'vegetation-pixels' within each photograph. Analysis follows ZEHM et al. (2003).

Horizontal vegetation structure was measured at 279 points by means of a PAR (400-700 nm) sensor (SunScan, Delta-T Devices Ltd., 1m - array with 64 light sensors). The light incidence at soil level (light penetration through the vegetation) is expressed as a percentage of the light intensity above the canopy. At 178 points we calculated from the 64 light sensors (on a light sensitive surface of 100 cm x 1 cm) the spread of light reaching the soil, as a value for vegetation heterogeneity. All parameters analysed in this study are listed in Table 3-2.

Statistical analyses

Data were checked for heteroscedasticity with the Fligner–Killeen test of homogeneity of variances. With no significant differences in variance, we applied one-way ANOVAs and for multiple comparisons Tukey's 'Honest Significant Difference' post-hoc comparison of means with a 95% family-wise confidence level. With significant differences in variance present, we used the Kruskal-Wallis rank sum test and for multiple comparisons the Mann-Whitney U test with Holm correction.

Table 3-2 Parameters analysed in this study

Parameter (codes)	**Definition**
Incidence of light [%] *(incidence.PAR)*	Light (PAR) reaching the soil surface, expressed as percentage of the light intensity above the canopy
Spread of light *(spread.PAR)*	Spread of the 64 light measurements (PAR) at the soil surface with a light sensitive surface of 100 cm x 1 cm
Mean column density [%] *(mean.density)*	Mean vegetation density calculated from densities per column (10 cm wide stripes of the picture analysed)
Difference of the column densities [%] *(diff.density)*	Difference of the lowest and highest density per column (10 cm wide stripes of the picture analysed)
Maximum canopy height [cm] *(max.height)*	Maximum height of the vegetation within each picture
Difference of the column heights [cm] *(diff.height)*	Difference between the maximum heights per column (10 cm wide stripes of the picture analysed)
Top-line length *(tl.length)*	Length of the line running along the crest of the highest plant elements divided by the width of the analysed picture
Height reaching specific percentage of density [cm] *(pc-50 / pc-75)*	Height below which 50 % / 75 % of the vegetation density is located
Row density [%] *(rdX-Y)*	Density of vegetation in an area between X and Y cm above the soil surface (10 cm wide rows of the picture)

For the analyses of the seasonal development of vegetation structure we calculated the change per sample point over time and divided this value by the number of days between the two measurements ('slope'). All statistical analyses were done using the R statistical software (R DEVELOPMENT CORE TEAM 2008).

Table 3-3 Means, standard deviations and sample sizes of the analysed parameters of vegetation structure. TMAP codes see Table 3-1, parameter abbreviations and units see Table 3-2; NA - not available

		Light measurement				**Photographic method / column and global parameters**							
		N	incidence.PAR	N	spread.PAR	N	mean.density	diff.density	max.height	diff.height	tl.length	pc-50	pc-75
grazed	S 1.2	5	0.49 ±0.25	5	0.41 ±0.20	6	23.53 ±14.46	6.57 ±1.80	42.75 ±21.40	14.9 ±6.68	5.75 ±1.58	13.48 ±5.00	20.03 ±7.81
	S 2.1	13	0.72 ±0.14	13	0.19 ±0.14	37	18.35 ±8.96	4.96 ±4.36	30.35 ±17.75	8.04 ±6.33	4.62 ±1.61	9.47 ±4.53	14.27 ±7.01
	S 3.0	14	0.57 ±0.20	13	0.27 ±0.15	22	19.12 ±5.05	4.57 ±3.31	34.16 ±12.46	12.23 ±10.54	5.52 ±1.67	9.68 ±2.48	14.65 ±3.77
	S 3.3		NA		NA	7	20.95 ±8.89	8.64 ±5.88	39.10 ±19.00	14.1 ±7.61	4.67 ±0.72	10.76 ±4.44	16.47 ±7.05
	S 3.5	7	0.31 ±0.17	7	0.70 ±0.25	7	36.61 ±4.67	13.23 ±6.66	51.64 ±7.28	11.81 ±7.48	4.51 ±0.94	18.36 ±2.33	28.29 ±3.39
	S 3.7	7	0.19 ±0.06	6	0.88 ±0.14	34	40.14 ±7.75	9.77 ±4.51	69.07 ±14.04	18.4 ±9.35	3.72 ±1.36	20.91 ±4.30	32.34 ±6.55
	S 3.9		NA		NA	5	40.73 ±8.23	11.26 ±6.04	66.56 ±10.84	18.7 ±7.85	4.03 ±1.45	20.72 ±4.12	32.48 ±6.23
fallow	S 2.1	78	0.23 ±0.18	39	0.67 ±0.27	65	31.77 ±6.73	11.44 ±7.64	54.65 ±18.65	14.15 ±12.99	4.97 ±1.56	17.04 ±3.79	27.04 ±8.05
	S 2.4	24	0.14 ±0.09	20	1.11 ±0.53	21	36.93 ±6.66	7.63 ±2.72	52.67 ±8.29	9.31 ±4.43	4.25 ±0.84	18.76 ±3.14	28.68 ±4.83
	S 3.3	14	0.15 ±0.09	6	1.03 ±0.11	9	38.82 ±5.96	14.43 ±5.16	63.12 ±18.50	19.04 ±15.53	4.21 ±0.96	20.1 ±3.07	31.30 ±5.92
	S 3.7	53	0.15 ±0.15	28	0.98 ±0.36	34	41.52 ±8.04	11.78 ±6.44	71.59 ±17.89	14.15 ±12.12	5.18 ±2.63	22.81 ±7.91	36.32 ±11.04
	S 3.9	23	0.19 ±0.21	12	0.86 ±0.35	17	40.49 ±9.48	19.71 ±8.99	73.89 ±20.72	21.76 ±13.37	6.14 ±3.81	22.53 ±5.07	35.84 ±8.35
mown	S 2.1	15	0.37 ±0.15	15	0.43 ±0.21	15	33.11 ±7.25	9.03 ±6.58	47.11 ±11.48	8.05 ±5.59	5.41 ±0.92	16.83 ±3.71	26.00 ±6.17
	S 3.7	22	0.20 ±0.24	14	0.68 ±0.31	18	53.72 ±10.70	16.64 ±8.37	94.85 ±17.24	15.13 ±7.77	6.41 ±2.29	28.76 ±5.90	45.79 ±8.85

Table 3-3 (CONTINUED)

		Photographic method / row parameters: Row density										
		N	rd0-10	rd10-20	rd20-30	rd30-40	rd40-50	rd50-60	rd60-70	rd70-80	rd80-90	rd90-100
grazed	S 1.2	6	84.02 ±37.84	74.72 ±36.05	45.08 ±45.15	22.3 ±31.77	6.58 ±13.52	2 .00±4.90	0.6 0±1.47	0.35 ±0.86	0 ±0	0 ±0
	S 2.1	37	96.06 ±4.94	53.53 ±38.80	22.72 ±33.94	8.23 ±16.22	2.43 ±6.35	0.77 ±2.76	0.19 ±0.74	0.03 ±0.16	0 ±0	0 ±0
	S 3.0	22	99.05 ±1.61	70.89 ±32.89	18.99 ±16.64	2.27 ±4.04	0.46 ±1.34	0.02 ±0.07	0 ±0	0 ±0	0 ±0	0 ±0
	S 3.3	7	96.81 ±3.11	65.1 ±39.05	34.29 ±33.29	10.86 ±15.52	2.10 ±3.73	0.54 ±0.94	0.13 ±0.34	0 ±0	0 ±0	0 ±0
	S 3.5	7	100 ±0	99.40 ±0.75	85.63 ±15.40	60.64 ±19.91	18.10 ±13.22	2.46 ±4.99	0.11 ±0.30	0 ±0	0 ±0	0 ±0
	S 3.7	34	98.57 ±4.30	94.80 ±6.87	84.59 ±13.66	65.73 ±22.52	36.99 ±25.39	13.7 ±15.27	4.60 ±7.63	1.90 ±5.36	0.71 ±2.08	0.2 0±0.71
	S 3.9	5	99.48 ±1.16	97.74 ±3.42	85.54 ±9.24	69.56 ±24.65	37.26 ±28.11	11.56 ±14.49	4.96 ±9.01	1.74 ±3.89	0 ±0	0 ±0
fallow	S 2.1	65	96.14 ±5.63	89.01 ±12.67	71.77 ±20.27	39.78 ±24.05	11.89 ±12.57	3.44 ±7.82	1.83 ±6.55	1.54 ±5.79	1.22 ±4.67	1.13 ±4.71
	S 2.4	21	99.17 ±3.16	97.29 ±7.15	88.63 ±12.26	57.73 ±25.06	22.00 ±23.33	4.54 ±11.19	0.30 ±0.70	0 ±0	0 ±0	0 ±0
	S 3.3	9	98.67 ±2.60	95.29 ±7.23	89.12 ±7.24	62.88 ±13.88	27.51 ±17.75	7.89 ±14.05	3.44 ±9.92	1.51 ±4.53	0.77 ±2.30	0.78 ±2.33
	S 3.7	34	96.28 ±15.55	93.26 ±14.29	84.83 ±16.22	63.54 ±23.34	37.02 ±23.95	19.15 ±19.42	10.59 ±17.66	7.33 ±18.12	2.87 ±7.58	0.74 ±2.27
	S 3.9	17	94.71 ±8.56	87.11 ±16.10	80.21 ±13.79	61.01 ±19.03	38.65 ±23.90	21.92 ±20.14	12.91 ±14.44	5.74 ±8.50	2.11 ±4.18	0.57 ±1.42
mown	S 2.1	15	99.27 ±2.34	96.41 ±4.87	75.16 ±24.90	42.23 ±29.79	14.33 ±17.65	2.94 ±8.68	0.99 ±3.82	0.09 ±0.34	0 ±0	0 ±0
	S 3.7	18	96.59 ±7.46	95.49 ±7.01	87.22 ±10.44	78.25 ±11.29	64.79 ±18.41	46.38 ±26.14	30.63 ±22.89	19.28 ±18.50	10.61 ±11.38	5.36 ±7.82

Results

For each analysed TMAP vegetation type (Table 3-1) the mean and standard deviation of vegetation structure characteristics per agricultural land use scheme are calculated (Table 3-3). An analysis of vegetation structure on fallow sites mirrors the natural variation between TMAP types without human disturbance. For the incidence of light and the top-line length we found no significant differences between the TMAP vegetation types on fallow sites (Table 3-4). However, the most distinct differences occur between the TMAP vegetation types S 2.1 (Low marsh, *Puccinellia maritima* type) and S 3.7 (High marsh, *Elymus* ssp. type), with the latter being significantly higher, denser and more heterogeneous (Table 3-3 and 3-4). But also S 2.1 and S 3.9 (High marsh, *Atriplex* ssp. type) differ significantly for six different parameters of vegetation structure (Table 3-4).

At all canopy heights, the *Elymus* ssp. type (S 3.7) is significantly denser than the *Puccinellia maritima* type (S 2.1) except for the lowest 10 cm. Above 70 cm, vegetation density approaches values of zero for both types (Fig. 3-1 and Table 3-3).

Additional analyses focused on the influence of agricultural land-use schemes on vegetation structure. Grazing and mowing as management tools on salt marshes have a strong impact on the structure of TMAP vegetation types investigated: On grazed sites the canopy height is lower and the vegetation is less dense as compared to fallow sites (Table 3-3).

Table 3-4 Levels of significance for differences between the TMAP vegetation types on fallow sites. Given are the p-values according to Tukey's HSD or Mann-Whitney U test (U). *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; n.s. not significant. For TMAP codes see Table 3-1

	Incidence of light (U)	**Spread of light (U)**	**Mean column density**	**Difference of the column densities (U)**	**Maximum canopy height**	**Difference of the column heights (U)**	**Top-line length**	**Height reaching 50 % of density**	**Height reaching 75 % of density (U)**
S 2.4 - S 2.1	n.s.	**	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.3 - S 2.1	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.7 - S 2.1	n.s.	**	***	n.s.	***	n.s.	n.s.	***	***
S 3.9 - S 2.1	n.s.	n.s.	***	**	**	n.s.	n.s.	**	**
S 3.3 - S 2.4	n.s.	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.7 - S 2.4	n.s.	n.s.	n.s.	*	**	n.s.	n.s.	*	*
S 3.9 - S 2.4	n.s.	n.s.	n.s.	***	**	**	n.s.	n.s.	n.s.
S 3.7 - S 3.3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.9 - S 3.3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
S 3.9 - S 3.7	n.s.	n.s.	n.s.	*	n.s.	n.s.	n.s.	n.s.	n.s.

When comparing structural components of the two focal TMAP vegetation types *Puccinellia maritima* type and *Elymus* ssp. type (S 2.1 and S 3.7, respectively), we again found less dense vegetation on mown as compared to fallow sites (Fig. 3-2), but for the *Elymus* ssp. type the canopy is significantly higher on mown than on fallow sites ($p < 0.001$; Table 3-3).

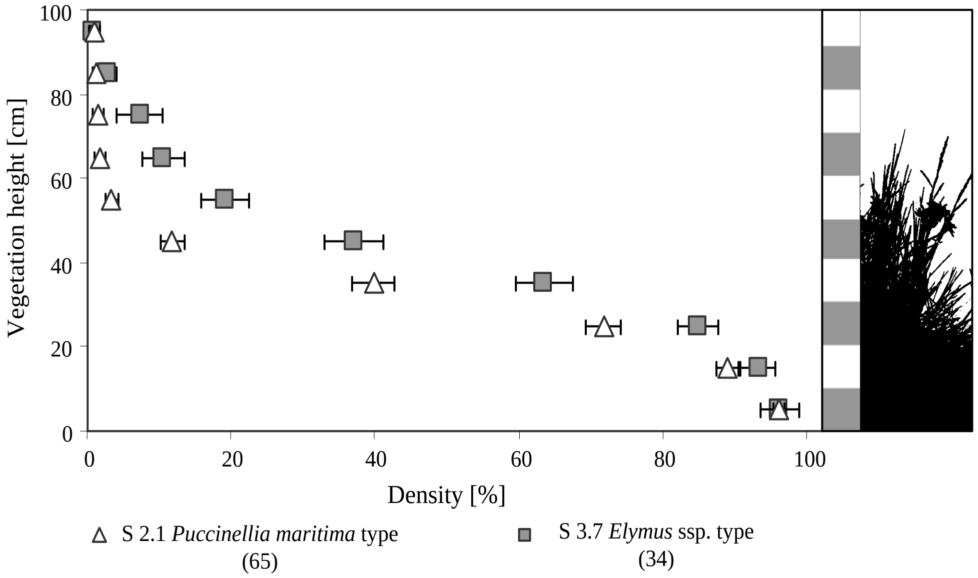

Figure 3-1 Row density of different heights above the soil surface for S 2.1 (Low marsh, *Puccinellia maritima* type) and S 3.7 (High marsh, *Elymus ssp.* type) on fallow sites

Agricultural land use has a strong and significant impact on most of the structural parameters investigated for the TMAP vegetation types S 2.1 (Low marsh, *Puccinellia maritima* type), S 3.3 (High marsh, *Festuca rubra* type) and S 3.7 (High marsh, *Elymus* ssp. type), whereas there is no significant impact on TMAP vegetation type S 3.9 (High marsh, *Atriplex* ssp. type; Table 3-5).

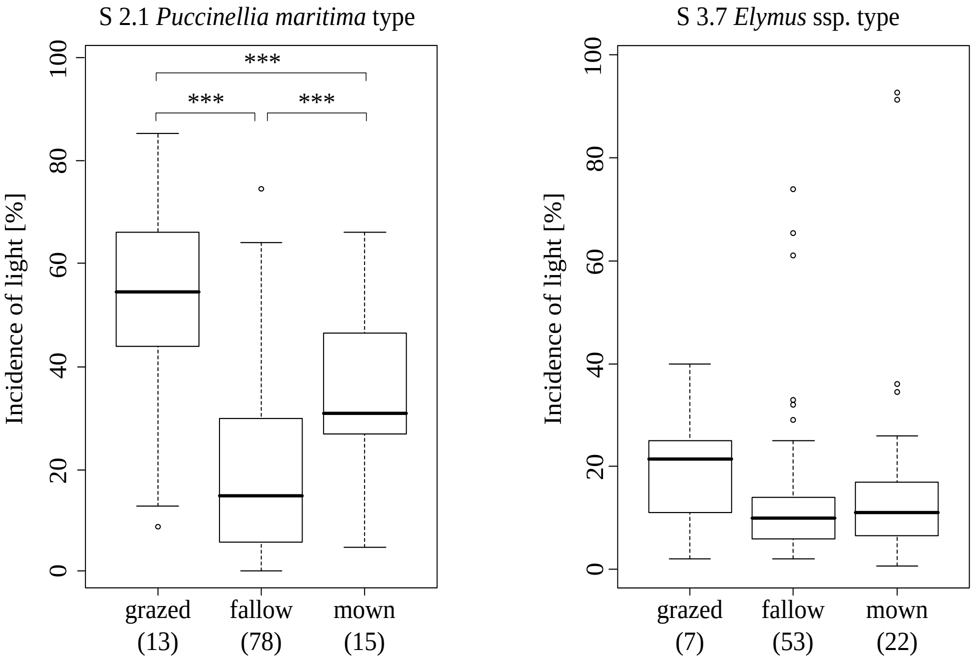

Figure 3-2 Influence of agricultural land use on the incidence of light. Shown are the TMAP vegetation types S 2.1 and S 3.7 (ANOVA S 2.1 $p < 0.001$ ***; S 3.7 $p = 0.49$)

As can be expected, we found a very consistent seasonal decline of light at soil level for all land-use schemes. This is attributable to the closing of canopies as the growing season progresses (Fig. 3-3). However, this decline is significantly steeper on mown than on grazed or fallow sites for both focal TMAP vegetation types S 2.1 (*Puccinellia maritima* type) and S 3.7 (*Elymus* ssp. type).

Table 3-5 Influence of agricultural land use on vegetation structure of different TMAP vegetation types. Shown are the levels of significance of ANOVA or Kruskal-Wallis rank sum test (K) calculated for each TMAP vegetation type with more than one agricultural land use schemes (Table 3-3). *** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; n.s. not significant; NA - not available. For TMAP codes see Table 3-1

	Incidence of light	**Spread of light**	**Mean column density**	**Difference of the column densities**	**Maximum canopy height**	**Difference of the column heights**	**Top-line length**	**Height reaching 50 % of density**	**Height reaching 75 % of density**
S 2.1	***	***	***	*** (K)	***	**	n.s.	***	***
S 3.3	n.s.	n.s.	**	n.s.	n.s.	n.s.	n.s.	***	**
S 3.7	n.s.	*	***	**	***	n.s.	***	***	***
S 3.9	NA	NA	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Spatial grazing patterns and forage avoidance by cattle create strong differences in light availability between a *Puccinellia maritima* type (open and short canopy) and an *Elymus* ssp. type (large amounts of standing dead early in season; Fig. 3-3 left panels top and bottom).

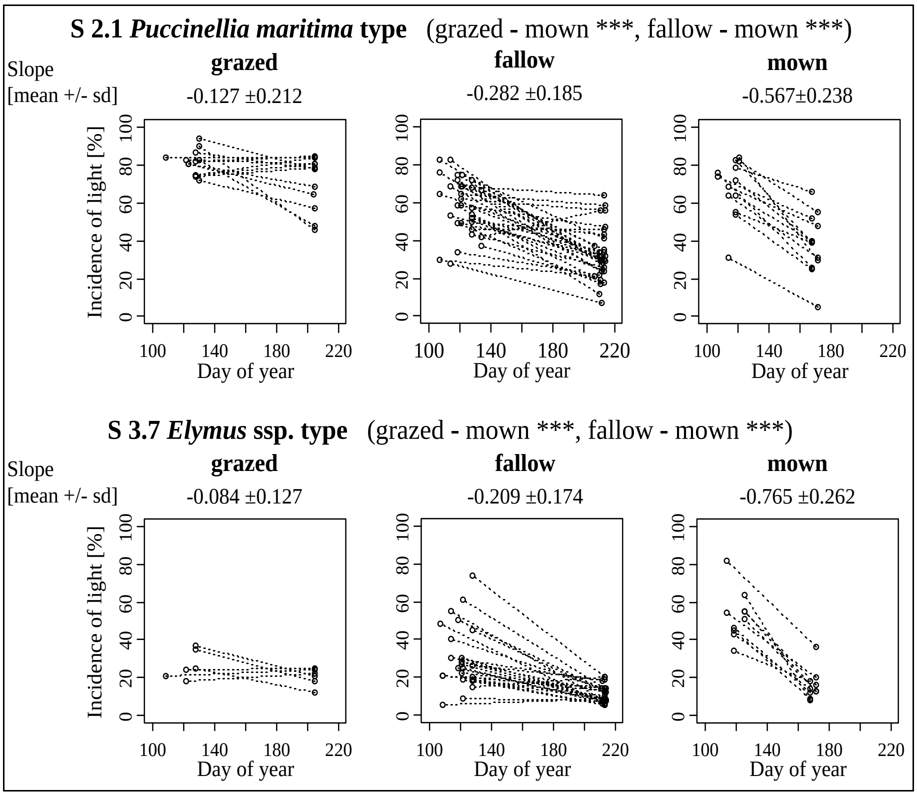

Figure 3-3 Seasonal development of incidence of light in different land use schemes for two focal TMAP vegetation types. *** $p \leq 0.001$

Discussion

Vegetation structure is an important determinant of habitat quality, influencing various ecological processes such as seed germination, predator escape and foraging efficiency. Our knowledge on the mechanisms behind these processes is still fragmentary, especially with regard to the influence of plant structure on higher trophic levels, i.e. herbivores and predators. Our study aims at providing necessary background information on vegetation structure of salt-marsh plant communities in order to facilitate further research on plant-herbivore and predator-prey interactions.

This study characterises vegetation structure for the most common TMAP vegetation types on mainland salt marshes (Table 3-3). Supported by the statistically significant differences found between focal TMAP vegetation types in different land-use schemes, it will be possible to extrapolate our findings to TMAP areas where vegetation mapping provides information on the occurrence of TMAP vegetation types and land-use, and to deduce information on vegetation structure for these areas.

As previous studies (ANDRESEN et al. 1990; BAKKER & DE VRIES 1992; KIEHL 1997) suggested already, our data confirm the strong impact of grazing and mowing on structural vegetation parameters, specifically canopy height and sward density. For an even more complete description of the structure of TMAP salt-marsh vegetation, we suggest future studies focusing on a comparison of mainland and island salt marshes, as well as on inter-annual variation with repeated measurements in different years.

Seasonal change of the vegetation structure attributable to plant growth is an important component and needs to be taken into account; especially when results are to be transferred to other regions. Therefore, it is necessary to conduct repeated measurements throughout the growing season at the same plots. Our study provides repeated measurements for only few sample points, but already these first results demonstrate a strong impact of agricultural land use on the development of vegetation structure during the period of plant growth.

In this study we used two largely differing methods for the analyses of the vegetation structure. On the one hand a quick assessment of the overall horizontal density of vegetation through light measurements, and on the other hand, the very detailed method of picture analyses in order to assess vertical structure. Both methods are suitable to obtain information about vegetation structure, but provide different parameters. As is often the case in ecological studies, the method of choice depends on the questions asked: for studies on the germination of seeds the incidence of light is a suitable parameter (BAKKER & DE VRIES 1992), while for the occurrence of arthropods a more detailed analysis on the density of vegetation in different canopy heights (cf. Fig. 3-1) will be necessary.

Box A

Artificial nest studies: observer bias and value as mimics

Introduction

Working with real bird nests is often a challenge, especially when dealing with rare or endangered species. The influence of observations on nest survival needs to be taken into account at all stages of the research including planning, analysis and data interpretation. When dealing with endangered or rare species, this ‘observer effect’ can have an impact on the whole breeding population, which is unacceptable when considering the targets set for species protection. Detecting and quantifying the influence of nest observations are challenging and, perhaps for this reason, not regularly done (IBANEZ-ALAMO et al. 2012).

The use of artificial nests is an alternative method for studying nest survival (e.g. MAJOR & KENDAL 1996 for a review). When working with rare species, the number of nests is limited and therefore the sample size is often insufficient for assessment of the focal research question (MOORE & ROBINSON 2004). Artificial nest experiments allow for a suitable sample size and for testing of various hypotheses concerning nest predation. Using artificial nest studies, it is possible to easily manipulate parameters such as nest abundance, nest location, timing and duration of nest exposure, number of eggs, and structural characteristics of nesting sites. By using artificial nests, the impact on real nests is minimized. However, it is still under discussion how well artificial nests can predict the survival rates of real nests (e.g. MOORE & ROBINSON 2004 for a review).

Our studies were conducted on salt marshes within the Wadden Sea National Park. The special protection status of the study sites increased the motivation to minimize disturbance caused by the observer. The focus of the project was on Common Redshank, a nearly threatened species in Germany (SÜDBECK et al. 2007). This species conceals its nests in vegetation and therefore all nest observations are likely to disturb the nests and leave marks of the observer. For concealed nests, using video cameras as an alternative to nest observation has limitations. The rates of predation and nest survival can be affected by nest observations. In order to reduce the impact of the research method on Redshank nests, we used artificial nests in our studies on nest predation. The artificial nests were constructed to mimic Redshank nests and were visited at regular intervals. These subsequent visits allowed us to control for the effect of repeated nest visits on nest survival.

Observer effect

The artificial nests were monitored at 3 to 5 day intervals for 15 to 20 days, starting from the first day after nest placement. This was done three times (3 time series in the experiment) per year (in May, June and July), with a respite of 8 or 12 days between periods of exposure to avoid predators from becoming habituated to the artificial nests (for details on the method, see chapter 4). The experiments were performed using comparable methods in 2007, 2008 and 2011.

Even though there was no observer effect apparent in our data from 2007 and 2008 (Fig. A-1, 2008), we found a clear observer effect in 2011. The daily predation rates increased with every additional nest visit on the salt marsh, *Beckmannsfeld* (Fig. A-1, 2011). As this increasing daily predation rate was not present in 2007 and 2008, this suggests that the effect caused by the repeated nest visits depends not only on the methodology of the artificial nest experiments but also on some external factors that had not been studied in detail in this project (e.g. predation pressure, predator community and weather conditions). As no general patterns for observer effects were found in this project, we expect the observer effect to be small because it was present at only one site and only in one of the three years (2011).

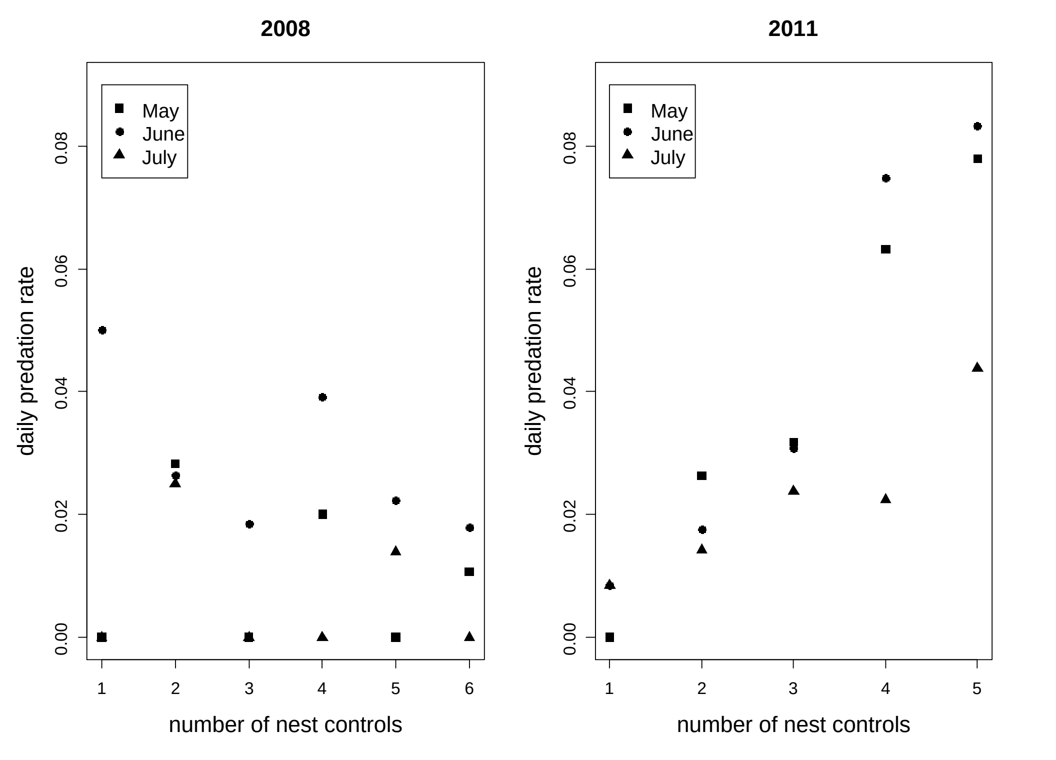

Figure A-1 Effect of subsequent nest controls on daily predation rates (according to MAYFIELD 1975) over two years at the study site, *Beckmannsfeld*

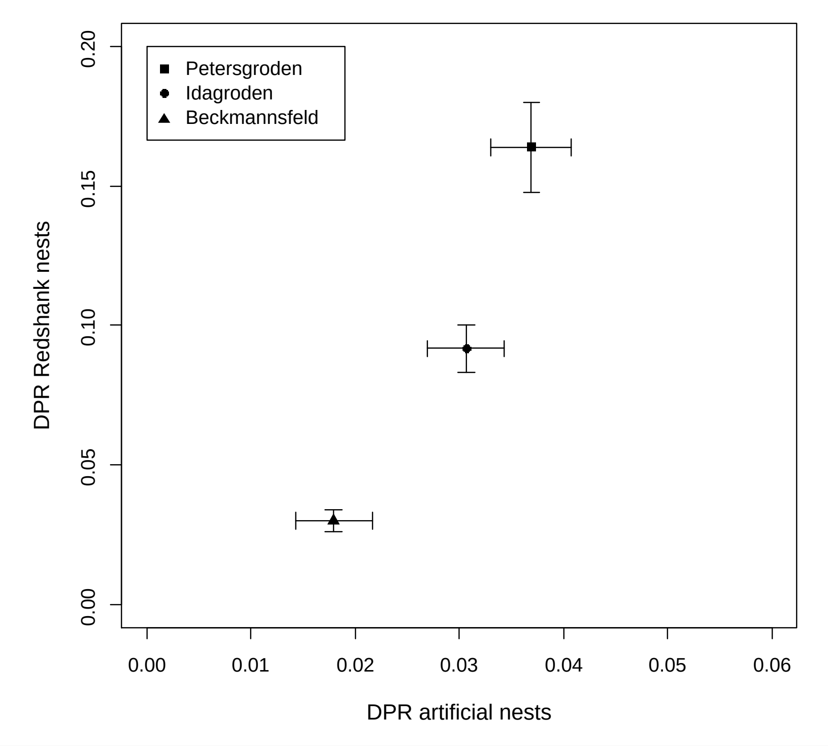

Figure A-2 Comparison of daily predation rates (DPR, according to MAYFIELD 1975) for Common Redshank nests and artificial nests at three study sites. The means ± standard error are shown

Value of artificial nests as mimic for real nests

In order to obtain results that could be compared to the actual breeding situation of Redshanks at the study sites, artificial nests were designed to mimic Redshank nests (for details see chapter 4). For evaluation purposes, nest monitoring of real Redshank nests was done at the same time (for details see chapter 5). Comparing the daily predation rates between artificial nests and Redshank nests showed differences between the two nest types. Daily predation rates of Redshank nests were generally higher than artificial nests (Fig. A-2). However, the spatial patterns of predation in both nest types were comparable (Fig. A-2), with highest daily predation rates at *Petersgroden* and lowest at *Beckmannsfeld*.

Comparing the temporal pattern between the nest types, this project showed that the predation rates of artificial nests resembled the temporal pattern of Redshank nests. The highest predation rates occurred in both artificial nests and Redshank nests during the second series of experiment (Fig. A-3).

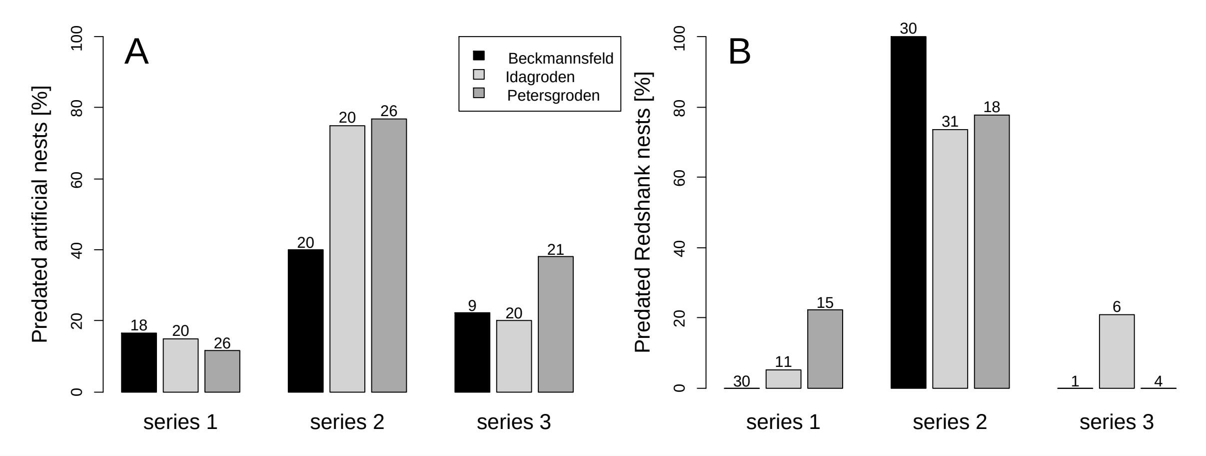

Figure A-3 Temporal variation in predation of artificial nests **(A)** and Common Redshank nests **(B)** at three study sites during the three experimental periods in 2008. Numbers above bars indicate total number of nests observed during the period (according to SCHLAICH et al. in prep.)

Conclusion

Within this project, an observer effect could only be detected for one year and at one site. For all other study sites and years, the effect of nest monitoring on predation rates was absent. Therefore, we tentatively conclude that the observer effect in our project was generally low. However, as an influence of the observer was found in one year and on one site, the use of artificial nests whenever possible is still recommended to avoid stress for the breeding birds in nest survival studies. Our results show that the use of artificial nests can give valuable insight into the spatial and temporal patterns influencing concealed ground nests on salt marshes. When using artificial nests, it is not possible to gather the exact daily predation rates of real nests. However, these experiments can be used to study general patterns in nest survival and predation because artificial nest experiments resembled the spatial and temporal patterns of well-concealed ground nests on salt marshes. Our results lead to the conclusion that artificial nests are suitable to assess the mechanics of predation over space and time. In addition, the use of artificial nests helps to disentangle the effect of nest properties from the influence of the behaviour of nest-guarding birds on predation rates (cf. chapter 4).

Chapter 4

High plants lead to low risk: implications of salt marsh management for ground-breeding waders

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Abstract

The salt marshes of the Wadden Sea National Parks are important breeding areas for ground-nesting bird species. Predation is known to have an enormous impact on the breeding success of birds. We analysed the mechanisms behind predation of concealed breeding waders on salt marshes. By using artificial nests, the influence of nest-guarding adults was excluded, allowing us to disentangle predation risks due to vegetation structure and thus land management from those due to the behaviour of parents.

Using survival analysis, we analysed the period of time to a predation event and factors influencing predation and survival rates. Twenty days after artificial nests were installed nearly 50 % (0.524, CI 95 %: 0.462 – 0.594) of nests were predated but predation rates differed significantly between sites and over time. On salt marshes, predation of ground nests was strongly influenced by vegetation structure and management. A higher canopy reduced the predation risk significantly: a decrease of 5 % per cm of canopy height. The impact of management activities differed clearly from inland grasslands, where mowing reduces breeding success. On salt marshes, mowing of couch grass vegetation (*Elymus spp.*) after the breeding season can lead to higher and denser vegetation in the following year and therefore reduced nest predation. The influence of spatial factors on predation was low. Our findings show that conservation management of salt marshes can strongly impact the predation rates of ground nests. Therefore, the effects of management on predation rates need to be taken into account during the decision-making process.

Introduction

During the second half of the 20th century, the intensification of agriculture throughout north-western Europe has caused a substantial loss and degradation of habitats suitable for birds that breed in grasslands (SUTHERLAND 1996; VICKERY et al. 2001; ROBINSON & SUTHERLAND 2002; EGLINGTON et al. 2010). In particular, open habitats like wet grasslands, moorlands and low-yielding grasslands have disappeared through drainage and conversion of grasslands into croplands. In addition, earlier mowing dates threaten nesting ground breeders (NEWTON 2004; SCHEKKERMAN et al. 2009; SCHROEDER et al. 2012). All these factors have caused an alarming loss of suitable breeding and rearing habitats for a large number of bird species ranging from waders to songbirds (WILSON et al. 2005; ROODBERGEN et al. 2012). Most ground-nesting birds, *i.e.* waders that breed mainly on wet grasslands, such as Northern Lapwing *Vanellus vanellus*, Black-tailed Godwit *Limosa limosa*, Eurasian Curlew *Numenius arquata* and Common Redshank (hereafter Redshank) *Tringa totanus*, have declined rapidly throughout central and north-western Europe during recent decades (BURFIELD & VAN BOMMEL 2004; VAN TURNHOUT et al. 2010).

The salt marshes of the Wadden Sea National Parks provide relatively safe breeding sites and have gained more importance since the loss of open habitats at inland sites. A vivid example of the importance of salt marsh habitats is provided by the breeding population of Redshanks: out of an estimated 14,500 breeding pairs in Germany, almost 50 % of the pairs breed in salt marshes along the mainland coast of the Wadden Sea (HÖTKER et al. 2007).

Although climate change is a growing threat for birds breeding in coastal habitats due to the increase in frequency of extreme tidal events (chapter 2), predation remains the major determinant for nest and chick loss in ground-nesting species next to agriculture land use. As in many inland habitat types, predation substantially decreases the breeding success of many meadow bird species (HÖTKER & SEBEBADE 2000; BURFIELD & VAN BOMMEL 2004; OTTVALL et al. 2005; KOFFIJBERG et al. 2006; ROODBERGEN et al. 2012). Predation has increased in the last decades on mainland salt marshes (KOFFIJBERG et al. 2006) and predation-induced changes in breeding behaviour have been reported (Redshanks: chapter 5). With our current study, we intend to gain insight into the factors that influence predation risk for concealed breeding waders on salt marshes.

In order to gain a systematic insight into mechanisms behind predation on salt marshes along the Wadden Sea mainland coast, we used artificial nests. This allowed us to disentangle predation risks due to vegetation structure from those due to the nest-guarding behaviour of parents. For ground nests in open habitats, it is possible to assess spatial differences and the fate of real nests using artificial nest experiments (BERG 1996; PEHLAK & LÕHMUS 2008; VOGELI et al. 2011), whereas this remains more complicated for other nest types (e.g. MOORE & ROBINSON 2004 for a review). Artificial nest experiments allow for testing of various hypotheses concerning nest predation and can lead to influential concepts in predation theory (MAJOR & KENDAL 1996). Factors such as nest abundance, nest distribution, timing of egg occurrence, number of eggs, and nest appearance can easily be varied (MCKINNON et al. 2010). In addition, experimental approaches using artificial nests allow for sufficient sample sizes for use in multi-parameter statistical testing (PEHLAK & LÕHMUS 2008). For ground-breeding species with hidden nests in dense vegetation, any nest monitoring will likely influence nest predation through observer effects. The disturbance of nests has to be minimised, especially when studying endangered species, so that working with many nests is not an option. To ensure a sufficient sample size without disturbance of nesting birds, the method of artificial nests was chosen. This systematic experimental approach to assess predation has never been applied on salt marshes before.

The aim of this study was to analyse factors influencing predation on well-concealed ground nests in salt marshes. We tested the influence of vegetation and land management on the fate of nests, while also including spatial information in the analysis. This study evaluates habitat conditions on salt marshes, aiming at conservation of meadow birds at retreat areas in a coastal landscape under intense agricultural pressure.

Material and Methods

Study area

The study was conducted on mainland salt marshes along the Wadden Sea coast of Lower Saxony, Germany: five sites at *Jadebusen* (*Idagroden* [JB1], in between *Ida*- and *Petersgroden* [JB2], *Petersgroden* [JB3]; *Nordender Groden* [JB4] and *Beckmannsfeld* [JB5]; 53°29'N, 8°12'E), one site at *Norderland* (ND; 53°39'N, 7°18'E) and one site at *Leybucht* (LB; 53°32'N, 7°06'E) (Fig. 4-1). Field work was carried out from March to July of 2008.

All study sites are part of the National Park Wadden Sea of Lower Saxony. Because of their overall international importance, salt marshes of the Wadden Sea are under the strict protection provisions of the European Habitats Directive (Council Directive 92/43/EEC). The vegetation of the study sites were representative of salt marshes. The upper salt marsh consisted mainly of the *Agropyretum littoralis* association dominated by *Elymus spp.*, whereas the lower salt marshes were mainly covered with the *Puccinellietum maritimae* association (*Puccinellia maritima, Limonium vulgare, Aster tripolium, Triglochin maritimum, Plantago maritima*) and the *Halimionetum portulacoidis* association (*Atriplex portulacoides*) (for details see MINDEN et al. 2012). Parts of the study sites in south-western *Jadebusen* (*Nordender Groden* and *Petersgroden*) were mown once a year, after the 1st of July. The other study sites were not used for agricultural purpose. Potential mammalian predators included Red Fox *Vulpes vulpes*, mustelids (*Martes spp., Mustela spp.*) and rodents such as the Brown Rat *Rattus norvegicus* and voles *Microtus spp.*. Potential avian predators included the Carrion Crow *Corvus corone* and gulls *Larus spp.* (THYEN & EXO 2003, 2005) as well as the Marsh Harrier *Circus aeruginosus* and the Short-eared Owl *Asio flammeus*. The temperature during the breeding season of 2008 was similar to the long-term average, whereas precipitation in May and June was very low and relatively high in July compared to the average of the long-term meteorological data (DWD 2012).

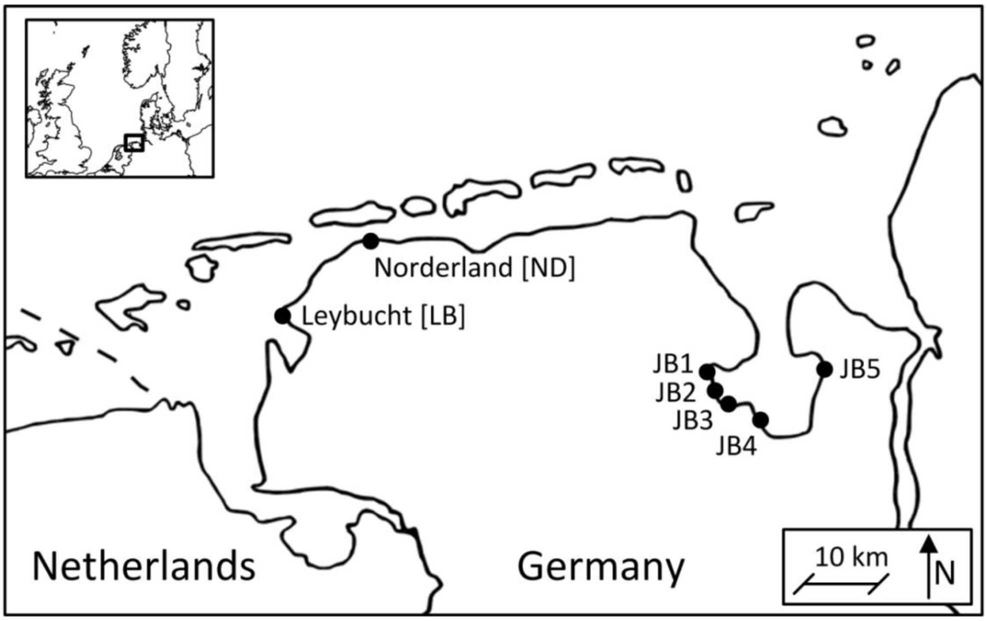

Figure 4-1 Study sites on the Lower Saxony Wadden Sea coast, Germany. JB1 = *Idagroden*, JB2 = in between *Petersgroden* and *Idagroden*, JB3 = *Petersgroden*, JB4 = *Nordender Groden*, JB5 = *Beckmannsfeld*

Artificial Nest Experiment

In order to obtain study results that could be compared to the actual breeding situation at the study sites, artificial nests were designed to mimic Redshank nests. Redshanks breed on the salt marshes of the study sites in densities up to 2 breeding pairs per hectare (chapter 5).

As Redshank nests usually contain four eggs (STIEFEL & SCHEUFLER 1984), the artificial nests contained three Quail eggs (*Coturnix coturnix*) and one artificial egg consisting of a core of plaster covered with modelling clay to conserve tooth or bill marks of predators. Quail eggs (33.7 mm × 26.3 mm, n = 62) are comparable in size to Redshank eggs (45.3 mm × 31.6 mm; STIEFEL & SCHEUFLER 1984). Artificial eggs were the same size and shape as redshank eggs and were fixed to the ground with a string and a tent peg to avoid being carried off by a predator. Quail eggs were rinsed in water and thereafter only handled with gloves in order to minimize odour trails (WHELAN et al. 1994).

The experiments with artificial nests were conducted in three series during the breeding season on the salt marshes: 1) end of April to mid May, when most Redshanks started egg-laying, 2) end of May to beginning of June, and 3) end of June to beginning of July. Each series lasted for 15 days and was extended to 20 days for four out of the seven study sites. A respite of 8 or 12 days was given between periods of exposure to avoid predators from becoming habituated to the artificial nests. The exposure period of 15 to 20 days allowed for the duration of each of the experiment series to be comparable to the incubation period of coastal waders (e.g. 24 days for Common Redshank; STIEFEL & SCHEUFLER 1984) in combination with three series of experiments during the breeding season (end of April till beginning of July). We used new eggs for each series of the experiment to avoid aging of the eggs. For each of the three series, we created about 20 artificial nests (along a 1,000 m transect) per study site. The actual positions of the nests were determined by creating random points using a randomized block design (4 nests per 200 m, min. distance 10 m). Positions of the nests were determined by Global Positioning System (GPS), and small markers (marking tape) were put on already existing fences or poles nearby. In total, 430 nests were deployed on mown (120 nests) and fallow (310 nests) sites.

We monitored nests at 3 to 5 day intervals for 15 to 20 days, starting from the first day after nest placement. During nest visits, we tried to avoid trampling of vegetation and used different paths to approach the nests in order to avoid building tracks easily perceived by predators.

Table 4-1 Environmental variables considered

Variable	Description	Range of Values
Exposure	Exposure of nest measured by light (PAR) reaching the soil surface, expressed as percentage of the light intensity above the canopy	0.02 % – 76.22 %
Canopy.height	Mean canopy height of the vegetation	14.0 cm – 100.0 cm
Veg.typ.grp (factor)	Vegetation type	*Elymus spp.* type / Others
Seawall.dist	Distance to seawall	19 m – 671 m
Mudflat.dist	Distance to mudflats	2 m – 667 m
Landuse (factor)	Agricultural land use	Mown / Fallow
Linear.structure (factor)	Narrow linear structure	Yes / No

Environmental variables

Seven environmental variables were measured at all nests (Table 4-1). We measured the mean canopy height of the vegetation per artificial nest in cm. To determine the exposure of nests, we measured photosynthetic active radiation (PAR) within the nest and above the vegetation (for details see chapter 3). A lower proportion of light reaching the nest indicates better nest concealment. Also the vegetation type and land management type were recorded at each nest. All vegetation types except the *Elymus spp.* type were grouped together, as the explanatory power of these vegetation types was negligible. For distance measurements (the nearest distance to the seawall and mudflats) we used a geographic information system (GIS) to integrate our GPS measurements of the individual nests. A binary variable for linear structures was assigned to a nest when the nest was inside a narrow strip of vegetation differing from the surrounding vegetation, *i.e.* high canopy along a fence. All correlation coefficients (Spearman’s rho) for numeric environmental variables were below 0.2 except for the correlation of distance to mudflats with distance to seawall, which had a Spearman’s rho of 0.21.

Definition of Predation

Nests were considered as predated if at least one egg was missing or if there were bite marks on the artificial egg (as described in PÄRT & WRETENBERG 2002). When we discovered a predated nest, we searched the area within a radius of approximately 5 m for eggshell remains and tracks of the predator. Nest surveys were stopped after the occurrence of a predation event.

Data Analysis and Statistics

Data were analysed by means of survival analysis. This technique allows for time-to-event analysis (time period until a predation event occurs) and the disentangling of factors influencing predation and survival rates. All analyses were performed in *R* (R DEVELOPMENT CORE TEAM 2010). The effects of environmental factors on the predation of nests were explored with Cox proportional hazard regression models (COX 1972; ANDERSEN & GILL 1982), using the R '*coxph*' function of the package '*survival*' (THERNEAU 2009).

After finding differences in predation rates between sites and over time, we focused the main model on the general pattern of predation on salt marshes. For the main model, we did not aim to include the influence of seasonal changes and different study sites on predation pressure. Therefore, for our analyses of the general pattern of predation on salt marshes, the influence of study site and time-related effects were excluded from the analysis by stratifying the data according to the three experimental series and the seven study sites.

The analysis started with the full model containing, as predictors, all environmental factors (see Table 4-1) and possible two-way interactions among them. This model was simplified by discarding independent variables that did not contribute to explaining the variability in the dependent variable. This was tested by an analysis of variance (ANOVA) for the two models. The final model was tested for proportional hazards using the *Schoenfeld residuals* and for nonlinearity using the *Martingale residuals*.

Table 4-2 Predation of artificial nests per time series

	Series 1 (end of April – mid May)		**Series 2 (end of May – early June)**		**Series 3 (end of June – early July)**	
Site	**Nests (N)**	**Number and percentage of predated nests**	**Nests (N)**	**Number and percentage of predated nests**	**Nests (N)**	**Number and percentage of predated nests**
JB1	20	3 (15 %)	20	15 (75 %)	20	4 (20 %)
JB2	12	0 (0 %)	12	5 (42 %)	12	3 (25 %)
JB3	32	4 (12.5 %)	32	21 (66 %)	32	8 (25 %)
JB4	20	7 (35 %)	20	15 (75 %)	20	10 (50 %)
JB5	18	5 (28 %)	20	8 (40 %)	20	2 (10 %)
ND	20	8 (40 %)	20	12 (60 %)	20	0 (0 %)
LB	20	12 (60 %)	20	18 (90 %)	20	4 (20 %)
Sum	142	39 (27 %)	144	94 (65 %)	144	31 (22 %)

Results

The experiments were conducted with a total of 430 artificial nests. The predation rate ranged from 0 % to 90 % (Table 4-2). In total, 164 nests were predated (38 % of all nests). Identification of the predator was possible for 104 nests (63 % of depredated nests). Of these, 100 nests were predated by birds and 4 nests by mammals.

With the survival analysis using Cox proportional hazard regression models, it is possible to calculate an estimated survival of nests over time and also in between nest controls. The model showed, that at day 20, nearly 50 % (0.524, CI 95 %: 0.462 – 0.594) of the nests were lost (Fig. 4-2). The decrease of survival probabilities – and thus the hazard – over time was rather constant.

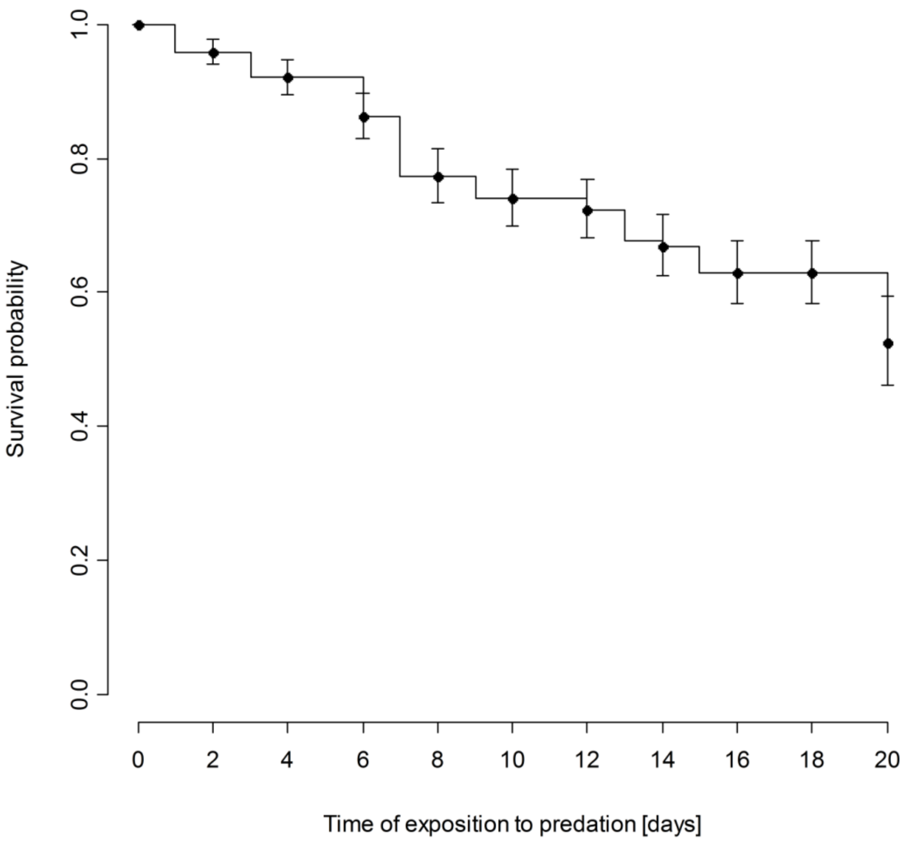

Figure 4-2 Estimated survival function for the Cox proportional hazard regression of nest survival (n = 430)

Survival of nests differed significantly between the sites and experimental series. For all study sites, the time of exposure to predation lasted at least 15 days. After this period of exposure, the estimated survival of the sites ranged from 0.32 (JB4) to 0.95 (JB2) (Table 4-3).

Table 4-3 Estimated survival (± standard error) per site after 15 days (for sample sizes see Table 4-2)

Site	Estimated survival after 15 days (± SE)	Confidence interval lower 95 %	upper 95 %
JB1	0.60 ± 0.07	0.47	0.76
JB2	0.95 ± 0.07	0.82	1.00
JB3	0.56 ± 0.07	0.44	0.71
JB4	0.32 ± 0.12	0.15	0.68
JB5	0.86 ± 0.05	0.76	0.97
ND	0.82 ± 0.07	0.70	0.97
LB	0.56 ± 0.11	0.38	0.83

A second important factor for the survival of nests was the timing of nesting within the breeding season. During the main breeding season (end of May to beginning of June; series 2), we found lower nest survival than in periods before and after the main nesting period (see Fig. 4-3: series 1 and 3).

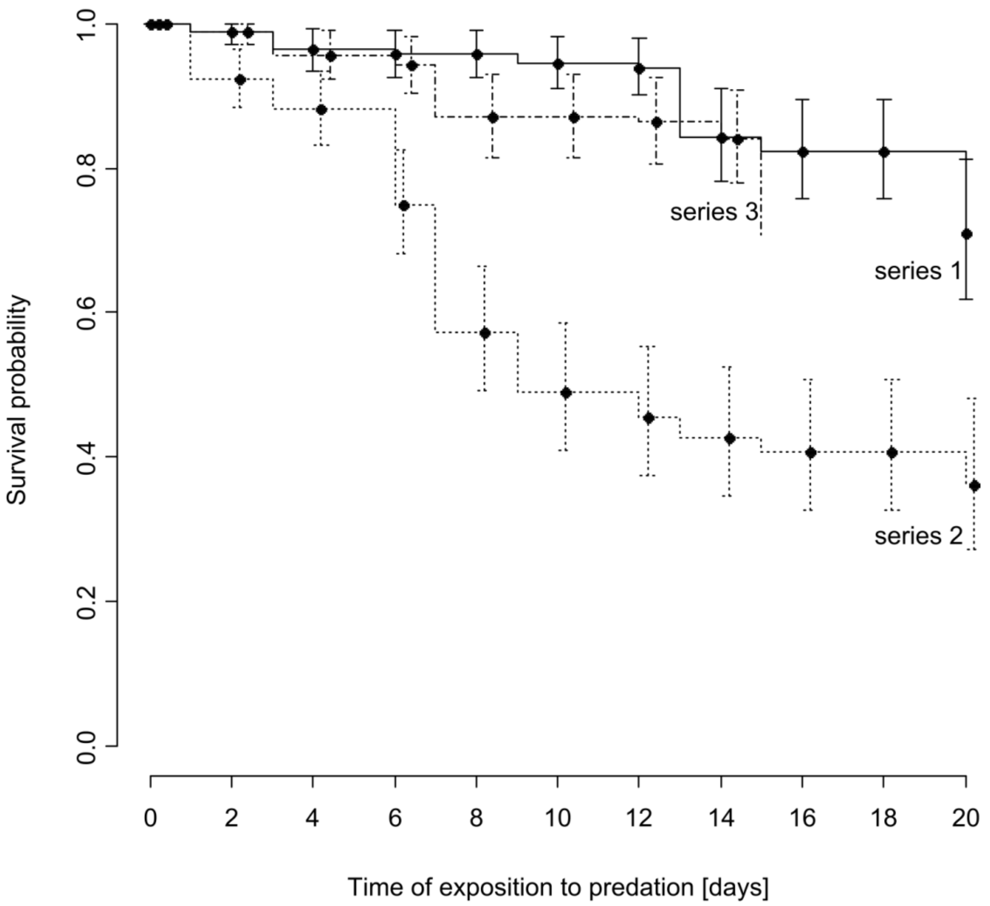

Figure 4-3 Estimated survival functions for the three time series pooled over all sites (n = 430; series1 = 142; series2 = 144; series3 = 144)

The final model (Likelihood ratio test = 46.75; df = 8; $p < 0.001$) included all explanatory variables as listed in Table 4-1 except for the linear structures. Vegetation (canopy height and vegetation types) had the highest impact on nest survival (Table 4-4). Higher canopy reduced the predation risk significantly: by 5 % per cm of canopy height.

If the artificial nest was situated in the *Elymus spp.* vegetation type, the risk of predation was just 2 % of the risk of an artificial nest in other vegetation types. In the *Elymus spp.* vegetation type, nest survival was generally relatively high but, surprisingly, decreased with increasing canopy height (4 % per cm canopy height).

Agricultural land use had a significant impact on the vegetation structure of salt marsh vegetation and therefore on nest survival. The model showed that the hazard of egg loss in *Elymus spp.* vegetation without agricultural land use was increased threefold compared to mown *Elymus spp.* vegetation (Table 4-4). Detailed measurements of vegetation structure at the study sites were done in a previous study (chapter 3). With those data, we could add detailed information of vegetation structure not measured at the artificial nest. These measurements of vegetation structure of *Elymus spp.* vegetation type showed significantly higher vegetation density and higher canopy at mown sites (Fig. 4-4). The lower survival on fallow *Elymus spp.* vegetation type, as shown in Table 4-4, could therefore be linked to the influence of mowing on the vegetation structure.

Table 4-4 Model parameters

	coefficient	exponentiated coefficient	standard error	z-value	p-value	
Veg.typ.grp (*Elymus* spp. type)	-3.8190	0.022	1.0440	-3.658	0.00025	***
Veg.typ.grp (*Elymus* spp.type): Landuse (fallow)	1.2230	3.398	0.5214	2.346	0.01897	*
Canopy.height	-0.0526	0.949	0.0163	-3.199	0.00138	**
Canopy.height:veg.typ.grp (*Elymus* spp. type)	0.0392	1.040	0.0158	2.484	0.01298	*
Seawall.dist:Landuse (fallow)	-0.0094	0.991	0.0041	-2.289	0.02207	*
Exposure:Seawall.dist	0.0004	1.000	0.0002	2.435	0.01487	*
Canopy.height:Seawall.dist	0.0002	1.000	0.0001	2.649	0.00807	**
Seawall.dist:Mudflat.dist	-0.0001	1.000	< 0.0001	-2.040	0.04132	*

Signif. codes: *** < 0.001; ** < 0.01; * < 0.05

Exponentiated coefficients represent the multiplicative change in risk due to each covariate

In addition to the vegetation, the spatial location of the nest (distance to seawall and mudflats) and the exposure of the nests showed an impact on the survival of nests (see Table 4-4). The interaction of distance to seawall with agricultural land use (fallow) increased the survival probability by approx. 1 %. This means that on fallow sites, survival was higher further away from the seawall.

The effects of the other interaction terms on the survival were low (less than 1 %), although they contributed significant to the explanatory power of the model.

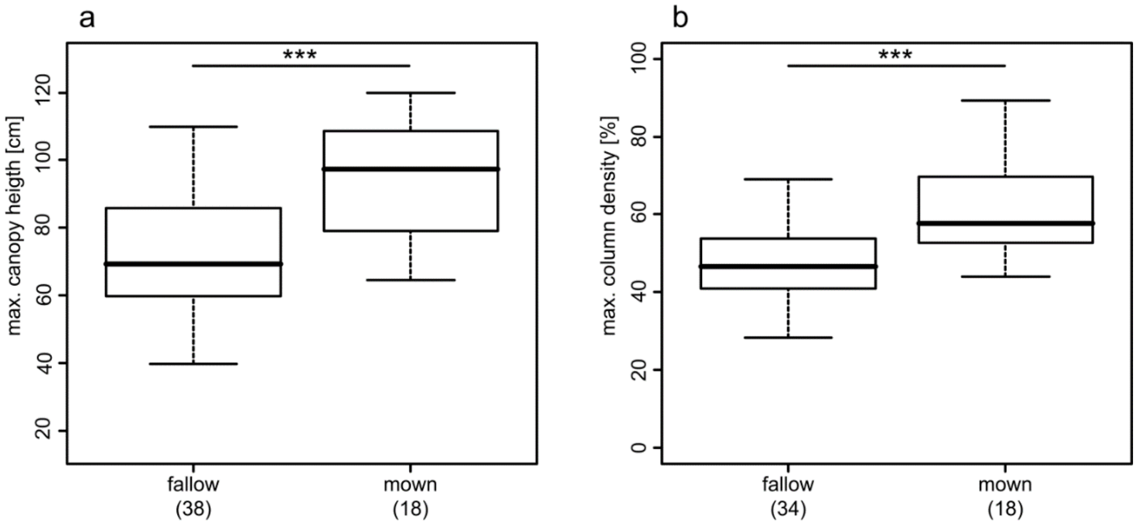

Figure 4-4 Canopy height **(a)** and density **(b)** of *Elymus spp.* vegetation measured in July with data from chapter 3 (boxes represent quartiles, whiskers extend to the most extreme data points which is no more than 1.5 times the interquartile range)

Discussion

Since we used study sites lying along approx. 140 km of coastline, we expected differences in the predator communities at those sites (cf. TEUNISSEN et al. 2008) and therefore differences between the sites with respect to the factors influencing survival rates. These differences between the sites were obvious in the survival probabilities (after day 15, ranging from 0.32 up to 0.95 over all sites). However, the pattern of survival with respect to the three series of experiment is comparable between all sites, with lowest nest survival rates in the 2nd time series of the experiments – the peak of the breeding season – at each of the study sites. As the sites were spread widely along the coastline of Lower Saxony, we conclude that this pattern of survival rates over time is general for mainland salt marshes in the Wadden Sea region. A comparison between artificial nests in this study with Redshank nests showed that predation rates differed between the nest types, but the spatial and temporal patterns of predation were similar (SCHLAICH et al. in prep., Box A). This means that, although a direct conclusion about predation rates of real nests based on artificial nests is difficult, the patterns of predation over space and time, and the factors influencing predation can be extrapolated from this study to breeding birds with well-concealed ground nests on salt marshes.

Identification of nest predators showed that a high number of nests were predated by birds (100 nests) and only few (4 nests) showed bite marks of mammalian predators. As many artificial eggs (60 nests) showed no marks of predators, even when predation on quail eggs took place, it is possible that all these nests had been predated by mammals. Due to this lack of information, it remains uncertain to what extend mammalian predators contributed to nest predation at the study sites, but their impact could be high. A high amount of predation by mammals at our study sites would be supported by the results of chapter 5, which showed predation avoidance strategies of Redshanks during night time at some of our study sites, indicating a high impact of mammalian predators.

Abundance of potential prey is likely to impact predator densities (BEINTEMA & MÜSKENS 1987; BEALEY et al. 1999; EVANS 2004). Knowledge of small mammals (e.g. mice and voles) – an alternative prey to eggs – on salt marshes is very limited. Regular flooding and especially winter storm surges render salt marshes as less suitable habitat for small mammals. High risks of drowning (ANDERSEN et al. 2000) or mortality due to hypothermia, stress and exhaustion (WIJNHOVEN et al. 2005) can lead to a total loss of the small mammal communities during a flooding event (BLUMENBERG 1982; GOLET et al. 2013). Recolonisation depends on vegetation structure, habitat connectivity and refugia, and is often site- and species-specific (WIJNHOVEN et al. 2005). Therefore, communities of small mammals on salt marshes are controlled by tidal flooding (SHURE 1971) and species richness and abundance are lower when compared to inland grasslands. This has important implications for predator communities. Predators can be attracted by high nest densities (EVANS 2004 and citations therein). Due to the low abundance of alternative prey to eggs on salt marshes, this habitat will be most attractive for predators during the peak of breeding season as the prey abundance is highest during this period. This results in the highest predation pressure and lowest nest survival during the main breeding season, as confirmed by this study. In contrast, on inland agricultural grasslands, the amount of alternative prey is more abundant. Nests here are mainly found in passing (SEYMOUR et al. 2003) when searching for small mammals. This leads to lower predation rates during the main breeding season on inland grasslands, in contrast to salt marshes, due to the higher supply of potential prey items (BEINTEMA & MÜSKENS 1987; BEINTEMA et al. 1995).

The impact of spatial variables (such as distance to seawall) in accounting for predation rates was only marginal even though mammalian predators are known to enter the salt marshes from inland areas (EXO 2008). This would imply a higher probability of predator occurrence and therefore higher predation rates closer to the seawall. This pattern was only confirmed for fallow salt marshes, where nest survival was indeed higher at nesting sites at greater distances from the seawall. We conclude that either the impact of mammalian predators on our artificial nests on mown sites was low or that, on mown salt marshes, mammalian predators could easily access wide parts of the salt marsh and spatial resistance was rather low. Therefore, predation rates were rather independent of nest locations on the salt marsh with respect to the seawall.

Vegetation structure appeared as the main factor influencing predation on ground-breeding birds on mainland salt marshes. High survival probabilities were found in vegetation with high canopy; predation risk decreased by 5% per cm of canopy height. This finding is in line with other studies which demonstrated an increase in nest crypsis with canopy height (BEINTEMA et al. 1995; NEWTON 1998; WILLSON et al. 2001; EVANS 2004). For ground-nesting bird species that rely heavily on concealment and show only limited nest defence by adult breeding birds, nest crypsis in higher vegetation grants lower predation rates (EVANS 2004). Our study on artificial nests provides, for the first time, experimental evidence for direct effects of canopy height and thereby habitat conditions on nest survival in a situation when predator defence by parental birds is absent.

The interaction term of couch grass vegetation (*Elymus spp.* vegetation type) with the canopy height showed a decrease of nest survival by 4 % with each centimetre of increase in canopy height. Generally, higher canopy leads to higher survival of nests but within the *Elymus spp.* vegetation type – the vegetation type with highest canopy on salt marshes – the highest stands were less suitable compared to couch grass stands with lower canopy. This could be due to the fact that high couch grass stands tend to tilt over during strong winds (cf. BAKKER et al. subm.), which can lead to a dramatic change of vegetation structure with a drastically reduced canopy height.

The exposure of nest sites – measured as the incidence of light passing through the vegetation – was not as relevant as canopy height in explaining the survival of nests. The exposure of a nest is influenced, on one hand, by the vegetation height and, on the other hand, by the density of vegetation (horizontal and vertical cover), which means that the exposure can differ in vegetation stands with comparable canopy height due to differences in vegetation density (chapter 3). It was expected that the exposure of nests was the main factor influencing the survival rates of ground nests (EVANS 2004). Based on our findings of canopy height playing the central role, we conclude that it is not nest concealment *per se* which drives predation risks but the changes in searching patterns of predators, which can be altered by canopy height. SCHEKKERMAN et al. (2009) found that avian predators tend to search for prey on fields with low canopy. Thus, it is possible to get exposed nests in high vegetation under low vegetation density where the nest survival is high because predators tend to search preferentially in the parts with low canopy. Besides canopy height and vegetation density, simplification of sward appearance can also lead to poorer camouflage of nests. Nest survival is lower in homogeneous swards than in heterogeneous vegetation (NEWTON 1998; FULLER & GOUGH 1999; VICKERY & ARLETTAZ 2012). Canopy height may form a complex clue for the attractiveness of sites for foraging predators (predation pressure and thus enhanced predation risk) and the actual detectability of nests (exposure of nests, heterogeneity of vegetation).

As the species composition of plant communities – and thus vegetation type – strongly influences the vegetation structure, the influence of vegetation type on the survival of nests is very high. The successional vegetation climax on the upper salt marsh is dominated by *Elymus spp.* (SCHRAMA et al. 2012) and shows the highest canopy and vegetation densities on salt marshes (chapter 3). This leads to high survival for cryptically nesting birds in this climax stage as compared to other vegetation types with lower canopy height and less dense vegetation. This was also shown in a study by THYEN & EXO (2005) where hatching success of Redshanks was highest in *Elymus repens* vegetation on mainland salt marshes. We found interesting effects of mowing on the *Elymus spp.* vegetation type and nest survival. Mowing as a conservation measure and for seawall maintenance takes place after the breeding season and plants will regrow until the breeding season of the following year. In the first place, mowing leads to a more homogenous vegetation as compared to fallow salt marsh. The removal of biomass in *Elymus spp.* stands leads to a higher productivity of this plant community with higher (MINDEN et al. 2012) and denser vegetation during the breeding season as compared to a situation without mowing (chapter 3). It is important to note that this effect contrasts sharply with the situation on inland grasslands, where mowing leads to lower and less dense vegetation during the breeding season, which in turn leads to higher predation rates on nests (EVANS 2004) and even on chicks (SCHEKKERMAN et al. 2009). On salt marshes, nevertheless, mowing of *Elymus* vegetation – the endpoint of salt marsh succession – after the breeding season can lead to a higher and denser vegetation structure and therefore reduces nest predation. The same effect was not found for other salt marsh vegetation types. This leads to the conclusion that mowing can improve survival rates of nests only at the latest successional stage of salt marshes. However, in order to enable mowing on wet salt marshes, a dense drainage network is necessary. Such drainage of salt marshes can have its disadvantages. With drainage, the heterogeneity of hydrological conditions and therefore the heterogeneity of salt marsh vegetation is decreased and can result in poorer food availability for breeding birds (EGLINGTON et al. 2010). Also, faster development to the vegetation climax stage is expected on well-drained salt marsh sites (VEENEKLAAS 2013). In addition, the building of infrastructure like crossing points over small ditches and creeks can improve the accessibility of salt marshes for mammalian predators. For conservation measures on salt marshes, these aspects have to be carefully balanced.

We show that predation of ground nests in salt marshes is strongly influenced by vegetation structure and management of the salt marshes. The results of this study are based on artificial nests where a parental bird is absent. With this method, the mechanisms behind predation at nests of a wide variety of ground-nesting species with nests hidden in vegetation can be detected, while disregarding the behavioural differences. As the probability of nest predation due to behaviour of adult birds is highly correlated with the time that nests are left unattended (SMITH et al. 2012), it will – in a second step – be possible to transfer our findings to species where the incubation pattern of adults is known (cf. DEEMING 2002; FONTAINE & MARTIN 2006; for Redshanks chapter 5). The use of artificial nests, which exclude the influence of breeding adults, is a suitable method to disentangle predation risks due to vegetation structure and thus land management form those due to the behaviour of parents. This renders information on habitat conditions necessary for effective conservation measures (ROODBERGEN et al. 2012). Our findings on management and vegetation structure can provide advice for effective conservation management measures on mainland salt marshes and help to support sustainable breeding sites for many breeding waders on salt marshes along the Wadden Sea mainland coast.

Acknowledgments

This study was conducted as part of the TREIBSEL project and was support by the Wadden Sea foundation of Lower Saxony (NWS 10/05) and the ‘Wasserverbandstag e.V.’. We thank K. Grote, J. Rößler, S. Treffler and K. Baipidi for assistance during field work and the administration of the National Park ‘Niedersächsisches Wattenmeer’ for permission to work on the salt marshes of the National Park.

Chapter 5

Can differences in incubation patterns of Common Redshanks *Tringa totanus* be explained by variations in predation risk?

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Abstract

The effects of predation on Redshank incubation patterns and behaviour was investigated in 2006 and 2007 at three mainland study sites at the *Jadebusen* and at one study site on the island *Wangerooge*, Wadden Sea National Park Lower Saxony (Germany), using temperature data loggers. At these sites, breeding Redshanks were naturally exposed to different predation pressures (as revealed by different hatching success) that varied between 10% and 90% amongst study sites. In areas with a higher predation risk, incubating Redshanks showed a lower nest attendance than in areas where predation risk was low. On the mainland two behavioural strategies could be distinguished. Some nests were unattended during the night for several hours whereas other nests were incubated for most of the night. Nocturnal absence behaviour was found only on the mainland, and then only in areas easily reached by ground predators. Since ground predators are often active during the night, and dangerous for the incubating birds, this behaviour has probably become established to avoid direct mortality of adult birds rather than avoidance of egg predation. This results from a trade-off between current and future reproduction. By leaving the nest unattended during the night, these birds probably put their own survival before reproduction to maximise their lifetime reproductive success. Since such long incubation recesses may have negative consequences for embryo development, the results of this investigation provide an example of an indirect effect of predation. However the behavioural trait of nocturnal absence from the nest may directly reduce reproduction and thus fitness of these individuals.

Introduction

For most birds, predation is one of the main causes of reproductive failure (RICKLEFS 1969) and thus plays an important role in life history evolution (MARTIN 1995). A high variation of adaptations to reduce the risk of nest predation has evolved among birds. Specifically waders as ground-nesting birds show many different kinds of anti-predator behaviour (VAN DE KAM et al. 2004) including active and passive nest defence behaviours (GOCHFELD 1984). Large waders mostly defend their nest aggressively against predators, in contrast to smaller waders, which tend to employ non-aggressive nest defence behaviour (LARSEN 1991). For instance Oystercatchers *Haematopus ostralegus* and Black-tailed Godwits *Limosa limosa* often attack potential nest robbers directly to drive away the intruder by ‘predator-mobbing’ (GOCHFELD 1984). Smaller waders e. g. Ringed Plovers *Charadrius hiaticula* and Dunlin *Calidris alpina* show a multitude of distraction behaviour and displays, e.g. the ‘exhausted bird display’, ‘false brooding’ or creeping through grass almost like a small mammal (NETHERSOLE-THOMPSON & NETHERSOLE-THOMPSON 1986). Common Redshanks are less aggressive, but do not try to distract or mislead potential nest predators as described for other non-aggressive waders (NIETHAMMER et al. 1968; NETHERSOLE-THOMPSON & NETHERSOLE-THOMPSON 1986). The only distraction behaviour observed in Redshanks is a collective scolding of intruders, observed in the presence of mammalian and also avian predators, for example Carrion Crows *Corvus corone* and Hen Harriers *Circus cyaneus* (GROßKOPF 1959; CERVENCL 2008). In contrast to many other wader species, the main strategy of Redshanks is to build a well concealed nest in relatively tall vegetation which reduces the chance the nest will be found (GROßKOPF 1958; STIEFEL & SCHEUFLER 1984). Furthermore, in some areas Redshanks tend to nest in association with more ‘aggressive’ waders, e.g. Lapwings *Vanellus vanellus* and Black-tailed Godwits, taking advantage of the nest defence behaviour of these “umbrella-species” (BUB 1957; DYRCZ et al. 1981).

Incubation patterns can also affect nest predation and therefore nest success (GHALAMBOR & MARTIN 2002; SMITH et al. 2007). A high activity near the nest due to many incubation recesses and nest visits can increase predation risk by drawing the attention of a predator to the nest (MARTIN et al. 2000; MUCHAI & DU PLESSIS 2005). On the other hand parental behaviour can be influenced by the risk of predation as well. The endemic New Zealand Bellbird *Anthornis melanura* has been shown to react to introduced mammalian predators (MASSARO et al. 2008). The authors found that females elongate their incubation bout length with increased predation risk to minimize activity near the nest. FONTAINE & MARTIN (2006) showed experimentally that birds can assess predation risk, resulting for instance in higher feeding rates by males in safer environments. Thereby not only the avoidance of nest predation, also the risk of predation on incubating adults may play an important role in shaping different incubation patterns (KEITT et al. 2004). Long-lived species specifically should reduce the risk to themselves to maximize their life time reproduction, as the risk taken by parental birds to increase current reproduction may have costs reducing survival and thus future reproduction (WILLIAMS 1966).

In this study we compared incubation patterns of Redshanks in different study sites which were naturally exposed to differential predation pressures. Former studies in two of these areas showed that Redshanks breeding on a Wadden Sea island had a higher hatching success (2003: 89 %) than those on a mainland study site (2000-2003: 2-11 %), where most nests failed due to predation (THYEN et al. 2005; BÜTTGER et al. 2006). An increase in nest attendance caused by a greater predation risk might be expected, if presence at the nest results in benefits from camouflaging or defending the nest (e.g. MONTGOMERIE & WEATHERHEAD 1988; ANDERSSON & WALDECK 2006). As this is not the case in Redshanks breeding in high and dense vegetation, we hypothesize that a decrease in nest attendance will occur in areas with a higher predation pressure. If the probability of nest success is low, it could be expected that the birds would spend less effort in the current clutch. This is potentially due to individuals saving energy for future breeding attempts, either as a replacement clutch in the same season (MARTIN 1995) or by maintaining higher adult survival for future breeding attempts (WILLIAMS 1966).

Methods

Study area

The study was carried out on salt marshes at four study sites within the Wadden Sea National Park Lower Saxony, Germany. In 2006 research was performed on the island *Wangerooge* (53°47’N, 7°54’E, c. 70 ha) and at the mainland study site *Petersgroden* (53°26’N, 8°05’E, c. 50 ha, Western *Jadebusen*). In 2007 two other mainland areas were included: *Idagroden* (53°28’N, 8°03’E, c. 70 ha, Western *Jadebusen*) and *Beckmannsfeld* (53°30’N, 8°19’E, c. 60 ha, Eastern *Jadebusen*). Vegetation types within the saltmarsh depend largely on the frequency of flooding and thus on the topographical height above mean sea level. The upper salt marsh consists mainly of the alliance *Armerion maritimae* with the association *Agropyretum littoralis* dominated by *Elymus spec.* Lower salt marshes are mainly covered with the alliance *Puccinellion maritimae* represented by the associations *Puccinellietum maritimae* and *Halimionetum portulacoidis* (nomenclature according to RENNWALD (2000), detailed description in POTT (1992)). Overall, differences in topographical height within the study sites are slight and there was no correlation between height and the distance to the dike or the coastline, respectively (NLWK 2004). Tidal creeks run perpendicular to the coast in a mean distance of ~30 m on all mainland study sites.

Most of the salt marsh areas of our study sites were not used for agriculture. However at the study site *Petersgroden* 15 % of the area was used for cattle grazing (1 animal/ha from May) and 15 % was mown once a year in July. Furthermore there is a clay pit (9 ha), which was created by the removal of clay for dike-building and which is now characterised by muddy sediments. Breeding densities of Redshanks were comparatively high with 1.4 –2.0 breeding pairs per hectare on the mainland study sites and 1.2 breeding pairs per hectare on the island *Wangerooge* (THYEN et al. 2005; OBERDIEK et al. 2007). Avian predators, such as gulls and corvids were present at all sites. In contrast to the mainland study sites, on *Wangerooge* neither Red Foxes *Vulpes vulpes* nor mustelids occur (JACOB et al. 2004). GROßKOPF (1989) found frequent predation of Redshank eggs by introduced Hedgehogs *Erinaceus europaeus* on the island *Wangerooge* in the 1960's. Also feral cats *Felis sylvestris f.* occur on the island, but as the hatching success (~ 90 %) reveals, these introduced predators had little to no effect on Redshank nest success on *Wangerooge* in the years of our study.

Nest Monitoring

Nest searching and monitoring was conducted from late April to the beginning of July at intervals of seven days (± 2 d, EXO et al. 1996). Usually nests were found by flushing the incubating bird or by observing a bird returning to its nest. Nests were marked with a bamboo stick placed 3 m away from the nest and the nest locations were recorded with a Global Positioning System (Garmin GPS 12). Length and breadth of the eggs were measured to the nearest 0.1 mm using a calliper. The egg mass was taken (± 0.1 g) with a digital balance. A nest was considered successful, if the nest was found empty after the estimated hatching date with small pieces of egg shells in the nest. A nest failure was recorded if eggs disappeared before the expected hatching date (see below) and if the nests showed clear signs of predation. Depredated nests were often found destroyed with egg shell and yolk remains close to the nest site.

In many studies (e.g. EIKHORST & BELLEBAUM 2004; EIKHORST 2005; GRIMM 2005; HARTMAN & ORING 2006; WEIDINGER 2006; BOLTON et al. 2007) temperature data loggers have been used to indicate when a predation event occurred (for example day- or night-active predators). Because of long incubation recesses some Redshanks take during the night, it was not possible to determine if the predation event took place before or during a recess. We therefore refrained from using temperature logger data in this way. We also chose not to determine predators by egg remains, since multiple visits of several predators and activity of parental birds at depredated nests can lead to wrong conclusions (LARIVIERE 1999).

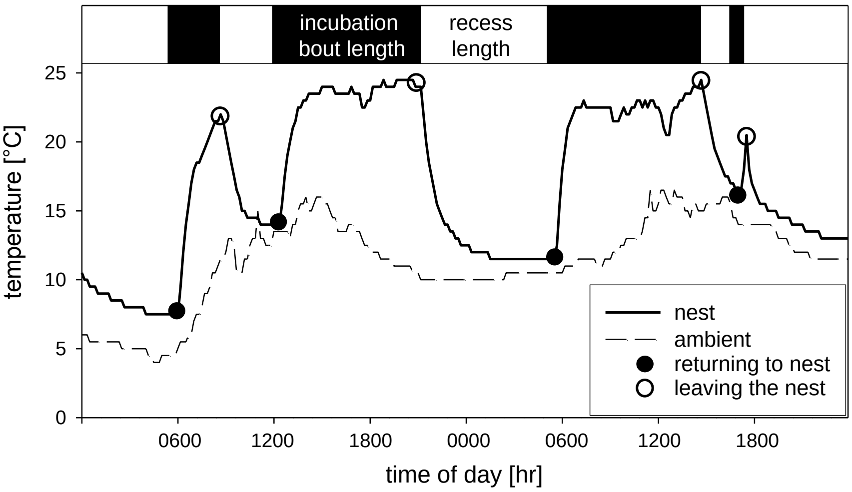


Figure 5-1 Example of an incubation record showing nest and ambient temperature for two days. Sudden changes in nest temperature indicate the moment a parental bird left or returned to the nest (denoted by white or black circles)

Incubation Behaviour

Incubation patterns of Redshanks were recorded using temperature data loggers (DS1921L-F52 Thermochron iButton, Dallas Semiconductor), which were programmed to measure nest temperature continuously at intervals of 10 min with an accuracy of 0.5 °C. The data loggers were fixed in the nests with pegs to avoid removal by parental birds or predators. No effects of iButtons on hatching success were observed in former studies in Common Redshanks and Long-billed Curlews *Numenius americanus* (Hartman & Oring 2006; Cervencl 2008). In total incubation patterns of 60 nests were recorded. On every study site ambient temperature was measured in the same way to facilitate incubation pattern analysis by comparing nest and ambient temperature (Fig. 5-1). A sudden drop or increase in nest temperature was recorded every time a parental bird left or returned to the nest. Thus the number of recesses per day, length of recesses and nest attendance (% time incubating) was obtained for each nest. A recess was defined as an absence of ≥ 30 min, as movements of adult birds on the nest (e.g. change breeding position or turning eggs) can cause variations in nest temperature. As only long recesses were measured, the number of recesses per day was not valid to analyse activity near the nest. To differentiate between day and night behaviours, night was defined as the time between sunset and sunrise using the U.S. Naval Oceanography portal sunrise data (www.usno.navy.mil/USNO) for each study site.

Data Analysis and Statistics

Since most nests were found with complete clutches (four eggs), the hatching date was estimated by calculating the remaining days till hatching using the egg metrics: $days = 446{,}508 \times mass\ [g] \times length^{-1}\ [mm] \times breadth^{-2}\ [mm] - 197$ (Green 1984). This was performed for all eggs in a nest. The earliest estimated hatching date was then used as the hatching date of the respective clutch. Assuming an average duration of incubation in Redshanks of 24 days (Niethammer et al. 1968), the start date of incubation could be assessed by subtracting 24 days from the estimated hatching date.

As only a few nests were monitored from the start of egg laying, daily survival probability (DSP), daily predation rate (DPR) and estimates of hatching success were calculated using the method developed by Mayfield (1975). Observation days from all nests were included, but only considered losses if resulted from predation. A total of 107 nests were used for hatching success analyses including the two years and all study sites. Standard errors were assessed following Johnson (1979). Pairwise comparisons of DSP were made according to Hensler & Nichols (1981). Within each year, we calculated separate estimates for each study site.

On the mainland two groups of different behavioural strategies could be distinguished by a hierarchical cluster analysis (Median method, Squared Euclidean Distance) using the date of clutch initiation, nest attendance, duration of recesses and number of recesses per day as grouping variables. The date of clutch initiation was included in the analyses, to verify if breeding experience and quality of parental birds may influence the incubation patterns. Older and thus more experienced Redshanks generally nest earlier in the season than inexperienced birds (Großkopf 1970; Thompson & Hale 1991). Only data of the first 12 days of incubation were included in the cluster analysis, since Redshanks change their behaviour as incubation progresses and increase nest attendance (see below). Thus, differences in incubation patterns were expected especially during this period. Afterwards the classification was tested by a discriminant analysis including the two groups from the mainland (named Mainland 1 and Mainland 2) and the nests from Wangerooge as a third group.

Results are given as mean ± SD. Statistical tests were two-tailed, according to Sachs (1997) and carried out in SPSS 13.0. Asterisks indicate significant differences (*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$). In pairwise comparisons of three groups, p-values < 0.017 have been considered significant after Bonferroni adjustment ($p = 0.05/3$).

Results

Hatching success

Similar to former studies (THYEN et al. 2005), hatching success of Redshanks in 2006 was significantly higher on the island *Wangerooge* (87.5 %, n = 10, z = 4.881, p < 0.001) than on the mainland study site *Petersgroden* (2.5 %, n = 27, Fig. 5-2). In 2007 hatching success at *Petersgroden* was also very low (1.1 %, n = 22) and thus significantly lower than at the other mainland study sites of *Idagroden* (51.8 %, n = 35, z = 4.041, p < 0.001) and *Beckmannsfeld* (47.2 %, n = 13, z = 3.707, p < 0.001), where hatching success was similar (z = 0.218, p = 0.827) The main cause of clutch loss was due to predation. Including nests from all areas and both years, 80.8 % of nest failure was due to predation, 16.4 % due to nest desertion and 2.7 % were flooded. At *Petersgroden* three adult birds were found predated next to their nests.

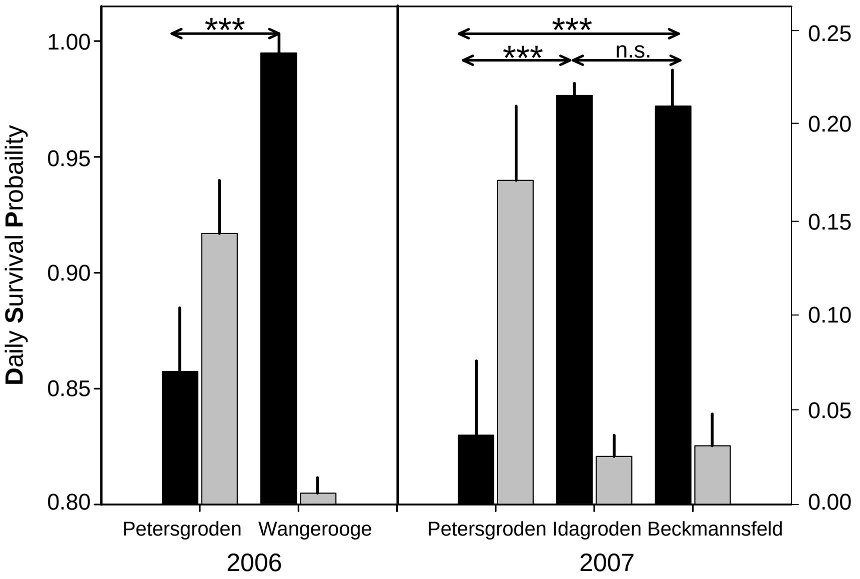


Figure 5-2 Daily survival probability (DSP, black bars), daily predation rate (DPR, grey bars) according to MAYFIELD (1975) and standard error (JOHNSON 1979) for Common Redshanks at four study sites in the Lower Saxonian Wadden Sea in 2006 and 2007. *** p ≤ 0.001 significance using HENSLER & NICHOLS (1981), corrected after Bonferroni

Incubation patterns of Redshanks

Averaging the nests from all study sites of both years and including the whole incubation period, Redshank nests were incubated 77.3 ± 19.8 % of the time (n = 60), with 2.0 ± 1.1 recesses per day, each lasting 126.2 ± 82.0 min. Incubation behaviour changed during the incubation period (Fig 5-3). From a plot of mean nest attendance, it can be seen that nest attendance increased over time from approximately 60% at the first day to 94% on the 24th day of incubation.

There was no significant difference in the number of recesses per day between the study sites, but recess durations on *Wangerooge* island were significantly shorter (69.3 ± 14.5 min, n = 10, p = 0.042, Kruskal-Wallis-Test) than recess durations from *Petersgroden* (152.4 ± 87.8 min, n = 25), *Beckmannsfeld* (108.9 ± 84.0 min, n = 11) and *Idagroden* (133.9 ± 81.2 min, n = 14). This tended to result in higher nest attendance on the island *Wangerooge* (87.4 ± 6.0 %, p = 0.067, Kruskal-Wallis-Test) compared to the mainland study sites *Petersgroden* (69.9 ± 21.1 %), *Beckmannsfeld* (81.4 ± 20.2 %) and *Idagroden* (80.1 ± 20.3 %).

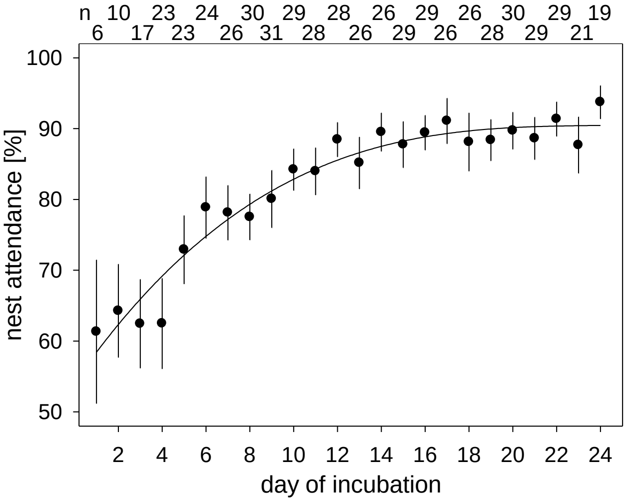


Figure 5-3 Relationship of nest attendance (mean values of nests of all study sites with SE) of Common Redshanks and the day of incubation. n Number of nests measured at the respective incubation stage is given along the top

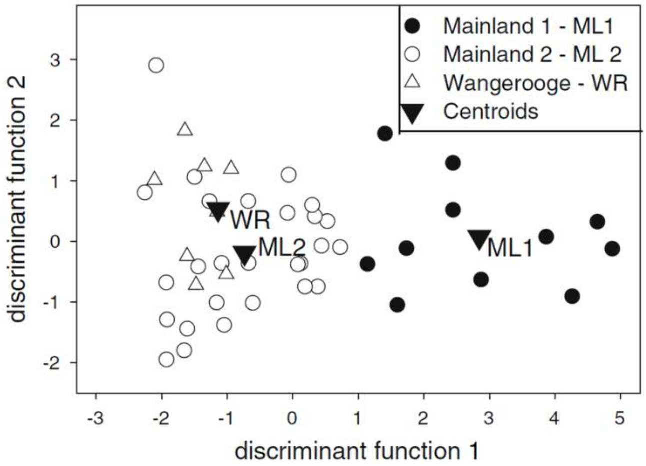


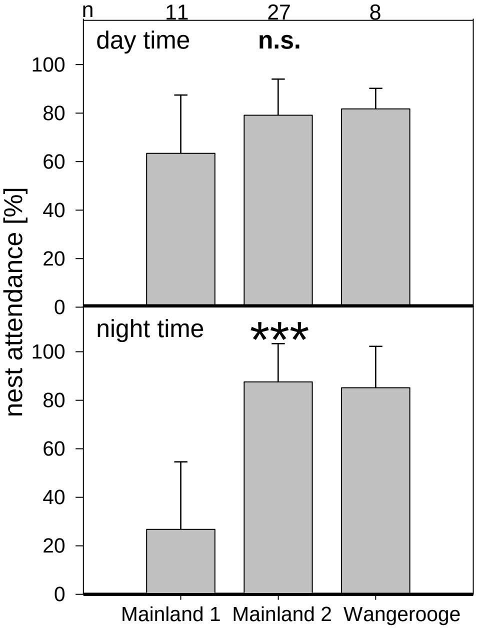
Figure 5-4 Results of a discriminant analysis separating groups of behaviour of Common Redshanks by nest attendance, mean duration of recesses, number of recesses, and the date of clutch initiation

Individual differences during the first 12 days of incubation

Individual differences in incubation behaviour in the first 12 days of incubation were shown by the discriminant analysis results (Fig. 5-4). Only function 1 discriminated between the groups ($\chi2 = 58.26$, $df = 8$, $p < 0.001$) and explained 97.3 % of variance. The variables that contributed most to this discrimination were duration of recesses and nest attendance. Function 2 was not significant ($\chi2 = 3.05$, $df = 3$, $p = 0.348$), so that the discrimination of the group takes place in a horizontal direction. It becomes apparent, that some birds from the mainland (Mainland 2 – ML2) showed a similar behaviour to the birds from *Wangerooge* (WR), whereas another group of Redshanks (Mainland 1 – ML1) behaved differently. There was no significant difference in the date of clutch initiation between the groups (p = 0.188). The mean recess duration of the group ML1 was significantly longer (261.0 ± 60.2 min, n = 11, p < 0.001) than in group ML2 (98.1 ± 44.5 min, n = 27) and *Wangerooge* (72.9 ± 18.7 min, n = 8). Since there was no difference in the number of recesses (p = 0.261), the difference in recess duration resulted in a significantly lower nest attendance in ML1 (52.1 ± 21.8 %, p < 0.001) compared to ML2 (81.7 ± 11.1 %) and *Wangerooge* (82.3 ± 6.7 %).

This considerable difference in nest attendance between the groups is mainly caused by the incubation behaviour during the night (p < 0.001, Kruskal-Wallis Test, Fig. 5-5). Pairwise comparisons of the three groups showed, that nocturnal nest attendance in group ML1was significantly lower (26.8 ± 27.8 %) than in nests of ML2 (87.6 ± 15.7 %, p < 0.0001, U-test) and *Wangerooge* (85.4 ± 17.1 %, p < 0.0001, U-test), which were incubated over most of the night-time. During daylight hours there was no significant difference in nest attendance (p = 0.159, Kruskal-Wallis Test). The mean recess duration of 260 min (or 4.3 h) in the group ML1 is also a reflection of these very long absences of adult birds at night, when recesses of 5-7 h were common. The longest recess on a successful nest was 670 min (=11.2 h). The parental bird left the nest 1.5 h after sunset and returned 3.5 h after sunrise.

Figure 5-5 Comparison of nest attendance (mean values ± SD) between groups of discriminant analysis separated for day and night time. *** p ≤ 0.001 significance from Kruskal-Wallis test; *n.s.* not significant; *n* number of nests



Even birds within the nocturnal recess group differed in behaviour in terms of complete incubation period (Fig. 5-6). Because of the high predation rate on mainland areas, only three nests of Redshanks which left their nest during night could be observed from a relatively early incubation stage until hatching of chicks. Two of the three pairs (Fig. 5-6a, one pair shown) changed their behaviour half way through incubation. Prior to more constant nest attendance, the last long recess for each pair during the night was shown on the 12th and 13th day of incubation respectively. After this the nests were also incubated at night. On the other hand, the third pair (Fig. 5-6b) continued with nocturnal recesses during the whole incubation period.

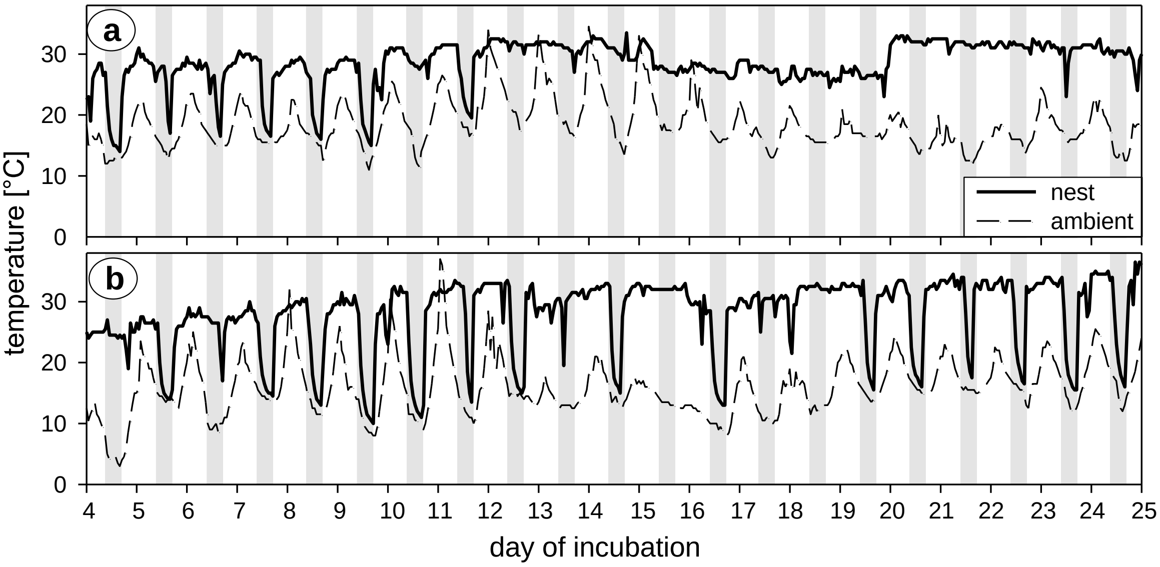


Figure 5-6 Temperature curves of two nests of Common Redshanks from *Idagroden*. Nest temperature and ambient temperature are shown for day 4 after clutch initiation to day 25. Night time is indicated by dark bars. Both nests were unattended at night during the first half of the incubation period. Birds in **a** changed behaviour from 13th day and incubated their nest during night, while birds in **b** continued with nocturnal recesses till the end of the incubation period

Unfortunately the sample size was too low to statistically compare the hatching success between nests with and without nocturnal incubation recesses. At *Petersgroden* site, five nests with data loggers were inside nest enclosures, which were used to protect some nests from predation for a separate study. Those nests could not be used for hatching success analysis because of the non-natural predation risk. Of the remaining 15 nests without nest enclosures at this site, two of these nests showed nocturnal incubation recesses and were depredated. However 10 out of 13 continuously incubated nests also failed due to predation. On the other hand, nests which were abandoned during the night at *Idagroden* and *Beckmannsfeld*, 1 out of 3 and 1 out of 2 respectively, failed. For the continuously incubated nests 3 out of 7 and 2 out of 6 (*Idagroden* and *Beckmannsfeld* respectively) were unsuccessful.

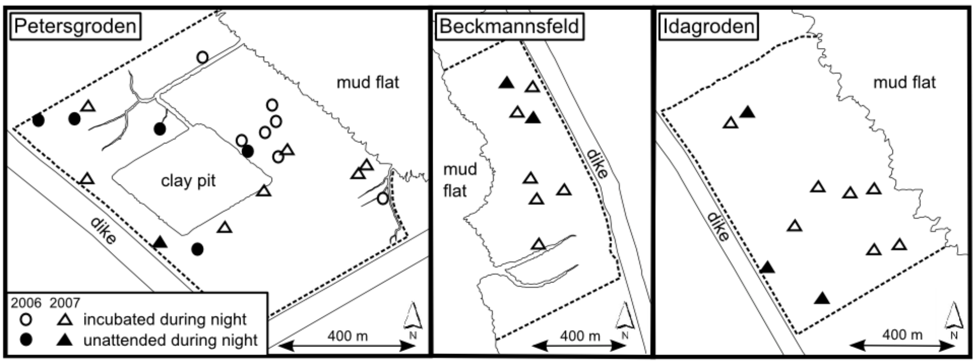


Figure 5-7 Locations of Common Redshank nests on the mainland distinguishing between nests which were unattended or incubated during night time. Dotted line indicates border of study area. Note that nests unattended during night are located relatively close to the dike compared to continuously incubated nests

The behavioural trait of leaving the nest unattended during night was only found on the mainland study sites. On the island *Wangerooge* none of the observed breeding pairs showed these nocturnal recesses. Nests which were unattended during night-time were located closer to the dike than other nests incubated at that time (Fig. 5-7). At *Petersgroden* the mean distance from the dike to nests with nocturnal absence was 225.5 ± 146.2 m (n = 6) and thus, significantly shorter (p = 0.012, U-test) than the other nests, which were 462.6 m ± 182.3 m (n = 14) away from the dike. On the two other mainland study sites the sample size was too low for a statistical analysis of nest distribution and distances to the dike.

Discussion

Incubation behaviour of birds can be influenced by a wide range of factors such as uni- or biparental incubation, stage of incubation or climatic circumstances (SKUTCH 1962). In the case of Redshanks, parental birds share incubation (GROßKOPF 1958; STIEFEL & SCHEUFLER 1984; HALE 1988), therefore nest attendance should be relatively high, because there is no need to leave the nest unattended for foraging. DEEMING (2002) reported for 24 biparental incubating species with precocial and semi-precocial young, an average nest attendance of 95.2 ± 5.5 % with two thirds of these species showing attentiveness of 95-100 %. For instance the nests of Semipalmated Sandpipers *Calidris pusilla* (also a biparental incubation species) were incubated 99.5 % of the time (CRESSWELL et al. 2003). Grey Plovers *Pluvialis squatarola* breeding in the Russian Arctic incubated their nests 97 % of the time (EXO & STEPANOVA 2000). Curlew Sandpipers *Calidris ferruginea* and Pectoral Sandpipers *Calidris melanotos* with only female incubation show a nest attendance of approximately 82 % (CRESSWELL et al. 2004; TULP & SCHEKKERMAN 2006). However, it should be noted that in these arctic breeding shorebirds egg heat loss plays an important role (ANDREEV 1999). Studies on other waders breeding in the temperate climatic zone found that e. g. Black-tailed Godwits and Lapwings incubate their clutches 89 % and 86 % of the time respectively (HEGYI & SASVARI 1998), though these results were based on direct observations and thus include only daytime incubation data. Investigations with nest cameras at Lapwing nests have also indicated a nest attendance of 84 % (JONGBLOED et al. 2006). GUNNARSSON (2002) found by measuring nest temperature, that Redshanks breeding in Sweden incubated 89 % of the time.

The studies mentioned above measured nest attendance more frequently, and therefore careful interpretation is required when comparing the results presented here with other studies of incubation behaviour. The nest attendance values from our study may be slightly overestimated as short recesses were not accounted for. The average nest attendance by Redshanks of 77 % reported in this study is comparatively low, particularly if this value is indeed overestimated. However, the apparent low average nest attendance of 77 % was mainly caused by a very low nest attendance of 70 % at *Petersgroden*, which was the area with the highest predation rate. Here most nests were found and included in the analysis and thus had a high impact on the average value. We expected decreased predation risk to increase nest attendance and we found that in areas with a low risk of nest predation parental birds did indeed spend more time incubating their nests. On the island *Wangerooge*, where nest predation risk was very low, mean nest attendance of Redshanks was about 87 % and similar to results found in (GUNNARSSON 2002). On the mainland study sites, *Beckmannsfeld* and *Idagroden*, with a medium risk of nest predation, nest attendance was approximately 80 % and thus between the values for *Petersgroden* and *Wangerooge*. We found that these wide differences in nest attendance between the island and mainland study sites were mainly caused by a few pairs of Redshanks, which left their nest unattended during night, probably to lower the predation risk for the breeding adults (see below).

Variation in predator communities

To explain these differences in incubation behaviour not only the predation risk per se should be taken into account. The predator community of the different study sites may play an important role as well, since antipredator behaviour of birds depends amongst others on the type of predator (BYRKJEDAL 1987; BURES & PAVEL 2003). On the mainland there is a wide range of potential nest predators. At the study site *Petersgroden*, where hatching success was only about 2 %, THYEN & EXO (2004) verified avian predators such as Carrion Crows *Corvus corone* as well as mammals e.g. rodents (*Microtus* sp., *Apodemus* sp., *Rattus norvegicus*), mustelids (*Mustela nivealis*, *Mustela erminea*) and Red Foxes as predators, using plasticine egg experiments. On the island *Wangerooge* no foxes or mustelids occur (JACOB et al. 2004), nevertheless there is a high number of potential nest predators including Carrion Crows and several gull species (*Larus ridibundus, L. canus, L. fuscus* and *L. argentatus*) (BÜTTGER et al. 2006). GROßKOPF (1989) reported predation on Redshank nests by hedgehogs, rats and feral cats on *Wangerooge* in the 1960s, but as the hatching success of circa 90 % reveals, nest predation played only a minor role on the island in the years of our study. Besides the lack of ground predators, a difference in the island breeding bird community compared to the mainland community may also have effects on predation risk and incubation behaviour. The presence of "aggressive" bird species may positively affect other breeding birds, even if it is a predator itself, because less aggressive birds take advantage of the anti-predator behaviour of these "umbrella species" (DYRCZ et al. 1981; LARSEN & MOLDSVOR 1992; VALLE & SCARTON 1999). Thus Redshanks on *Wangerooge* could benefit from the anti-predator behaviour of e. g. Oystercatchers and gulls (BÜTTGER 2004). In an area with such favourable breeding associations and mainly visual oriented predators, the better strategy in the presence of a potential nest robber might be sitting tight, covert in vegetation and waiting for other birds to distract or drive away the predator, resulting in the observed higher nest attendance of Redshanks on the island.

Spatial variations in incubation behaviour

The low average nest attendance on the mainland study sites was caused by just a few pairs of Redshanks. This may be an indication of higher disturbance by predators on the mainland, where birds spent a high percentage of time away from their nests. On the mainland sites two behavioural strategies could be distinguished; 1) some nests were unattended every night for several hours, at least in the first half of the incubation period and 2) other nests were incubated most of the night-time. However, no interrelation between these differences in behaviour and the date of clutch initiation was found. This was to be expected, since higher quality and more experienced Redshanks start breeding earlier in the season (GROßKOPF 1970; THOMPSON & HALE 1991). Instead, there is a spatial distinction associated with these two behavioural strategies. The behavioural trait of leaving the nest unattended during the night was only found on the mainland and here mainly on nests located closer to the dike. These upper parts of the salt marsh are potentially more reachable by ground predators, e.g. Red Foxes and mustelids. Since these predators are often active during night (LANGE et al. 1994) the nocturnal absence of the adult birds might be an indirect nest protection behaviour that reduces cues given to predators. WOLF (1998) found that nests of inland breeding Oystercatchers were, in contrast to birds breeding in the Wadden Sea, only incubated by males during night. During that time no breeding exchanges took place, probably to reduce activity near the nest, which could draw attention of predators to the nest. However, absence from the nest not only reduces activity, but also olfactory cues available to mammalian predators. RENEERKENS et al. (2002) have shown that Redshanks, as with other sandpipers, reduce their own scent during incubation periods by switching from monoester to diester preen waxes. Although the birds emit some smell, the strength of this signal to predators is lessened and therefore absenteeism seems not primarily be due to "scent-avoidance" behaviour.

Current versus future reproduction

Incubation during night also means a high predation risk for adult birds. Even though a well concealed nest may be an advantage in the presence of visually oriented predators, the reduced visibility can lead to an increase in predation risk for the incubating bird (GOTMARK et al. 1995), especially by olfactory oriented predators. By leaving the nest unattended during night the adult birds potentially put their own survival before reproduction of offspring. The life-history theory predicts, that animals optimise their reproductive effort to increase their lifetime reproductive success, which may result in a trade-off between current and future reproduction, especially in long-lived species such as Redshanks (WILLIAMS 1966; BENNETT & OWENS 2002). That means, if the reproductive costs in the current breeding season lead to a decline in future reproductive output (e.g. by an enhanced adult mortality), then the optimal effort in the current season is less than the effort which would maximise the number of young produced in that season. Thus, Redshanks breeding in areas which are more accessible for ground predators may react to higher and varied predation risk by leaving the nest unattended during night. Therefore, this kind of behaviour is not considered as an avoidance of egg predation, but as avoidance of direct mortality of adult birds.

There was no relationship between these behavioural patterns and the date of clutch initiation, which was assumed to be related to breeder quality and/or experience. This may indicate that it is difficult to assess the risk of predation when occupying a territory. This is possibly due to the fact, that predation risk is highest later in the breeding season (THYEN & EXO 2005). Furthermore, after arriving in the breeding area, even territorial birds spend a major part of their time on foraging grounds until the beginning of egg laying (GROßKOPF 1959). It is therefore possible that the birds have no information on the presence of nocturnal predators prior to breeding. At the onset of incubation, the birds may have to “face” a trade-off between reproduction and survival. Parental birds performing these nocturnal recesses may take lower risks to themselves, but also reduce the chance to breed successfully.

For the current hatching success, nocturnal absence may have negative consequences by increasing the risk of egg predation, since the unattended nest is accessible for small mammal predators, which may take advantage when parents are absent from the nest (BLIGHT et al. 1999). Furthermore, any absence from the nest may negatively affect egg temperature and subsequently embryo development (e.g. WEBB 1987). Even if the heat loss from eggs is slower in tall vegetation (KIM & MONAGHAN 2005), the egg cooling caused by such long recesses may lead to delayed chick hatching. This might result in a higher predation risk, as the time the eggs are exposed to potential nest predators increases (CONWAY & MARTIN 2000).

Temporal variation in incubation patterns

We found that Redshanks increased nest attendance as incubation advanced. This may result from the fact that avian embryos become less tolerant to cold temperatures as they develop (BATT & CORNWELL 1972). Similar patterns were also recorded for Ruffs *Philomachus pugnax*, where nests were incubated 83.3 % of time in the first week of incubation and up to 89.6 % in later incubation stages (SCHEUFLER & STIEFEL 1985). Other studies have not shown any correlation between stage of incubation and percentage of time nests were incubated, e.g. for Lapwings and Black-tailed Godwits (HEGYI & SASVARI 1998). The strong increase in nest attendance found in Redshanks from approximately 60 % at the beginning of incubation up to 94 % a few days before chick hatching, was caused by those birds, which left their nest unattended during night. Some of these changed their behaviour in later incubation stages and were present at the nest during the night as well. Thus, these parental birds appear to take higher risks to lower any exemplified negative effects of nocturnal absence as incubation progressed, probably as a consequence of decreasing re-nesting potential within the current breeding season. Furthermore the already provided investment and increasing probability that the eggs will hatch enhances the reproductive value of the offspring (MONTGOMERIE & WEATHERHEAD 1988).

Conclusion

The present study shows, that the behavioural trait of leaving the nest unattended during the night, was mainly performed by incubating adult Redshanks breeding in high risk areas. Thus it appears to be an adult prevention predation tactic rather than egg predation avoidance, since this strategy may have negative effects on hatching success by increasing the risk of nest predation. CRESSWELL (2008) reviewed the non-lethal effects of predation in birds and emphasised the impact these effects may have. There the main focus was on foraging costs caused by avoiding predation, leading to reduced resources for long-term survival or reproduction. Our study shows another potential example of indirect effects of predation, however here we found that the behavioural trait of nocturnal absence from the nest may directly reduce reproduction and thus fitness of these individuals. In terms of the trade-off between current and future reproduction, more data are needed to prove that in fact nocturnal incubation recess behaviour is primarily due to predation risk, and also to make predictions about the fitness consequences of such modifications in the incubation patterns under high predation risk.

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Influence of soil compaction on terrestrial invertebrates in salt marshes

Introduction

Salt marshes comprise habitat for a large number of specialized invertebrate species (FORD et al. 2013). Invertebrate communities on salt marshes can be influenced by many environmental factors such as flooding frequency, soil grain size, soil moisture, bulk density of the soil, plant species composition and vegetation structure. Some of these factors can, in turn, be influenced by the management of salt marshes. Grazing of salt marshes alters bulk density, soil aeration, plant species composition and vegetation structure. The majority of salt marsh arthropods respond to grazing management (VAN KLINK et al. 2013). Within this project, the most important factor influencing the number of terrestrial invertebrates on salt marshes was grazing by livestock. On grazed sites, invertebrate numbers were significantly lower than on mown or fallow sites (Kruskal-Wallis chi² = 92.85; $p < 0.001$; Figure B-1). It has been suggested that the effects of livestock grazing on plant species composition and vegetation structure lead to changes in the invertebrate community (VAN KLINK et al. 2013). As we found only minor changes in vegetation structure and plant species composition on the moderately grazed sites, as compared to mown or fallow sites (see chapter 3), we expect that soil compaction by grazing cattle is the main reason for the lower invertebrate numbers on grazed sites. When large livestock walk on the clay-rich sediments, it can increase the bulk density (FORD et al. 2013). Compaction of soil by grazing cattle can lead to less suitable habitat conditions for invertebrates, thus resulting in lower invertebrate numbers as found at our study sites.

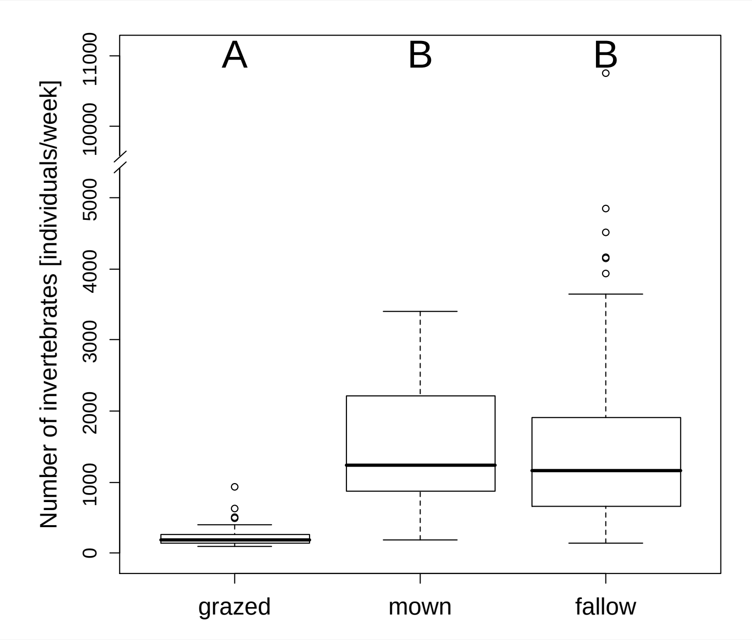

Figure B-1 Numbers of invertebrates caught with pitfall traps (within one week in spring) on salt marshes with three different types of land management. Capital letters show significant differences between categories of land management ($p < 0.001$)

Method

In order to test the effects of livestock grazing on bulk density and consequent effects on invertebrate numbers, measurements of soil resistance to penetration were taken at all locations where invertebrate numbers had been recorded with pitfall traps (see chapter 6 for information on pitfall trapping method). The measurements of penetration resistance were performed on three different dates (04-06-2009, 25-06-2009 and 07-07-2009) at each pitfall trap. Penetration resistance was measured in kilo-Newton per square meter (kN/m²) using a pocket penetrometer (CL 700A). Additionally, I conducted measurements of soil moisture using a frequency domain sensor (ThetaProbe Soil Moisture Sensor ML2x) in order to control for the effects of soil moisture on terrestrial invertebrate numbers. Sites with high soil moisture were excluded from correlation analyses with invertebrate groups showing decreased abundances on those sites.

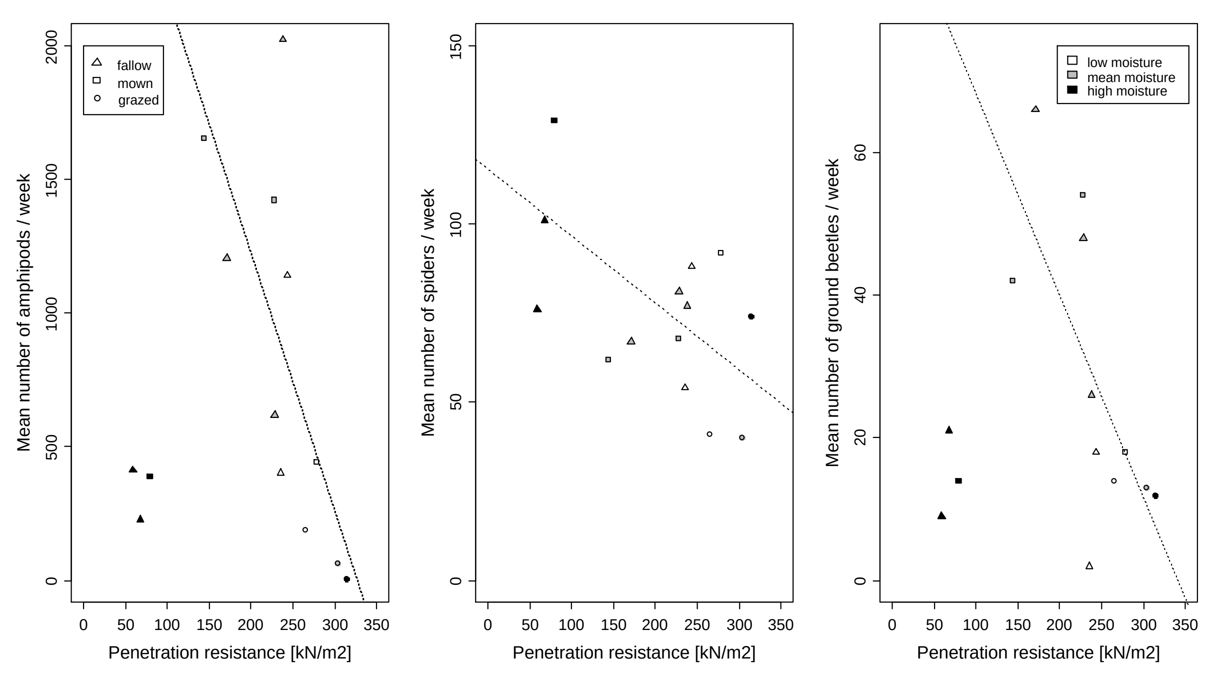

Figure B-2 Correlation of soil penetration resistance with numbers of amphipods (R² 0.45), spiders (R² 0.30) and ground beetles (R² 0.43). Sites with high soil moisture were excluded from correlation analyses with amphipods and ground beetles.

Results

The numbers of amphipods, spiders and ground beetles were significantly correlated with the penetration resistance of the soil (Fig. B-2). Not only penetration resistance but also soil moisture influenced the abundance of amphipods and ground beetles. On sites with the highest soil moisture, only few amphipods and ground beetles were present. The highest penetration resistances were measured on grazed soils (Table B-1).

Table B-1 Soil penetration resistance for different management types

	Mean ± SD [kN/m²]	**Range [kN/m²]**	**N**
fallow	177 ± 82	59 – 243	7
mown	182 ± 88	79 – 278	4
grazed	294 ± 25	265 – 313	3

Conclusion

Strong evidence was found that livestock grazing of clay-rich salt marshes can lead to soil compaction, which in turn has negative impacts on the frequency of specific invertebrate groups. In this study, penetration resistances higher than 278 kN/m² were found only on grazed sites. As numbers of amphipods, spiders and ground beetles show a correlation with penetration resistance, it can be shown that high soil penetration resistances impact the invertebrate communities and may explain the low numbers of invertebrates on the grazed sites. Although grazing can help to increase the species richness of plants on salt marshes (ANDRESEN et al. 1990), this is not always true for invertebrate (RICKERT et al. 2012). On clay-rich salt marshes, the impact of grazing on bulk density has negative effects on the numbers of invertebrates and this should be considered whenever grazing is applied as a management tool on clay-rich salt marshes.

Chapter 6

Dilemma of quantity versus quality for invertebrate-feeding birds on salt marshes

MARTIN MAIER, ROBERT BIEDERMANN & JULIA STAHL

Summary

For reproduction of coastal birds on salt marshes, the local food supply is a key factor for breeding success. For chicks, the highest demand on energy for growth and maintenance occurs during the period from hatching to fledging. It is especially crucial for precocial chicks on salt marshes that feeding locations provide enough prey to supply their energetic needs. We studied the foraging condition on salt marshes along the mainland coast of the Wadden Sea. These salt marshes are important breeding sites for a wide range of coastal bird species.

Studies on breeding birds that forage on terrestrial invertebrates very rarely take energetics into account, although this is a commonly used value for studies on foraging in herbivores and invertebrate-feeders on mudflats. In this study, we aim to give insight into the foraging quality of salt marshes for invertebrate feeders by analysing of the abundance of potential prey and their energy content.

We measured the energy content for different size classes of the most abundant invertebrate prey groups on mainland salt marshes. Based on this study, we show that salt marshes provide foraging locations differing in availability of total energy and quality of prey. We found a range of invertebrate communities from those rich in insects and spiders to those dominated by amphipods. High abundance of invertebrates on salt marshes does not always translate into high-quality foraging habitats. The quality of food (measured as energy per gram dry weight) was negatively correlated with the total energy (sums of energy per week). Thus, either very high abundances of low-quality prey or low abundances of high-quality prey were available on the salt marshes we studied. The ultimate profitability of a site, which depends upon a trade-off between quantity and quality, is predicted to be highly influenced by the foraging behaviour of chicks and therefore, to be species-specific.

Introduction

The salt marshes along the coast of the Wadden Sea are important breeding areas for a wide range of breeding bird species (KOFFIJBERG et al. 2006). Through the establishment of three German national parks along the coast of the Wadden Sea, agricultural intensification of these coastal salt marshes was prevented in contrast to the situation of inland grasslands. While inland breeding populations of waders have declined significantly with the intensification of agricultural land use (ROODBERGEN et al. 2012), the breeding populations of some species on coastal salt marshes have remained stable or even increased (HÖTKER et al. 2007). This development has significantly increased the importance of salt marshes for some coastal bird species and nowadays, these salt marshes within the national parks act as important refuges in a landscape dominated by intensive agriculture (EXO 2008; THYEN et al. 2008).

To ensure that successful reproduction of coastal birds continues in this important habitat, an understanding of the factors that influence breeding success is needed. In addition to predation (LANGGEMACH & BELLEBAUM 2005, chapter 4 and 5), the local food supply is the key factor for breeding success on salt marshes. Recent declines in meadow birds have not been caused by low adult survival but rather by decreased reproductive output (ROODBERGEN et al. 2012). Therefore, it is important to gain insight into the foraging conditions available for chicks of coastal bird species on salt marshes. During the period from hatching to fledging, the highest energy demands are made by the young for growth and maintenance. This period is regarded as an energy bottleneck in the breeding cycle (WEATHERS 1992). It was shown by AUSDEN & BOLTON (2012) that although adult Black-tailed Godwits *Limosa limosa* fed in pools, the main food source of Black-tailed Godwit chicks were terrestrial arthropods. As precocial chicks forage on salt marshes, the abundance of potential prey items and their energy content are crucial for the breeding success of many coastal bird species. During chick rearing, the abundance and accessibility of terrestrial invertebrate prey on salt marshes must supply enough energy for the survival and growth of chicks. Food shortages can manifest directly through poor chick growth and lower survival of chicks (SCHEKKERMAN & BOELE 2009) or indirectly through changes in behaviour that also can lead to higher mortality (NEWTON 2004).

Analysing the energy contents of prey items is important for studies on the forage conditions for breeding birds. Only analysing the biomass of potential prey is not sufficient. For herbivores, plant nitrogen content is often used as a proxy for the nutritional quality of plant material (VAN DER WAL et al. 2000; HARTLEY & JONES 2003; BOS et al. 2005a) and energy content of invertebrate prey serves as an indication of forage quality for waders on mudflats (ZWARTS & WANINK 1993). On inland grasslands, the abundance and accessibility of prey items for breeding birds is often known (SCHEKKERMAN & BEINTEMA 2007) but the amount of energy contained in prey is only rarely taken into account (BEINTEMA et al. 1991). The same holds true for salt marshes where the invertebrate communities are well known (FINCH et al. 2007; PÉTILLON et al. 2008; RICKERT et al. 2012; FORD et al. 2013; VAN KLINK et al. 2013), but information on energy contents of salt marsh invertebrates is very limited (CUMMINS & WUYCHECK 1971). Salt marshes show a characteristic arthropod community (VAN KLINK et al. 2013) with high numbers of coastal specialist species (FORD et al. 2013). By combining information on the abundance of invertebrate groups and their energy content, the suitability of salt marsh habitats for foraging birds can be evaluated. To close this gap of missing information on energetics, the energy content of invertebrate prey items on salt marshes was measured in addition to the analysis of the invertebrate communities.

In this study we aim to give insight into the foraging quality of salt marshes by analysing the quantity of potential prey and their energy content. We expect sites with high invertebrate numbers to be the most preferable foraging habitats on salt marshes, allowing for the highest energy intake during the growth period of chicks. The results of the study will enable evaluation of the foraging quality of specific salt marshes based on their invertebrate communities.

Methods

Study sites

The study took place on mainland salt marshes within the Wadden Sea National Park of Lower Saxony. Two study regions differing in land-use practice (*Jadebusen* and *Norderland* were chosen (Fig. 6-1). In the region, *Jadebusen* (53°29’N, 8°12’E), parts of the salt marshes are traditionally mown in late summer (1st of July onwards). The salt marshes in the region of *Norderland* (53°39’N, 7°18’E) are partly grazed by cattle (1 LSU per ha) from May till October each year. In both regions, fallow sites were included in the study (Table 6-1). The vegetation of the study sites reflects a typical mainland salt marsh. The upper salt marsh consisted mainly of the plant community *Agropyretum littoralis*, dominated by Couch Grass *Elymus spp.*, whereas the lower salt marshes were mainly covered with the plant communities *Puccinellietum maritimae* (*Puccinellia maritima, Limonium vulgare, Aster tripolium, Triglochin maritimum, Plantago maritima*) and *Halimionetum portulacoidis* (*Atriplex portulacoides*) (for details see MINDEN et al. 2012). In both study regions, upper and lower salt marshes were included in the study. Elevation heights of the study sites were between 0.3 m and 1 m above mean high tide.

Invertebrates – pitfall traps

We chose in total 14 sites to place pitfall traps, covering upper and lower salt marshes as well as all vegetation types present under the different land-use regimes. The locations of these sites for pitfall traps within each vegetation type were randomly generated in GIS (stratified random sampling). At each of the 14 sites, three pitfall traps with a distance of 1.5 m between them were installed. To provide information during main chick rearing period on salt marshes, sampling was done in 2007 and 2008 starting from the end of

May (23rd – 29th) till the end of June (19th – 26th). The traps were emptied weekly. We used pitfall traps (7 cm in diameter) filled one-third of the way up to the brim with a 3.7 % formalin solution and 0.1% of 'Agepon' to break the surface tension.

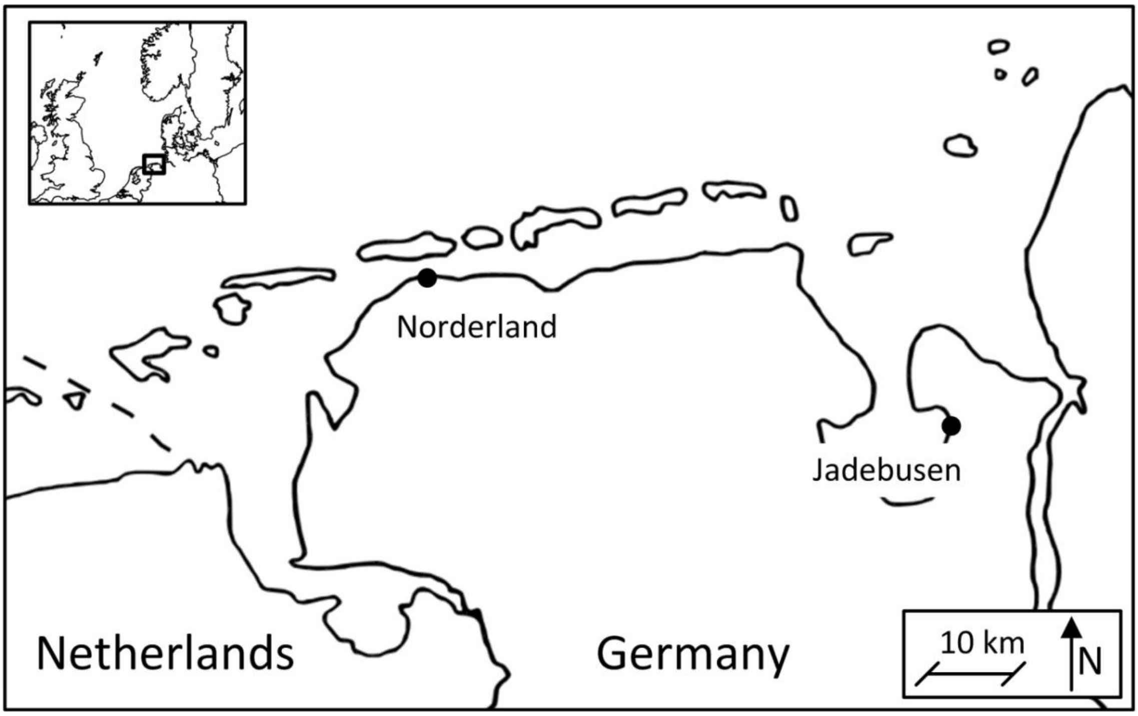

Figure 6-1 Study sites on mainland salt marshes along the German Wadden Sea coast. Black dots mark the study sites within the study regions

All trapped invertebrates were sorted, counted and determined at least to class level (for *Carabidaea*, *Malacostraca* and *Mollusca*, to family or species level). The size of each animal was measured and the material was dried at 60°C until constant weight was reached (usually after 2 days). Afterwards, the dry weight was measured and the amount of ash was determined by incinerating a weighed subsample of the material at 650ºC for 12 hours in a muffle furnace. From this, the ash free dry weights (AFDW) of the samples were calculated.

Analysis of caloric content

For analyses of caloric content (i.e. energy) the dried samples were ground and analysed in an adiabatic calorimeter (IKA C5000). The analysis of the caloric content was done with samples of at least 1 gram of dry matter. Therefore, the individuals of one systematic group within one size class per trap were pooled for the measurements. If there was not enough material to do the analysis per trap, the material was pooled for more than one trap. For less abundant prey groups or small-sized prey groups, this led to a single measurement of caloric content per prey group of one size class, even though these single measurements contained many individuals (see Table 6-2, columns *Samples for caloric analysis* and *Total no. of individuals*) and therefore gave mean values for the prey group per size class. The samples used for the analysis in the calorimeter had been analysed beforehand with NIRS (near infrared spectroscopy; Bruker MPA) to validate the measurements of the calorimeter. Values differing significantly between NIRS and calorimeter measurements were discarded from the data analyses.

Environmental information

At each site with pitfall traps, environmental information was gathered. The height above mean high tide was extracted for each trap using a digital elevation model (resolution 1x1 m, based on LIDAR data) in combination with Differential GPS measurements of pitfall trap locations. In addition, the land use of the salt marshes was noted together with the vegetation type present at the sites. The nearest distance from the sites with traps to mudflats was calculated in GIS (Table 6-1).

Table 6-1 Locations of pitfall traps with environmental information

Region	Agricultural land use	No. of vegetation types (sites)	Height above mean high tide [m]	Distance to mudflat [m]
Jadebusen	Fallow	6	0.36-0.70	7-190
Jadebusen	Mown	3	0.30-0.56	260-528
Norderland	Fallow	2	0.60-0.73	156-212
Norderland	Grazed	3	0.59-0.98	173-321

Data analysis

The sum of energy per trap per one week was calculated based on the numbers of individuals per prey group within size class and the mean caloric contents of the group analysed using the calorimeter. Energy per gram dry weight was calculated per trap as a weighted mean of joules per gram of dry weight. The mean body weights of animals per prey group and size class was used as the basis of the weighting. All calculations were based on the most detailed information available. This means that for some prey groups, the caloric content per trap was based on measurements of this single trap, whereas for other prey groups, the mean caloric content per animal was calculated based on samples from many traps if no specific value for this trap was available (see above). For mean weights per individuals, the same method was used. The calculations of required intake rates of Common Redshank *Tringa totanus* chicks were based on a digestion efficiency of 74 % (CASTRO et al. 1989), a daily food requirement of 160 kJ/day (BEINTEMA et al. 1991) and an available foraging period for chicks of 14 hours per day.

For correlations of two samples, we checked both samples for normal distribution by using the *Shapiro-Wilk* test. Based on the results, we calculated the *Pearson's* product-moment correlation coefficient for normally distributed samples and the *Spearman's* rank correlation coefficient for samples that were not normally distributed. For tests with more than two samples, we checked for homogeneity of variance using the *Fligner-Killeen* test. Based on these results, we performed an *ANOVA* (parametric) or *Kruskal-Wallis* rank sum test (non-parametric). Pair-wise comparison was done either using the *Tukey Honest Significant Differences* or *pair-wise Wilcoxon* rank sum test with *Holm* correction. All calculations and statistical analyses were performed with the help of the statistical software package, *R* (R CORE TEAM 2013).

Results

More than 253,000 individuals of invertebrate prey items were analysed in search of abundance patterns of salt marsh invertebrates and in order to calculate weekly total energetic contents per site. As not all individuals of abundant prey groups were necessary for the analyses using the calorimeter, only around 111,700 sampled prey items were combusted. Based on the calorimeter measurements, it was possible to assess the nutritional content of the most abundant invertebrate groups and prey items on salt marshes (Table

6-2).

Highest caloric contents were found in spider eggs with 25.1 kilojoules per gram dry weight (kJ/g DW), lowest amounts in woodlice with 15.9 kJ/g DW. In general, prey groups with low energy per gram showed high ash contents. Highest ash contents were present in woodlice (32 %) and amphipods (approx. 20 %).

Table 6-2 Energy amount, weight and ash content of invertebrate groups

Prey group	**Common name**	**Size class [mm]**	**Samples for caloric analyses**	**Total no. of individuals**	**kJ/g DW (+/- SD)**	**mg DW/animal (+/- SD)**	**ash % (+/- SD)**	**kJ/g AFDW**	**J/animal**
Araneae	spiders adult	< 5	2	6 431	20.2 (0.1)	0.22 (0.02)	7 (1.4)	21.6 (0.11)	4.37 (0.02)
Acari	mites	< 5	1	2 122	20.6 (-)	0.25 (-)	6 (-)	21.8 (-)	5.24 (-)
Auchenorrhyncha	leaf-hoppers	<5	1	927	19.4 (-)	0.49 (-)	5 (-)	20.4 (-)	9.42 (-)
Diptera (Brachycera)	flies	< 5	1	3 266	20.2 (-)	0.19 (-)	7 (-)	21.6 (-)	3.77 (-)
Araneae (eggs)	spider eggs	5-10	1	50	25.1 (-)	6.20 (-)	5 (-)	26.3 (-)	155.42 (-)
Isopoda	woodlice	5-10	1	287	15.9 (-)	5.92 (-)	32 (-)	21.0 (-)	94.25 (-)
Amphipoda (Orchestia gammarellus)	amphi-pods	5-10	30	12 166	18.7 (0.9)	3.22 (0.58)	20 (1.2)	22.5 (1.11)	60.31 (2.97)
Carabidae (Pogonus chalceus)	ground beetles	5-10	1	179	22.2 (-)	4.64 (-)	3 (-)	22.8 (-)	102.80 (-)
Staphylinidae	rove beetles	5-10	2	2 806	21.4 (0.5)	0.87 (0.02)	4 (0.0)	22.2 (0.37)	18.55 (0.31)
Elateridae	click beetles	5-10	2	182	19.8 (0.5)	8.04 (0.29)	3 (0.0)	20.4 (0.46)	159.33 (3.63)
Formicidae	ants	5-10	27	48 849	21.2 (2.3)	0.71 (0.14)	4 (1.5)	22.1 (2.41)	15.06 (1.65)
Diptera (Brachycera)	flies	5-10	2	562	21.7 (0.1)	3.26 (0.61)	7 (0.7)	23.2 (0.09)	70.97 (0.27)
Araneae	adult spiders	10-15	1	26	20.3 (-)	25.00 (-)	6 (-)	21.5 (-)	508.05 (-)
Amphipoda (Orchestia gammarellus)	amphi-pods	10-15	67	29 067	19.4 (0.7)	5.96 (0.96)	20 (1.9)	23.3 (0.87)	115.50 (4.29)

Table 6-2 (CONTINUED)

Prey group	Common name	Size class [mm]	Samples for caloric analyses	Total no. of individuals	kJ/g DW (+/- SD)	mg DW/animal (+/- SD)	ash % (+/- SD)	kJ/g AFDW	J/animal
Carabidae (Poecitus cupreus)	ground beetles	10-15	2	68	21.7 (0.0)	26.32 (0.62)	4 (0.0)	22.5 (0.01)	570.60 (0.24)
Cantharidae	soldier beetles	10-15	1	37	18.2 (-)	8.11 (-)	6 (-)	19.3 (-)	147.69 (-)
Amphipoda (Orchestia gammarellus)	amphipods	>15	46	4 647	17.4 (1.0)	10.34 (1.77)	22 (1.9)	21.2 (1.20)	179.49 (10.13)
Silphidae	carrion beetles	>15	1	9	20.3 (-)	63.33 (-)	3 (-)	20.9 (-)	1287.06 (-)

kJ/g AFDW (kilojoules per gram ash free dry weight) and J/animal (joules per animal) were calculated based on kJ/g DW (kilojoules per gram dry weight), mg DW/animal (milligrams dry weight per animal) and ash % (percentage of ash)
mm = millimetre; SD = standard deviation; (-) = data not available

To fulfil the energy requirement of Common Redshank chicks, 11.15 g dry weight of the very abundant *O. gammarellus* (size class 10-15 mm) was needed (Table 6-3). This energy requirement equals to an intake of 1872 individuals of *O. gammarellus* per day or 2.23 individuals per minute. The intake rates ranged for different size classes of *O. gammarellus* between 4.27 and 1.43prey items per minute. For heavy prey species with high energy, intake rates of less than 0.5 prey items per minute are possible.

Table 6-3 Required intake rates of *Orchestia gammarellus* and *Poecitus cupreus* to meet energy demands of Common Redshank *Tringa totanus* chicks

Prey	Size class [mm]	Mean dry weight per animal [mg DW/animal]	Mean caloric content per animal [kJ/g DW]	Required intake [g DW/ day]	[items/ day]	[items/ hour]	[items/ minute]
Orchestia gammarellus	5-10	3.22	18.7	11.55	3585	256	4.27
Orchestia gammarellus	10-15	5.96	19.4	11.15	1872	134	2.23
Orchestia gammarellus	> 15	10.34	17.4	12.45	1205	86	1.43
Poecitus cupreus	10-15	26.32	21.7	9.97	379	27	0.45

We assumed daily energy requirements of 160 kJ/day (Beintema et al. 1991), 14 hours / day available for feeding and a digestion efficiency of 74 % (Castro et al. 1989)

Based on the caloric measurements and analysis of prey abundance, it was possible to calculate the sum of energy per week and the amount of energy per gram of dry weight for each pitfall trap. This resulted in sums of energy ranging from 0.95 kJ/week (grazed site in *Norderland* on 20th June 2007) to 548 kJ/week (fallow site in *Jadebusen* on 16th June 2008). The highest energy value per gram dry mass found for a trap was 22.12 kJ/g DW (grazed site in *Norderland* on 14th June 2007) and the lowest was 18.66 kJ/g DW (mown site in *Jadebusen* on 13th June 2007).

As shown in Fig. 6-2, the energy sum per week was negatively correlated with the energy per gram dry weight (Spearman's rho = - 0.57, S = 1 630 006, $p < 0.001$). As the prey items caught with pitfall traps could be seen as potential prey per site, the total amount of energy caught per trap equals the potential energy available per site. This means that on sites with a high amount of available energy, the quality of prey (i.e. energy per gram dry weight) was worse than at sites with a low energy sum available per week.

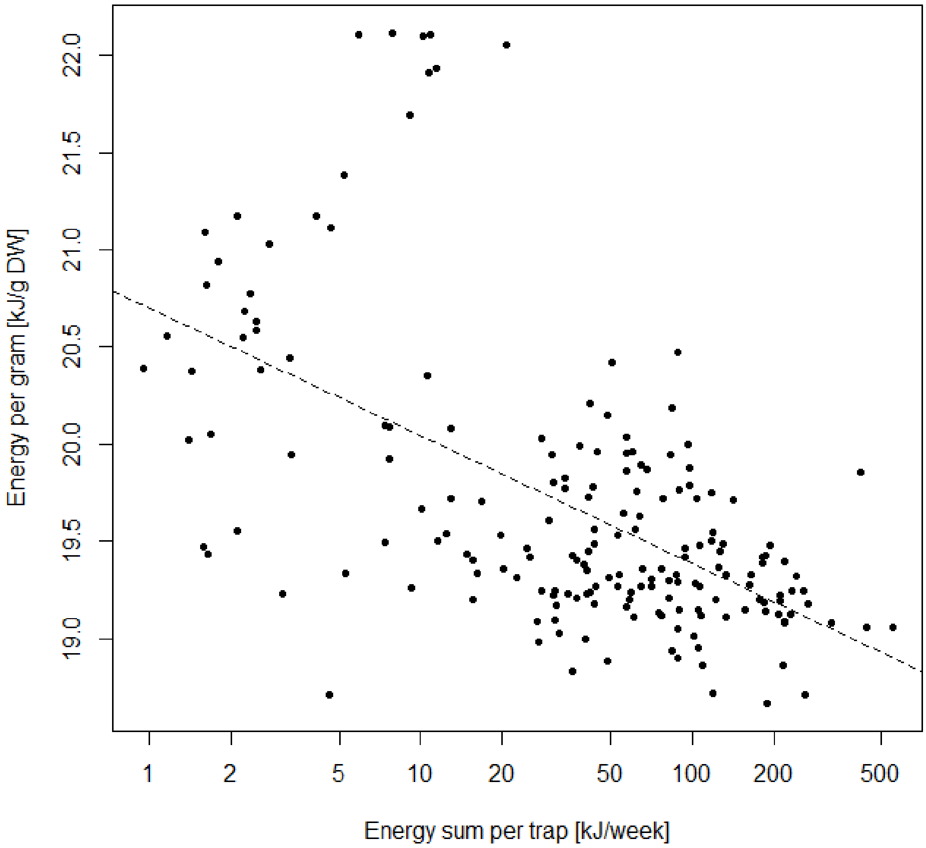

Figure 6-2 Correlation of energy sum with energy per gram of trap material, R^2 adj. = 0.33, regression line: $y = 20.70 - 0.66 \cdot \log10(x)$

To explain this pattern, a detailed look at the components making up the sum of energy per trap is necessary. Regarding the absolute abundance of prey groups, the energy sum per trap was highly correlated with the number of amphipods per trap (Spearman's rho = 0.98, S = 16 715, $p < 0.001$; Fig. 6-3A). The correlation between the energy sums and insects was weak (Spearman's rho = 0.61, S = 400 860, $p < 0.001$; Fig. 6-3B); with spiders, it was not significant (Spearman's rho = -0.01, S = 1 047 631, p = 0.903; Fig. 6-3C).

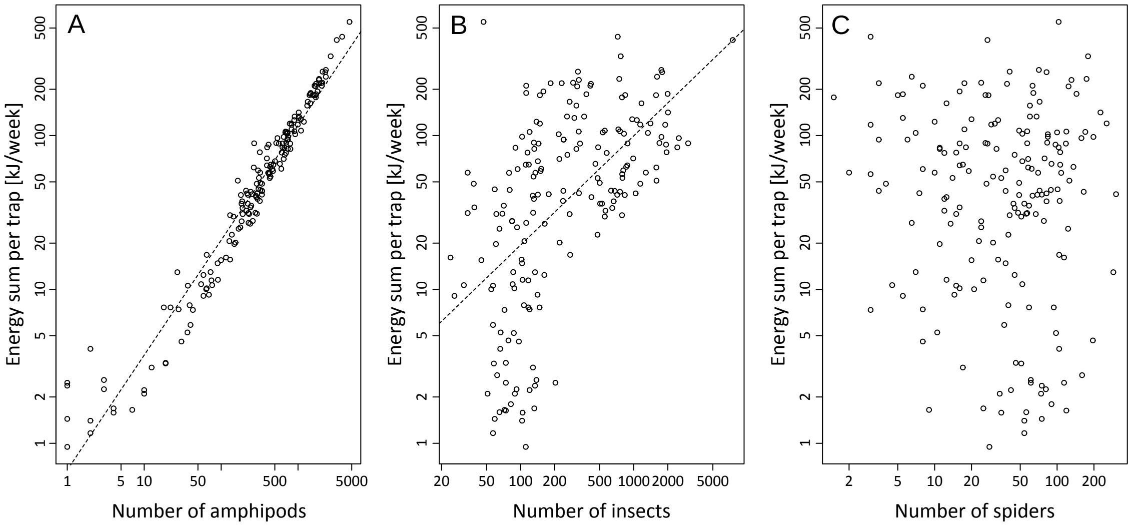

Figure 6-3 Correlation of energy sums per trap per week with abundance of invertebrate groups. **(A)** amphipods, R² adj. = 0.95, regression line: log10(y) = -0.17+0.75log10(x); **(B)** insects, R² adj. = 0.32, regression line: log10(y) = -0.13+0.71log10(x); **(C)** spiders, not significant

Regarding the relative abundance, composition of the invertebrate community showed a shift from insect- and spider-dominated communities to amphipod-dominated communities with increasing energy sums per week. The relative fraction of the different prey groups to the total number of individuals was correlated with the sum of energy per trap (data not shown). The relative abundance of amphipods were positively correlated with the sum of energy per trap (Spearman's rho = 0.67, S = 339 708, p < 0.001), whereas the relative abundance of spiders showed a negative correlation (Spearman's rho = -0.71, S = 1 774 310, p < 0.001). For insects, there was only a weak negative correlation (Spearman's rho = -0.35, S = 1 405 386, p < 0.001).

Amphipods showed significantly lower amounts of energy per gram dry weight (ANOVA, F = 58.24, df = 2, p< 0.001; mean = 18.580 kJ/g DW ± 1.244) than insects (mean = 20.870 kJ/g DW ± 2.031) and spiders (mean = 20.920 kJ/g DW ± 0.894) (Fig. 6-4). This pattern, in combination with the high abundance of amphipods on sites with high energy sums per trap (cf. Fig. 6-3), led to the negative correlation between the energy contained per gram unit mass and the total available energy, as shown in Fig. 6-2. Therefore, on sites with a high amount of available energy for foraging, the amount of energy per gram (quality of prey) was low and *vice versa*.

The availability of amphipods strongly determined the energy content of prey items on salt marshes. We found significant differences in amphipod abundance between sites with different types of agricultural land use (Kruskal-Wallis rank sum test: chi² = 80.13, df = 2, p < 0.001) and the occurrence of the successional climax vegetation (*Elymus spp.*) (Kruskal-Wallis rank sum test: chi² = 16.94, df = 2, p < 0.001) (Fig. 6-5). However, the distance to mudflats and the height above mean high tide showed no significant correlation with amphipod abundance.

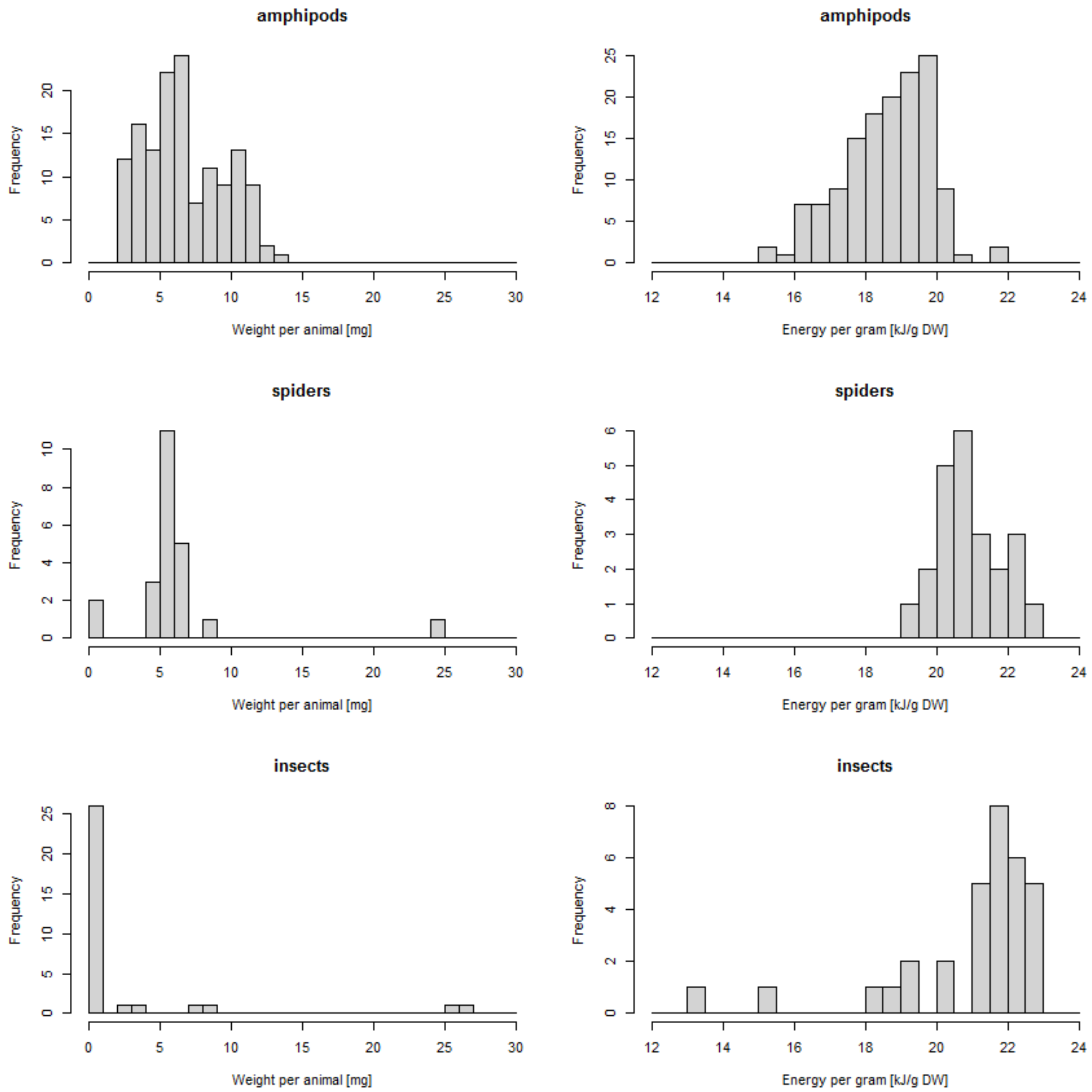

Figure 6-4 Weight per animal (left panel; ANOVA, F = 1.98, df = 2, n.s.) and energy per gram dry weight (right panel; ANOVA, F = 58.24, df = 2, p < 0.001) of three invertebrate groups

Discussion

Animals balance their energetic budget through maintaining a rate of energy intake that is able to sustain the needs of maintenance and growth (MAURER 1996). For precocial chicks on salt marshes, it is crucial that the feeding locations provide enough prey of sufficient quality to maintain their energetic needs. A lack of high-quality feeding locations precludes growth and ultimately results in starvation (SCHEKKERMAN & BOELE 2009). Low-quality foraging sites can lead to chicks with poorer body condition and less vigilant adults, which can make chicks more vulnerable to predation (AUSDEN & BOLTON 2012), and thus indirectly can result in lower reproductive output. In order to unravel the factors affecting growth and survival of chicks, detailed research on their feeding ecology and energetic needs is a crucial prerequisite (BEINTEMA et al. 1991).

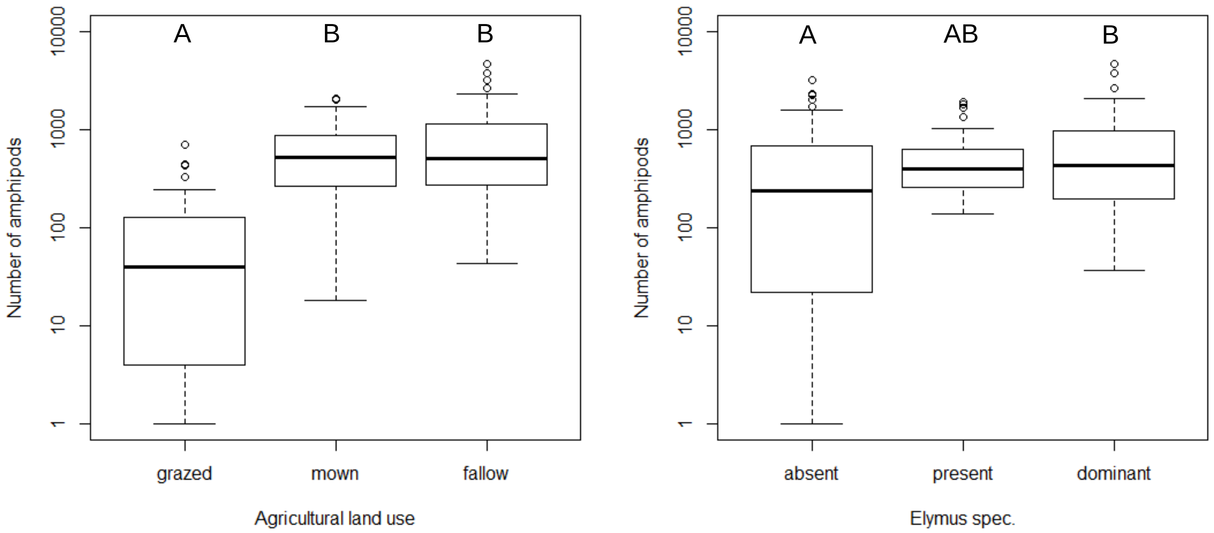

Figure 6-5 Abundance of amphipods based on type of agricultural land use and occurrence of the late successional species, Couch Grass (*Elymus spp.*); capital letters show significant differences ($p < 0.001$)

In this study, we showed that salt marshes vary largely in the total availability of energy and quality of prey. We found different invertebrate communities ranging from insect- and spider-rich communities to communities dominated by amphipods, which were mainly composed of *Orchestia gammarellus*. This strongly impacts the foraging conditions for breeding birds on salt marshes. *O. gammarellus* is a soil-burrowing and litter-fragmenting amphipod (SCHRAMA 2012). Highest abundances with up to 3,690 individuals/m² (DIAS & SPRUNG 2003) can be found on sites with tall and dense vegetation, and high litter production, which describes the situation for fallow, late successional stages on salt marshes (SCHRAMA 2012) dominated by Couch Grass (*Elymus spp.*). Thus, that the shift in invertebrate communities on salt marshes is driven by vegetation development during succession and highly influenced by abundances of *O. gammarellus*. On younger salt marshes, litter production is generally low and nutrient input is mainly from marine sources. During succession to more highly productive salt marsh plants, the system shifts from being driven by outside nutrient inputs to nutrient cycling and results in altered food webs (SCHRAMA et al. 2013b). Due to these changes in productivity, the abundance of *O. gammarellus* increases during salt marsh succession and leads to a the shift from low abundance of high-quality prey items to high abundance of low-quality prey items dominated by *O. gammarellus*. However, the succession of salt marshes leads not only to a shift in the invertebrate community but also to a change in vegetation composition and structure (chapter 3). This is likely to impact the detectability and accessibility of prey (VICKERY et al. 2001) as well as predation risk for foraging chicks (SCHEKKERMAN et al. 2009).

Due to the vast numbers of amphipods at some of our study sites, a closer look at the detectability of this prey can provide insights in foraging decisions of birds. *O. gammarellus* is active throughout the whole year (DIAS & SPRUNG 2003), but hides in vegetation during daytime (COLOMBINI et al. 2013), thus leading to possible difficulties in detection for foraging chicks. However, their movements are associated with the moisture condition of the substratum (COLOMBINI et al. 2013); on wet salt marshes in spring, *O. gammarellus* is expected to be rather mobile. This is in contrast to findings by COLOMBINI et al. (2013) on Mediterranean dune slacks where *O. gammarellus* was rather immobile. Our own field observations on the salt marshes of this study indicated that *O. gammarellus* is easily detectable in high numbers during the daytime throughout the breeding season.

For the most abundant size class of *O. gammarellus* (10-15 mm) a mean intake rate of 2.23 prey items per minute is needed to fulfil the energy requirement of Common Redshank chicks. As invertebrate groups differ in body mass and energy available per unit mass, a whole range of different qualities in prey items can be found at each study site. For *Poecitus cupreus,* which is a heavier prey species with higher energy, an intake of 0.45 prey items per minute is needed. As SCHEKKERMAN & BOELE (2009) found prey ingestion rates of up to 25 prey items per minute for Black-tailed Godwit chicks, the ingestion rates of 4 or less prey items per minute as calculated lead to the conclusion that at least some parts of the mainland salt marshes of this study are foraging sites of high quality for precocial chicks. BEINTEMA et al. (1991) postulated that chicks near fledging need to switch their diet from arthropods to earthworms, which are more profitable prey. Although the energy content of earthworms per unit mass is relatively low (19.1 kJ/g dry weight; CUMMINS & WUYCHECK 1971), they are still a profitable prey due to their high body mass. On salt marshes, there are no earthworms but the chicks can use the nearby intertidal mudflats for foraging grounds as soon as the development of the chicks allows probing for soil invertebrates.

The total arthropod density may be a poor predictor of prey availability if it includes many animals that are not prey or profitable prey (SCHEKKERMAN & BOELE 2009). Therefore, it is necessary to assess the food choice of focal breeding bird species in order to evaluate the foraging quality of a site, based on its invertebrate communities. For many waders, the diet of the adults is known (GOSS-CUSTARD & JONES 1976; CRESSWELL 1994; AUSDEN et al. 2003), whereas there is hardly any information on the food choice of wader chicks on salt marshes. Additional feeding experiments with captive Common Redshank chicks in a cafeteria design have been conducted to fill this gap, and showed that virtually all common prey groups found on salt marshes can serve as forage for growing Common Redshank chicks (KUHNIGK 2013). However, Common Redshank chicks started to reject prey of sizes less than 2.5 mm as they grew older (MAIER et al. subm.).

To better understand profitability, we used energy content instead of invertebrate abundances for the calculations in this study. General conclusions about the foraging quality of salt marshes were difficult to draw, as our data depicted large spatial differences in prey abundances and energy content. Total energy content of pitfall traps ranged from about 1 kJ/week up to about 548 kJ/week. Daily energy expenditure (DEE) of arctic shorebirds chicks ranged from 14 kJ/day (young chicks of smaller species) to 365 kJ/day (older chicks of larger species) as measured by KRIJGSVELD et al. (2012). A comparison of these DEE values with our data demonstrates that there is sufficient energy available for the energetic needs of chicks of smaller species at the better feeding locations, even with this untargeted collection of prey items. However, not only the amount of energy matters for foraging chicks but also the quality of prey items needs to be taken into account. Even with plentiful food of low nutritional value or digestibility, a bird may be unable to process enough forage to maintain its daily energy needs (NEWTON 2004). The quality of the prey in this study ranged from about 19 kJ/g dry weight up to 22 kJ/g dry weight. The caloric content of salt marsh invertebrates measured in this study did not significantly differ from results gathered in other studies (Table 6-4) and are within the theoretical range of energy values contained in organisms: 17 kJ/g dry weight up to 40 kJ/g dry weight (CUMMINS & WUYCHECK 1971).

A general finding of this study is that the quality of food (i.e. energy per unit mass) was negatively correlated with the quantity of good (i.e. total energy content available per site). Thus, either a great abundance of low-quality prey items or a low abundance of high-quality prey items were available. In order to optimize foraging decisions (high quantity *versus* high quality), it is crucial to account for the time of handling, the searching and catching effort, and also the detectability of prey as these actions require the expenditure of energy as well (MAURER 1996). The behaviour of the breeding bird species determines handling time, searching and catching effort as well as the detectability of prey. However, little is known about the foraging behaviour of precocial chicks on salt marshes because observing foraging chicks in high vegetation is very challenging (cf. Schekkerman & Boele 2009). Nevertheless, we showed that high abundances of invertebrates on salt marshes do not always translate into high-quality foraging habitats, contrary to our expectations, as the energy per unit mass of prey is generally lower on sites with high abundances of invertebrates. Therefore, the final assessment of the foraging quality of sites will strongly depend on the behavioural patterns of the different breeding bird species on salt marshes. Further research on the foraging behaviour of chicks, in combination with the results of this study, will allow for better assessment of the foraging quality of sites.

Table 6-4 Overview of caloric content of invertebrate prey found in study and from literature

Prey group	**Common name**	**This study[1]** kJ/g DW	kJ/g AFDW	**Literature** kJ/g DW	kJ/g AFDW	**Source**
Araneae	adult spiders	20.3	21.6	20.2		Cummins & Wuycheck (1971)
				23.5		Robel et al. (1995)
Acari	mites	20.6	21.8		24.3	Cummins & Wuycheck (1971)
Auchenorrhyncha	leafhoppers	19.4	20.4	21.4[+]		Southwood & Cross (2002)
Diptera	flies	21.0	22.4	24.2		Cummins & Wuycheck (1971)
				22.2		Bryant (1973)
				22.5		Southwood & Cross (2002)
				21.4		Robel et al. (1995)
					24.0	Theberge & West 1973
Isopoda	woodlice	15.9	21.0	15.9		Cummins & Wuycheck (1971)
Amphipoda	amphipods	18.5	22.4	17.0		Cummins & Wuycheck (1971)
Carabidae	ground beetles	21.9	22.7		23.7	Cummins & Wuycheck (1971)
				25.1*		Bryant (1973)
				21.4*		Southwood & Cross (2002)
				22.2*		Robel et al. (1995)
Elateridae	click beetles	19.8	20.4	22.8		Cummins & Wuycheck (1971)
Formicidae	ants	21.2	22.1	19.0		Cummins & Wuycheck (1971)
				21.4		Bryant (1973)

* mixed Coleoptera

[+] mixed Heteroptera

[1] data represent mean values for all size classes pooled together; Table 6-2 gives mean per size class and values may therefore be different

DW = dry weight; AFDW = ash free dry weight

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Chapter 7

Managing mainland salt marshes for breeding birds – a synthesis

Mainland marshes – safe sites for breeding birds?

In the second half of the 20th century agricultural intensification caused degradation and a substantial loss of suitable grassland habitats for many bird species throughout Northwestern Europe (SUTHERLAND 1996; VICKERY et al. 2001; ROBINSON & SUTHERLAND 2002). The agricultural intensification led to a conversion of wet grasslands into croplands and a rapid decline of numbers of ground-nesting birds (BURFIELD & VAN BOMMEL 2004; VAN TURNHOUT et al. 2010). Along with an advancement of mowing dates the former breeding grounds for ground-nesting birds disappeared, with effects ranging from waders to songbirds (NEWTON 2004; WILSON et al. 2005; SCHEKKERMAN & BOELE 2009; ROODBERGEN et al. 2012; SCHROEDER et al. 2012).

The mainland salt marshes of the Wadden Sea are largely of anthropogenic origin (ESSELINK et al. 2009). The development of the marshes has been promoted with the help of sedimentation fields and ditching (STOCK 2011). These man-made salt marshes differ in morphology to natural ones (i.e. island salt marshes), especially due to their artificial drainage patterns (CWSS 2010). Through land reclamation and shortening of the coastline for coastal protection, the formerly extended salt marshes have been reduced to a narrow band of open habitat in front of the seawall (ESSELINK et al. 2009). In contrast to inland grasslands, no agricultural intensification took place on salt marshes. Salt marshes may therefore act as safe sites for breeding birds with regards to threats originating from modern agriculture. Although the risk for breeding birds due to modern agriculture is not comparable to inland grasslands, with respect to climate change salt marshes can be a risky environment for breeding birds: the impact of storm surges and sea level rise is high. This study demonstrates increased flooding risks for nests of many breeding bird species on Wadden Sea salt marshes (chapter 2). This risk is expected to further increase with progressing climate change. Higher flooding risks will lead to increased nest losses if breeding birds are unable to behaviourally adapt to the changes in abiotic dynamics. Studies along the Dutch coast show that birds preferentially select elevated parts of the marsh as nesting sites under high flooding risks (KOFFIJBERG et al. 2013). This leads to the expectation that breeding birds may be able to avoid flooding with changes in nest site selection. Therefore, adaptive management of salt marsh sites is necessary to develop breeding habitats of high quality at the higher parts of salt marshes. At present, the higher parts of the mainland salt marshes are dominated by successional climax stages (mainly Couch Grass communities) and make it impossible for many breeding birds to use these higher elevated parts as nesting sites.

Management objectives of mainland marshes

The salt marshes within the Wadden Sea are strongly protected under European and national conservation acts (CWSS 2008). But for a successful conservation within protected sites, the management plays a governing role (COOK et al. 2010). The management aims for salt marshes within the Wadden Sea have changed dramatically in the past: agricultural exploitation and land reclamation have ceased in favour of nature conservation purposes, whereas on parts of the coast are managed for coastal protection (ESSELINK et al. 2009). The Wadden Sea Plan (CWSS 2010) states that the management and nature conservation policy within the Wadden Sea is directed towards the creation of natural and sustainable ecosystems, in which natural processes proceed in an undisturbed way. This means that ecosystems contain the full range of natural and dynamic habitats showing natural dynamics, presence of typical species, but also absence of disturbance and pollution (CWSS 2010). To reach this goal for salt marshes, the following targets are set within the Wadden Sea Plan for salt marshes: further increase of the surface area of natural and dynamic salt marshes, increase of natural morphology and dynamics, improvement of natural vegetation structure of artificial salt marshes through further cessation of intensive grazing, reduction of artificial drainage in salt marshes without any agricultural use, and de-embankment of summer polders where this is appropriate and compatible with the needs for coastal flood defence and protection (CWSS 2010).

On salt marshes where the natural dynamics are low and no management in form of mowing or grazing is present, the salt marsh succession leads on higher elevated parts to a domination of Couch Grass *Elymus athericus* and *Elymus repens* (BAKKER et al. 1993), the climax stadium of salt marsh succession. This kind of ageing of salt marshes is often present on salt marshes with high sedimentation rates (CWSS 2010), as sedimentation is the main source of nutrients to salt marshes and salt marsh plants. The nitrogen pool in the topsoil increases by 43 g/m² with every centimetre of silt added through accretion (OLFF et al. 1997). Accretion rates measured on mainland salt marshes ranged from 5.4 to 34.6 mm/year and showed great differences between and within salt marsh sites (NOLTE et al. 2013). Nevertheless, with such accretion rates, mainland salt marshes are a naturally nutrient rich system, favouring successional processes leading to tall and dense vegetation stands dominated by few species. Management of salt marshes can slow down the process of aging and can support the biodiversity on salt marshes (BAKKER et al. 2005). In the Netherlands and Denmark, objectives of management for nature conservation are focussed on the preservation of biodiversity. In order to halt vegetation succession, livestock grazing is advocated in these countries, especially in the man-made mainland salt marshes, whereas in the German national parks the undisturbed course of natural processes is by law the declared prime objective (ESSELINK et al. 2009). The foundation of the German Wadden Sea national parks therefore came along with drastic changes in salt marsh management. In Lower Saxony the size of intensively grazed salt marshes declined from 23 % in the 1980s to 4 % in 2003 (KOFFIJBERG et al. 2006).

Managing marshes for breeding birds

The impact of changes in salt marsh management on breeding birds and their number is largely unknown (WOLFF et al. 2010). In this project the effects of management on the three main habitat properties for breeding birds on mainland salt marshes were studied. The focus was set on vegetation structure, predation risk and food availability. In addition the changes in flooding risk of nests due to climate change were assessed. Fig. 7-1 shows a conceptual framework of the main effects of management on habitat quality for breeding birds. Management measures impact the abiotic properties, vegetation and fauna of salt marshes. These impacts result in changes of the main habitat properties for breeding birds, altering the nest site selection.

This project showed that management on salt marshes can have a direct impact on bulk density, vegetation structure, invertebrate abundance and risk of nest predation. To enable management on salt marshes, a functioning drainage system is necessary, which accelerates the succession (VEENEKLAAS et al. subm.) and the accessibility of the salt marshes for mammalian predators. But the main and most obvious impact of management is on the vegetation structure. The strength of the impact of management on the vegetation structure depends on the vegetation type (chapter 3). Significant changes due to management in most vegetation types were found for canopy height and sward density. The vegetation structure is important for breeding birds on salt marshes. By the vegetation structure the nest concealment is altered, which is one of the main factors to influence the predation risk of well concealed ground nests, but also the search patterns of predators are influenced by vegetation structure, resulting in changed predation pressure (chapter 4). In vegetation with low canopy, highest nest predation rates were found. High predation risk resulted in changed behaviour of breeding birds. Breeding Redshanks showed adaptation to high predation risk with lower nest attendance during night, compared to sites where predation risk was low (chapter 5).

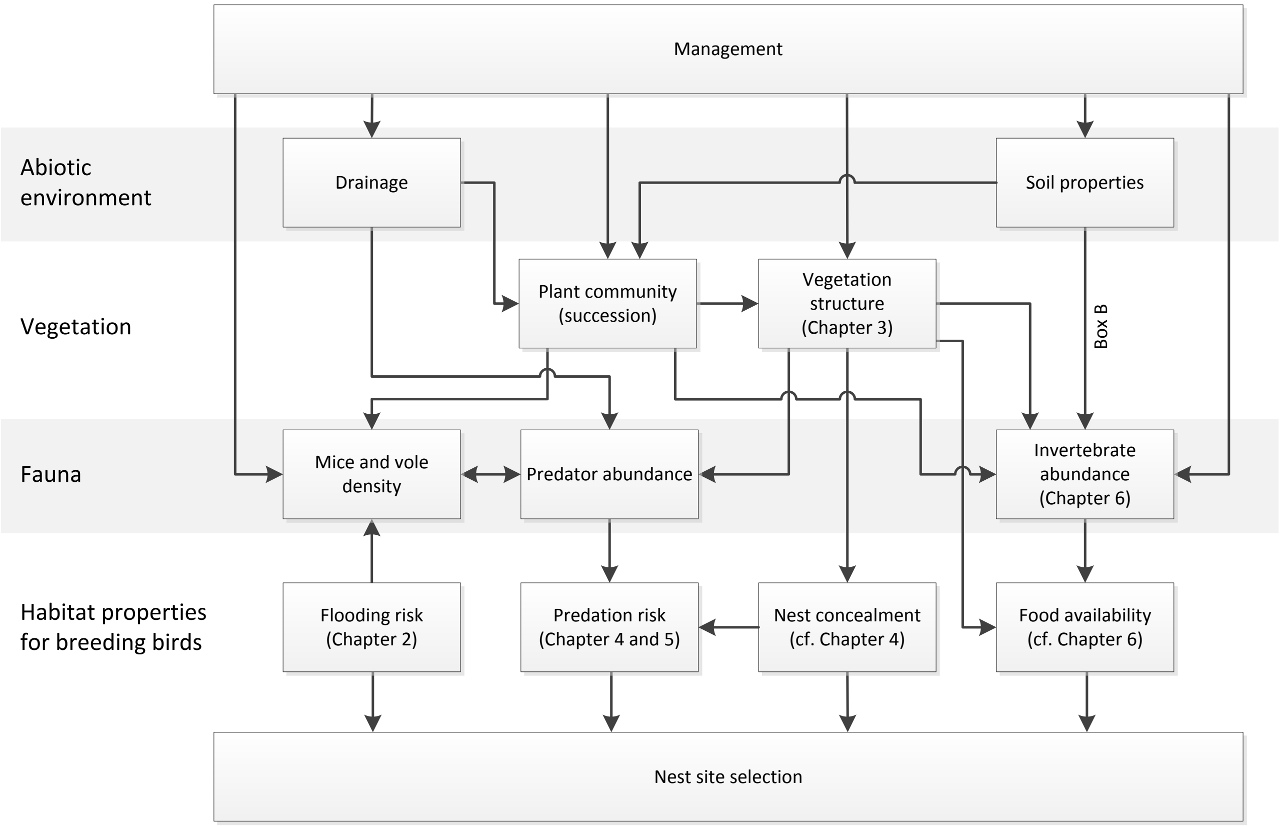


Figure 7-1 Conceptual model of management effects on habitat properties for breeding birds on salt marshes

Another effect of changes in vegetation structure is on the abundance of invertebrates and the accessibility of invertebrate prey for breeding birds. The composition of the invertebrate community is the main driver for the food availability for invertebrate feeding chicks on salt marshes (chapter 6). The invertebrate community is altered by management and the occurrence of Couch Grass. We found high numbers of potential prey of low nutrition quality in Couch Grass vegetation and low numbers of potential prey but of high quality when Couch Grass was absent. The shift between these two stages in invertebrate numbers and quality is mediated by salt marsh succession. Grazing can slow down the succession but on clay rich soils grazing can result in soil compaction and a decrease in numbers of some invertebrate groups (Box B).

Orchestia gammarellus, a soil-burrowing and litter-fragmenting amphipod, is responsible for the changes in invertebrate community on salt marshes with proceeding succession. The abundance of this amphipod is strongly dependant on the plant community and therefore the successional stage of salt marshes. Main occurrence of *O. gammarellus* is in tall and dense vegetation with high litter production, which describes the situation for fallow, late successional stages on salt marshes dominated by Couch Grass (SCHRAMA 2012). With highest abundances of *O. gammarellus* in this vegetation and the low-quality of this prey, the late successional stages show a high abundance of low-quality prey items (chapter 6).

Our calculations for prey energetics (cf. chapter 6) only hold true, if diet choice of breeding birds is congruent to the available prey. To assess diet choice for foraging wader chicks, we performed feeding choice experiments with three Redshank chicks. Indeed, all prey types collected on salt marshes were used. However, chicks selected for bigger prey items as soon as different size classes were on offer. Still, smaller prey groups were taken, if no bigger prey was available. The preference for bigger prey increased with the age of chicks. Near fledging age, the very small prey items (< 2.5 mm) were not used any more (Fig. 7-2).

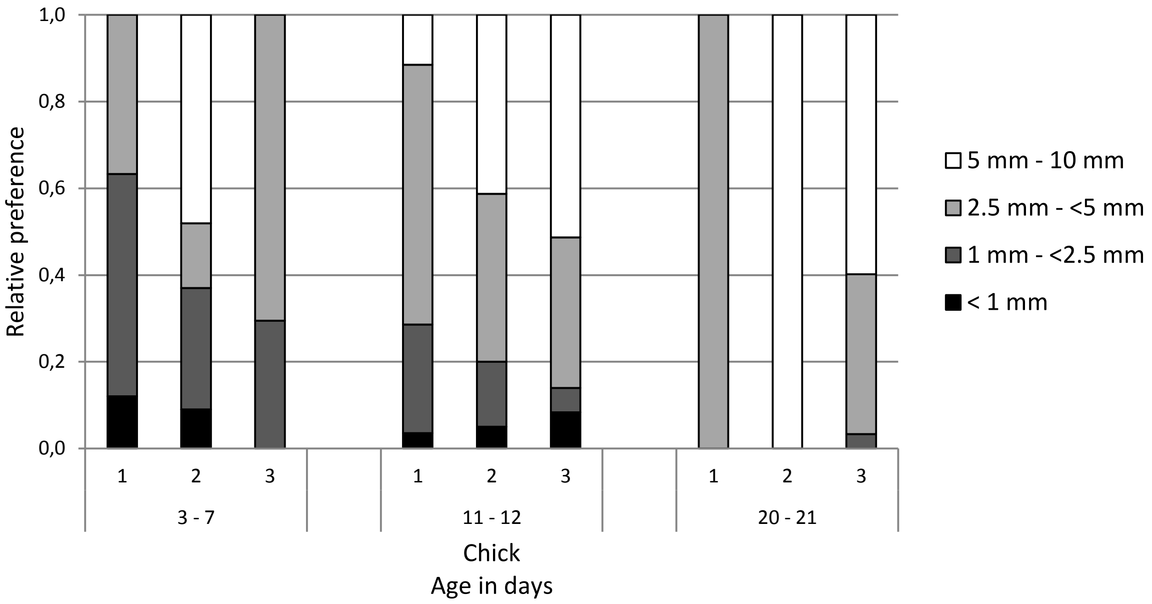


Figure 7-2 Relative preferences (sum of preferences per chick equals 1) for different size classes of prey per Redshank chick and age of chicks

Predation is the main cause for nest losses on mainland salt marshes (cf. chapter 5). Food availability can trigger predation on chicks. Low food availability leads to hunger of chicks and increased begging intensity which in turn can lead to higher predation rates (EVANS 2004). Therefore, on fallow sites low forage quality of invertebrates may increase predation risk, whereas the higher canopy of fallow salt marshes will at the same time reduce the predation risk. We found that adult Redshanks try to prevent predation with nocturnal absence from their nests under high predation risk. This behaviour is more often present near to the seawall than further away and illustrates the high impact of nocturnally active mammalian predators, which enter the salt marshes from behind the seawall (Fig. 7-3, for details see chapter 5).

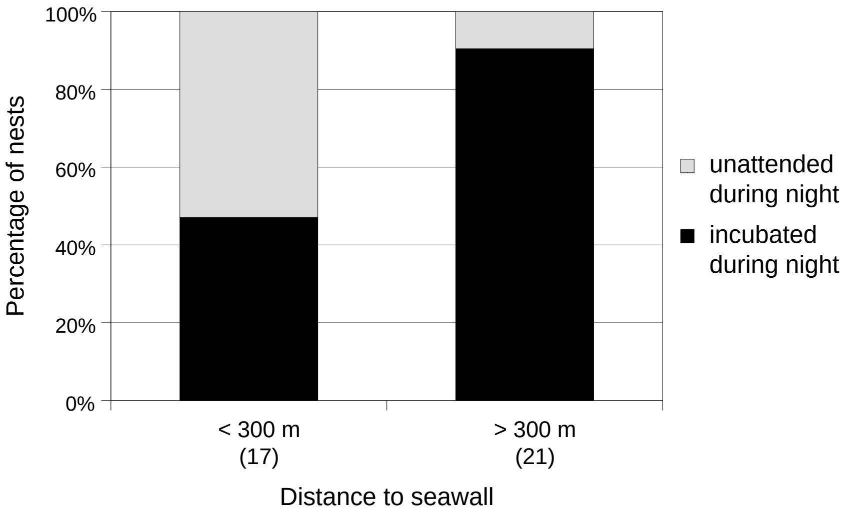


Figure 7-3 Incubation patterns of Redshank in different distances to the seawall

The artificial nest study supports this finding on fallow salt marshes, where our data indicate an effect of distance to seawall on predation pressure (chapter 4). But it should be noted that the general importance of nocturnally active mammalian predators was not proven by our artificial nest experiments, where only a very small number of predation events were evidently connected to mammalian predators. However, as many predation events left no bite marks of predators the actual contribution of mammalian predators in the artificial nest study remains diffuse.

Based on the artificial nest studies, we found a pattern of highest predation rates at times with highest numbers of nests on salt marshes (peak of the breeding season; see chapter 4). Predators are obviously attracted by the high numbers of nests. On inland grasslands the contrary was found. There, lowest predation rates occur during the main breeding season (BEINTEMA & MÜSKENS 1987; BEINTEMA et al. 1995). Our findings illustrate that apart from the main breeding season potential prey is limited and therefore salt marshes are less attractive for predators. We conclude that the number of alternative prey (i.e. mice or voles) is crucial for the understanding of predation patterns on salt marshes. Although small mammals are important ecological players on salt marshes through their influence on predator presence and also on vegetation succession (KUIJPER & BAKKER 2012), present knowledge on numbers of small mammals on salt marshes is very fragmentary. As compared to inland grasslands, numbers are expected to be relatively low and flooding events on salt marshes will regularly lead to a strong reduction of the small mammal communities (BLUMENBERG 1982; GOLET et al. 2013).

Impact of mowing

Mowing takes place within the Wadden Sea national park to slow down succession processes on salt marshes and for reasons of seawall maintenance. Mowing within the national park is postponed to July in order to protect ground-breeding birds. In general, mowing leads to a rather homogeneous vegetation structure as compared to grazed salt marshes (chapter 3). These more homogeneous vegetation stands increase the detectability of nests for predators (NEWTON 1998; FULLER & GOUGH 1999; VICKERY & ARLETTAZ 2012). In our study the impact of mowing on nest predation risk depended strongly on the vegetation types. In Couch Grass stands mowing can lead to higher and denser vegetation, and therefore lowers the risk of detectability of nests (chapter 4). In other vegetation types no effect of mowing on predation risk was found within our artificial nest studies. However, the effect of distance to seawall on predation rates changed along with the management. On fallow salt marshes nest survival was higher at nesting sites with larger distance to the seawall. This is expected when mammalian predators enter the salt marshes from inland in search for prey. On mown salt marshes the effect of distance to seawall on predation rates was absent which indicates that either the impact of mammalian predators on our artificial nests on mown sites was low or predators can easily access wide parts of the mown salt marshes.

Mowing bares risks for breeding birds when clutches or chicks are still on the site. Mowing can lead to crushing of eggs and chicks (KRUK et al. 1996; SCHEKKERMAN et al. 2009). Therefore, the timing of mowing is crucial for optimal management. The present practice of mowing after 1st of July can lead to a substantial loss of Redshank nests and chicks. At two study sites in the western *Jadebusen*, on average 56 % of broods were at risk of being lost to mowing. This proportion ranged from 33 % in early to 75 % in late breeding years (EXO et al. in prep.). Therefore, flexibility in mowing dates depending on the phenological progress of the breeding season will be a first step towards adaptive management of salt marshes.

Next to these direct effects there are indirect effects of mowing on food availability and predation rates. In order to logistically enable mowing on salt marshes, an effective drainage system is necessary to provide access for machinery. This leads to rather uniform abiotic conditions with loss of shallow water bodies important for foraging waders (SMART et al. 2006). The drier salt marshes are easily accessible for mammalian predators and the availability of bridges over ditches further supports this accessibility. The drainage of salt marshes is also known to speed up the succession towards the climax vegetation (VEENEKLAAS et al. subm.). Therefore, mowing can indirectly lead to an increased succession towards Couch Grass stands in combination with a higher accessibility of the salt marsh for mammalian predators.

Impact of grazing

Grazing by livestock can slow down or even reverse successional processes on salt marshes (BAKKER et al. 2005). Therefore, grazing is an often used management tool to increase biodiversity on salt marshes (ESSELINK et al. 2009). However, VAN KLINK et al. (2013) showed that arthropod diversity on grazed salt marshes does not exceed that of fallow salt marshes. The general effects of grazing can be split up into three major components of impact on the ecosystem: (1) herbivore forage consumption resulting in defoliation of plants, (2) physical disturbance caused by trampling of grazers and (3) nutrient return by deposition of faeces and urine of grazers (HOBBS 2006; VAN KLINK et al. in prep.). Defoliation changes vegetation structure, vegetation productivity and plant species composition towards plant species tolerant to grazing. Trampling leads to changes in plant species composition and additionally to changes in soil properties, which in combination with faeces and urine input modulates nutrient cycling and nutrient availability (HOBBS 2006; SCHRAMA et al. 2013a). Light grazing results in higher heterogeneity of vegetation types and vegetation structure: a mosaic of high and low canopy at small spatial scale. For many breeding birds such a combination is expected to be beneficial, as many ground-nesting species prefer dense vegetation for nesting and open vegetation for foraging (VICKERY & ARLETTAZ 2012). Under low stocking rates the vegetation mosaic provides high vegetation for hidden nests but also low vegetation for foraging. Own data on Redshank showed the importance of small scale heterogeneity in vegetation structure (for details on method see spread.PAR in chapter 3) for breeding success (ANOVA F = 9.96, df = 2, $p < 0.001$; Fig. 7-4).

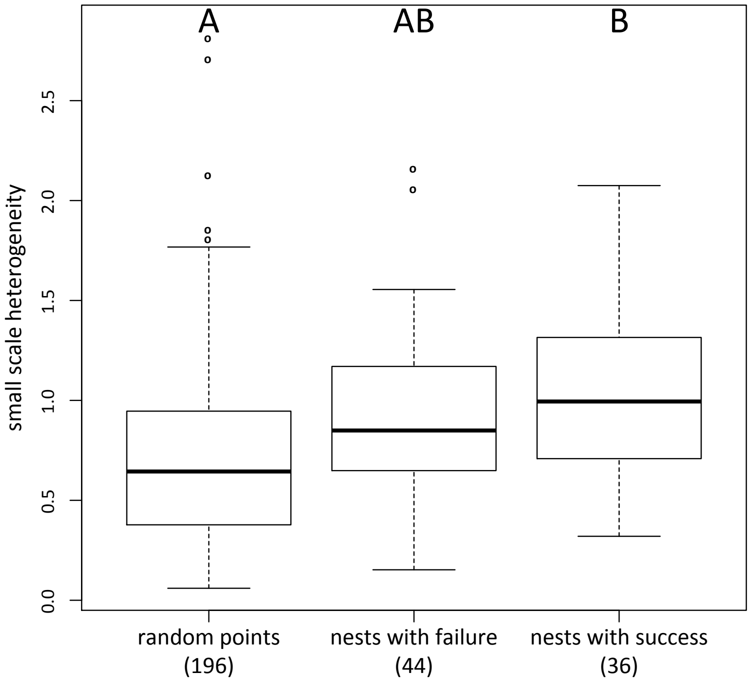


Figure 7-4 Small scale heterogeneity at random points and Redshank nests (capital letters show significant differences with $p < 0.001$)

The same pattern of nest site preference for vegetation mosaics was found for Meadow Pipits *Anthus pratensis* on one of our study sites (FRANKE 2013). In contrast, on a Dutch salt marsh no preference for short vegetation by foraging Meadow Pipits was found (VAN KLINK et al. in press), which could be due to the overall short vegetation on that particular salt marsh.

Grazing on fine textured soil can lead to soil compaction (cf. Box B). Compaction of soil changes the redox potential, which is known to be the most important determinant (besides elevation) for plant species composition on salt marshes (DAVY et al. 2011). This can lead to grazing induced changes in plant species composition resulting in changed vegetation structure, a key habitat feature for ground-nesting birds. In addition soil compaction is associated with a loss of air filled porosity, resulting in low abundance of soil microarthropods (VAN KLINK et al. in prep.) and terrestrial invertebrates (Box B). Besides these indirect effects, grazing involves the risk of trampling of nests. The risk of nest trampling depends highly on the stocking rates and the type of livestock (MANDEMA et al. 2013). But in contrast to mowing, precocial chicks are not in danger as they can physically avoid herds of grazing livestock. Light grazing with stocking densities ranging from 0.5 to 1.0 livestock units/ha is proposed to reduce the risk of trampling of nests on salt marshes, whereas the effect of these stocking densities on the vegetation depends on the productivity of the specific salt marsh (VAN KLINK et al. in press).

Outlook

Management of salt marshes changes the habitat quality in many different ways as illustrated above. The logistics of salt marsh management by grazing and mowing generally require access to the salt marsh through bridges and paths. For deployment of machinery and to secure dry places for cattle drainage of salt marshes is necessary. As most of the mainland marshes are man-made, such a drainage system is present on most of the mainland marshes (ESSELINK et al. 2009). These artificial drainage systems fundamentally change abiotic properties in favour of a homogeneous morphology. Increased drainage in combination with missing dynamics of biomass removal in a naturally highly dynamic system leads to salt marshes featuring rapid vegetation succession (BAKKER et al. 2005; VEENEKLAAS et al. subm.).

A removal of the artificial drainage network on man-made mainland salt marshes in combination with cessation of land use is theoretically possible and promotes a shift to a more natural situation. The rewetting of sites can lead to more diverse vegetation stands and an enhanced diversity of habitats (BAKKER et al. 2005). The Wadden Sea Plan (CWSS 2010) aims at an increase of these natural situations. But for such a change, it is necessary to thoroughly analyse the functions of the man-made structures for the salt marsh development. Just a cessation of maintenance of the drainage system in combination with cessation of management is often not successful and can even lead to a speeding-up in succession. Unmaintained drainage systems can have long-term effects on the landscape, even 20 years after discontinuation of maintenance (ESSELINK et al. 2009). However, a removal of the artificial drainage system implies top soil removal, a major impact on the system as a whole.

These conflicting trade-offs illustrate the challenges of management decisions on salt marshes. Science-based decisions for management of salt marshes should therefore start with an analysis of present conditions (on site) including the main abiotic drivers such as flooding frequency and sedimentation. If changes of management aim at improving the habitat quality for breeding birds, the main causes for low breeding pair densities and / or low breeding success need also to be assessed. In a second step any adjustment of salt marsh management needs to account for the effects on abiotic drivers, vegetation, invertebrates and predation as these are key determinants for breeding performance of salt marsh bird species. This is especially difficult in times of climate change when probabilities for extreme summer floods are already increasing. With higher flooding risks, changes on abiotic properties (sedimentation, salinity), vegetation and fauna of salt marshes can be expected and need to be considered (DUARTE et al. 2013). But for detailed prediction of these changes further studies are necessary.

Within this project I performed the analysis of the general pattern of the main factors influencing habitat quality for breeding bird species nesting hidden on salt marshes. This information is crucial for management decisions but is also valuable for a detailed understanding of breeding ecology of bird species on mainland salt marshes. For further research on the ecological requirements of breeding bird species the application of habitat suitability models will be valuable (HIRZEL & LE LAY 2008). The results provided by this project can be included in habitat suitability models and add important information on habitat quality of salt marshes. This will be an important future step to take. The results of this project are applicable for a wide variety of breeding birds on salt marshes. One example: Songbirds are an often overlooked species group on salt marshes but there is evidence for rapid declining numbers of songbird breeding pairs on salt marshes (WELLBROCK et al. 2010). The results of the present study can be used for studies on the ecological requirements of this and further species group (e.g. waders) on salt marshes. But the different nest types, nest sizes and foraging behaviours need to be taken into account when applying the results from this study.

Although detailed information on food availability could be gathered in this study, there is still a gap in our knowledge concerning the foraging behaviour of bird species on salt marshes. As soon as first insights on feeding behaviour become available it will be possible to assess the energetic needs, including the energy expenditure for catching of prey and prey processing (MAURER 1996), and the most preferential foraging situation. This information is strongly depending on the species specific foraging behaviour and is missing for most breeding bird species on salt marshes. The present study provides detailed information on the curious link between forage quality and forage quantity for invertebrate prey items on salt marshes and additional behavioural data will allow a proper interpretation of the findings with respect to food availability.

As the focus of this project was on mainland salt marshes, the results are not applicable for island salt marshes. It would be interesting to compare the results gathered in this project with results from island salt marshes. In general, the predation rates on islands are lower, due to differences in predator communities (cf. chapter 5). Only through further studies, the applicability of the present results for island salt marshes can be evaluated. It should be part of future research agendas to elaborate differences and general systematics in breeding ecology on mainland and island salt marshes.

This study entangles the complex impacts of management on the habitat quality of salt marshes for breeding birds and provides information on the interactions of management, abiotic environment, vegetation and fauna. The study results on salt marsh ecology support the development towards science-based management decisions for mainland salt marshes in the Wadden Sea region.

Appendix

List of figures

List of tables

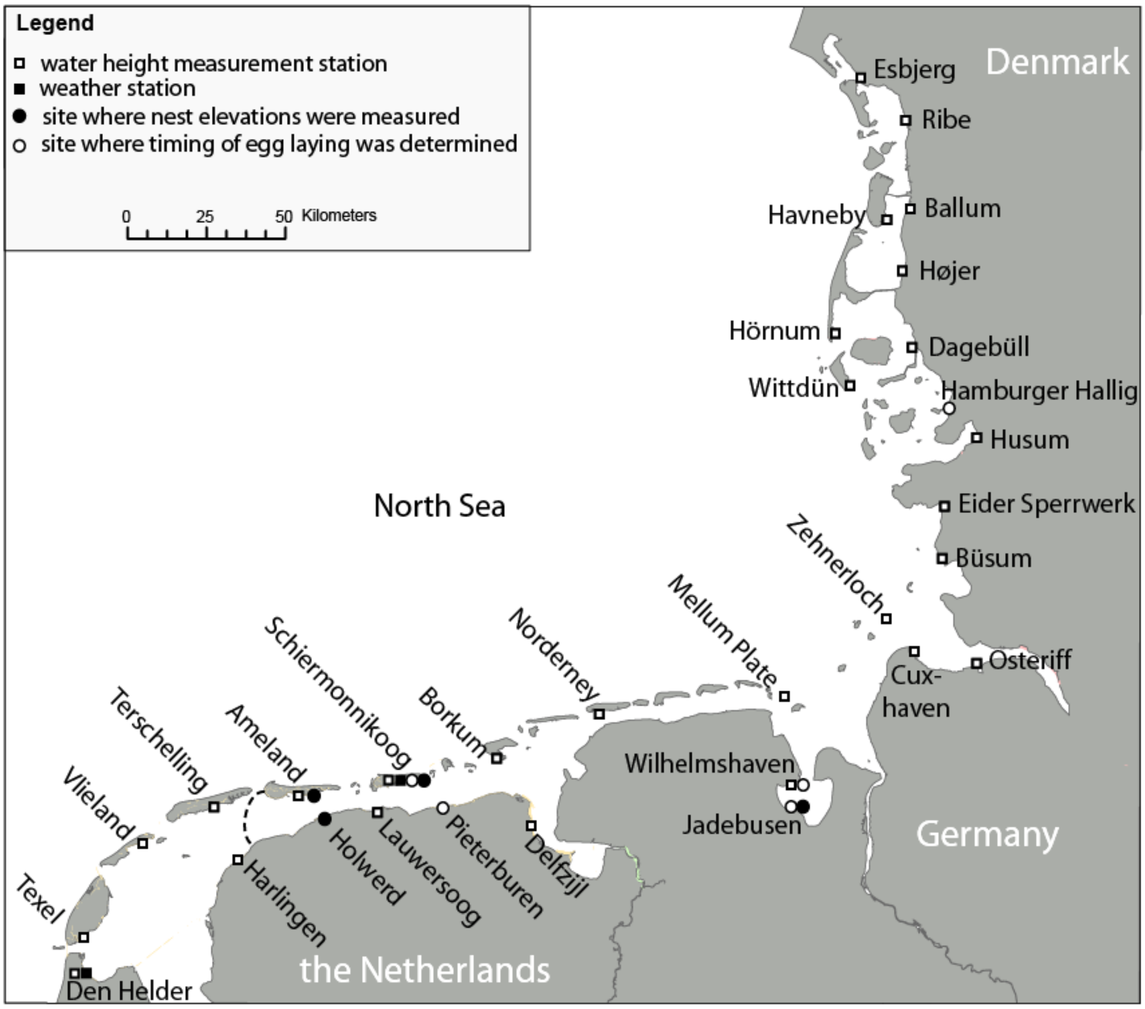


Figure 8-1 Map with location and names of measurement stations

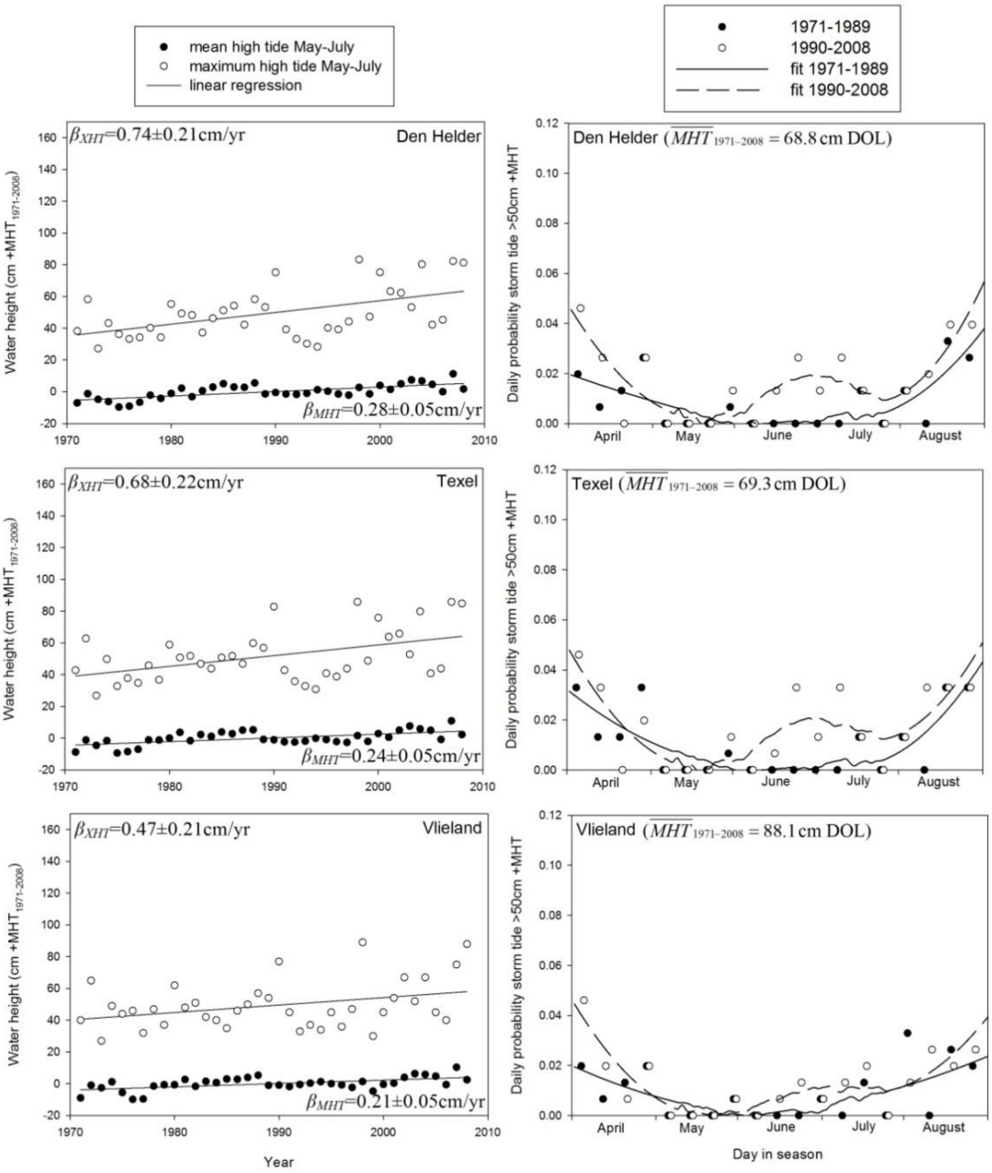
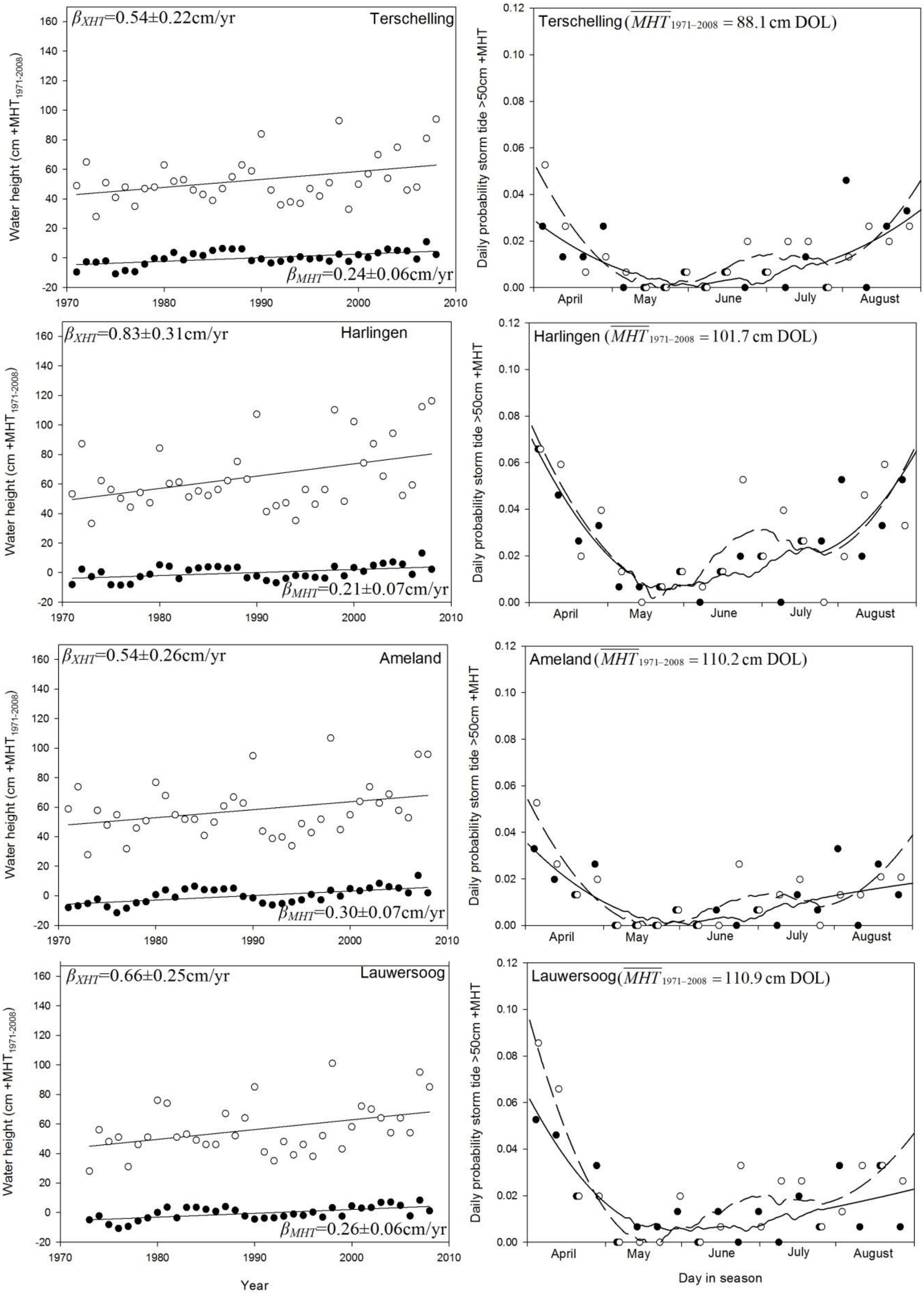


Figure 8-2 Left panels: Changes in mean high tide (MHT) and maximum high tide (XHT) over the period 1971-2008 during the months May-July for each of the 27 stations shown in Fig. 8-1. Right panels: Seasonal changes in the daily probability that the lower salt marsh (0-50cm above MHT) floods for each of the 27 stations for the periods 1971-1989 and 1990-2008. Dots represent averages per week; lines are fitted on raw daily data using negative exponential smoothing functions. For each site the absolute MHT is given in cm above Dutch Ordnance Level (DOL). Data sources: Dutch Directorate for Water Management, German Federal Institute of Hydrology and Danish Coastal Authority

Figure 8-2 (CONTINUED)



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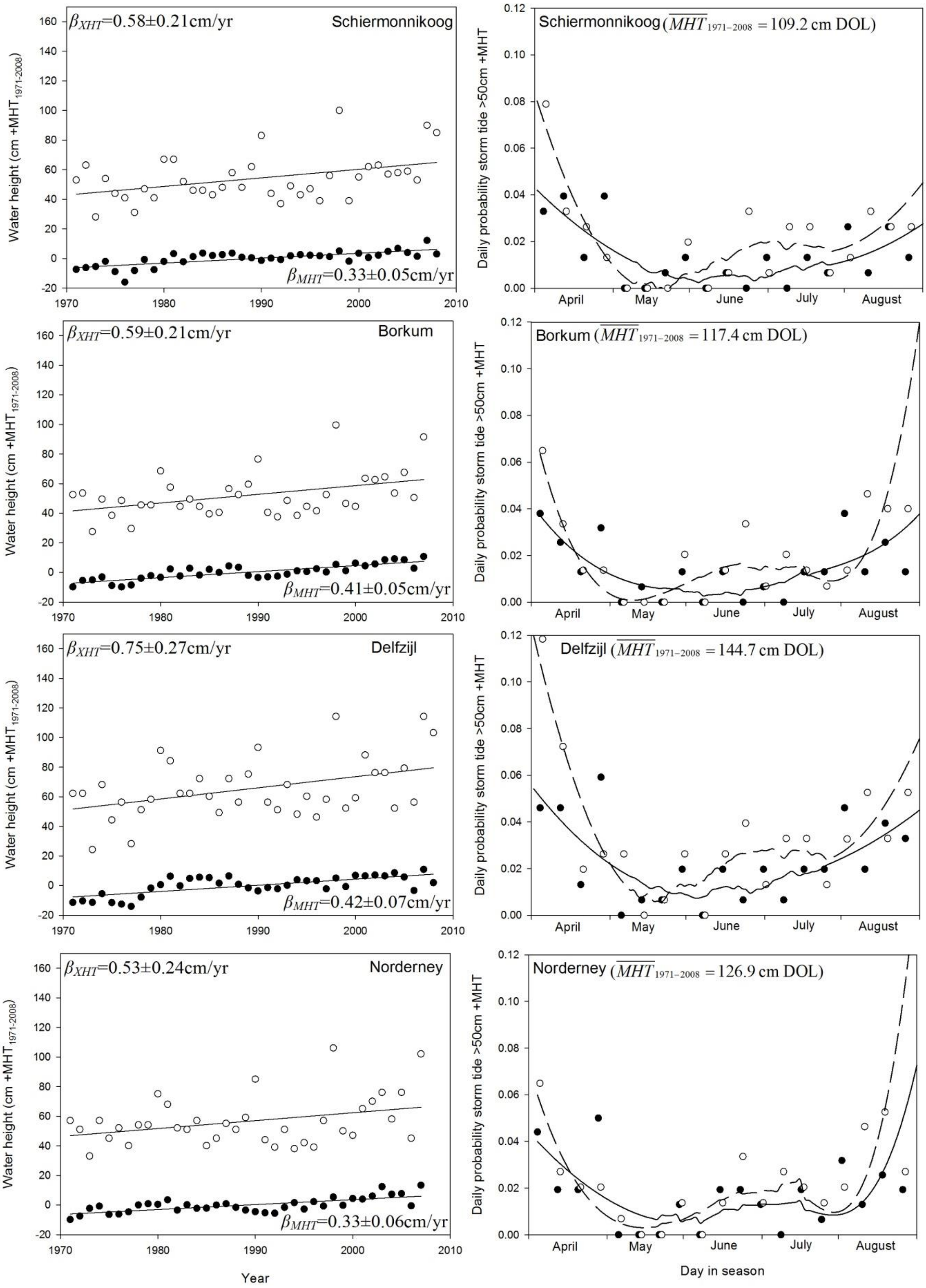

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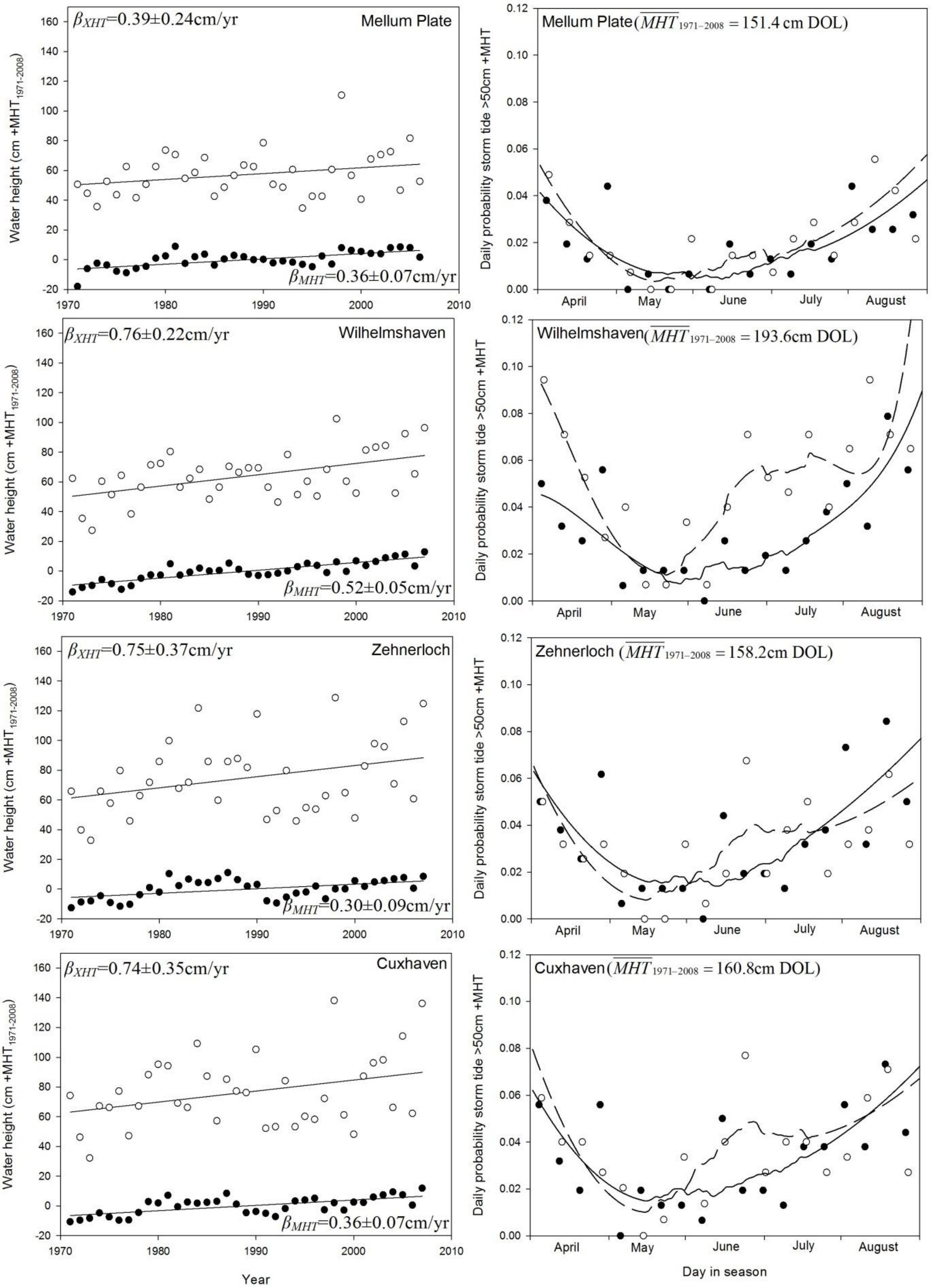

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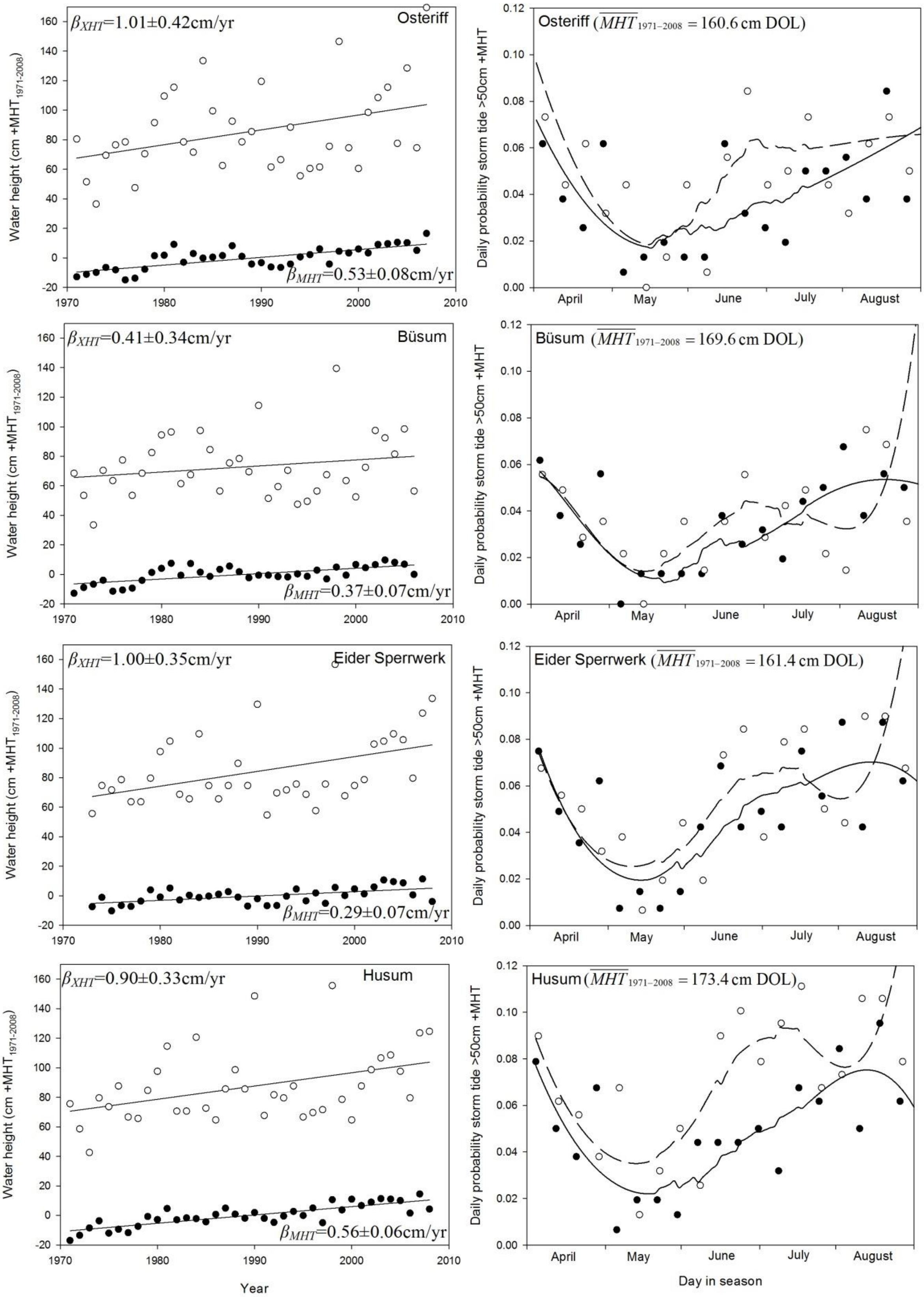

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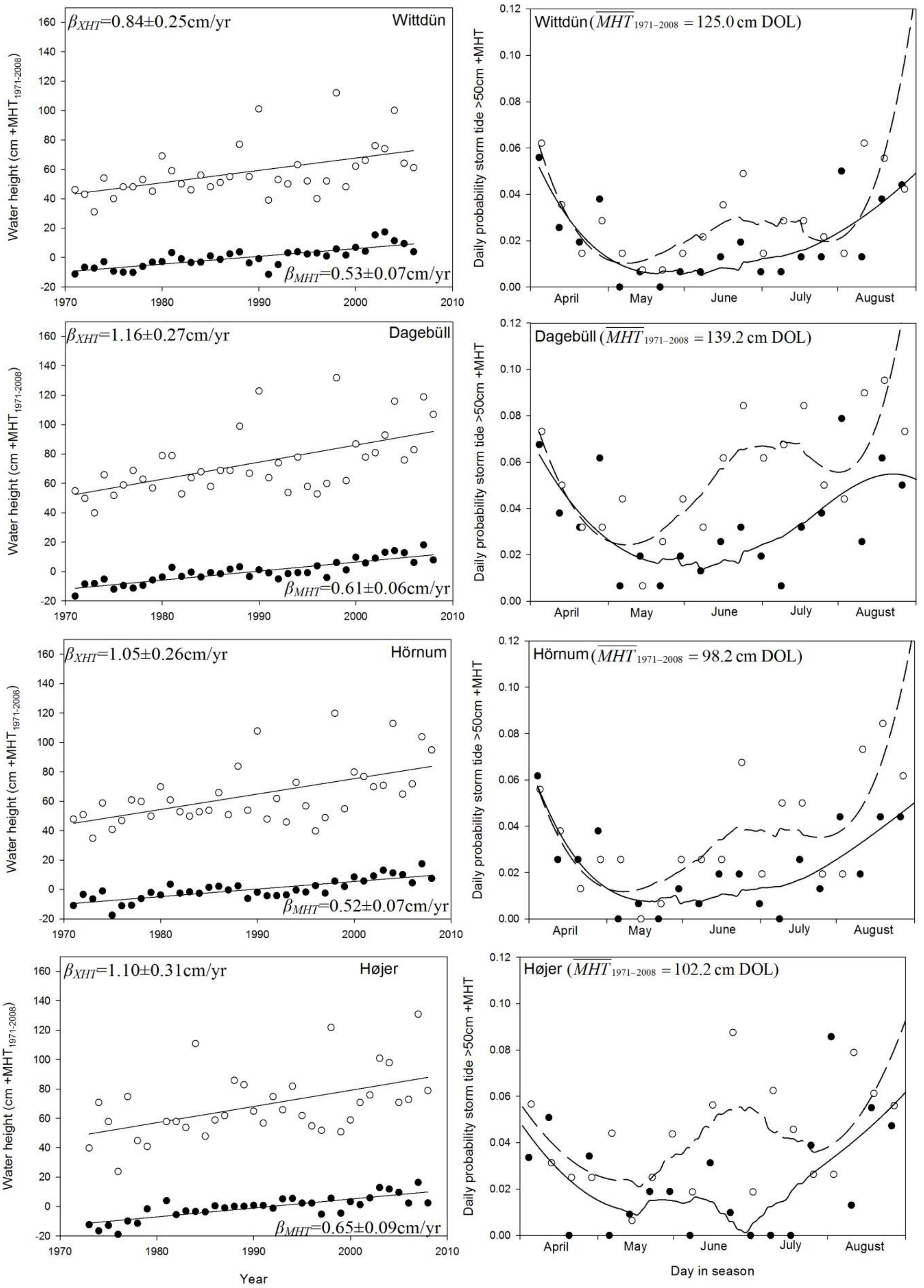

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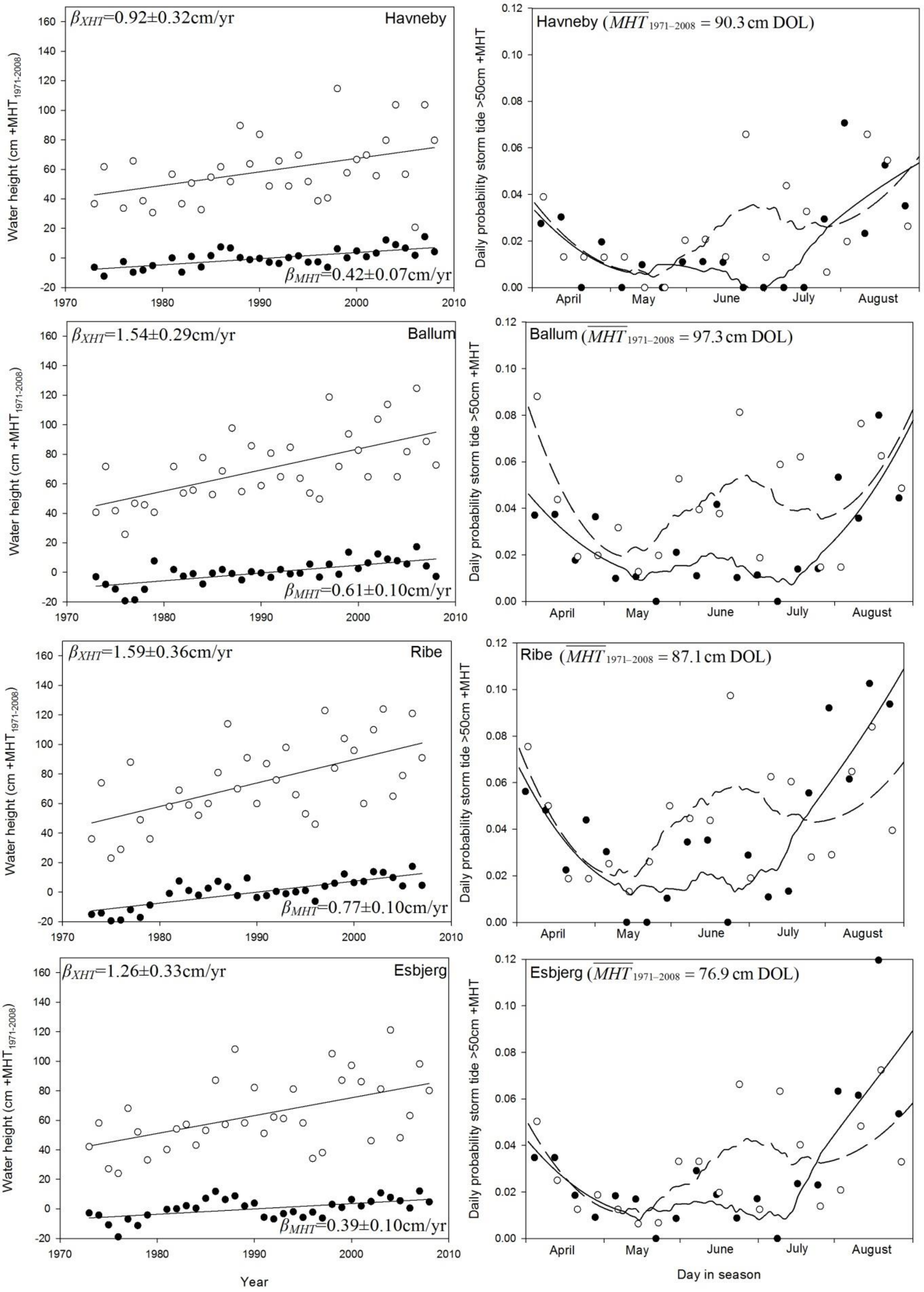


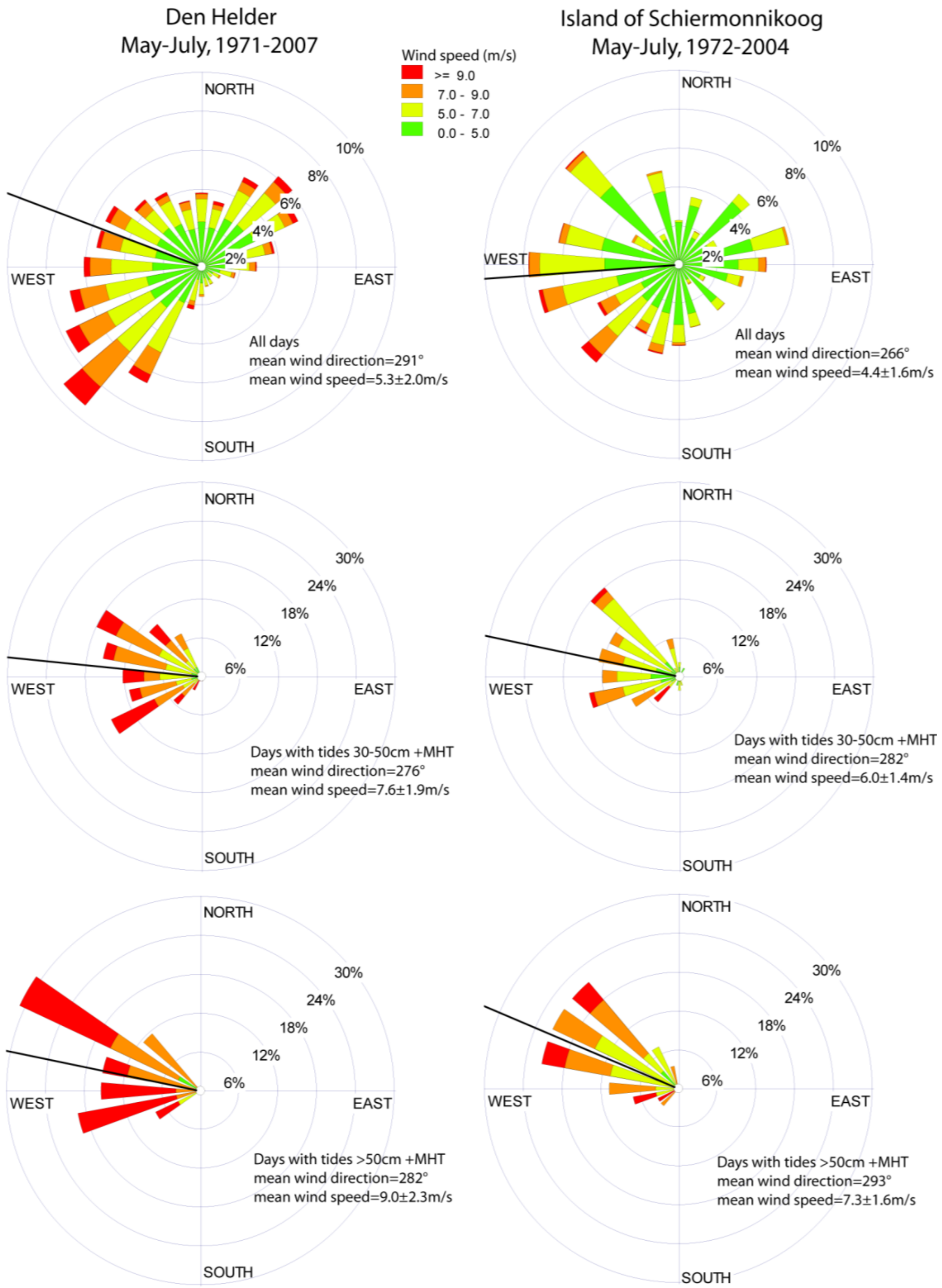
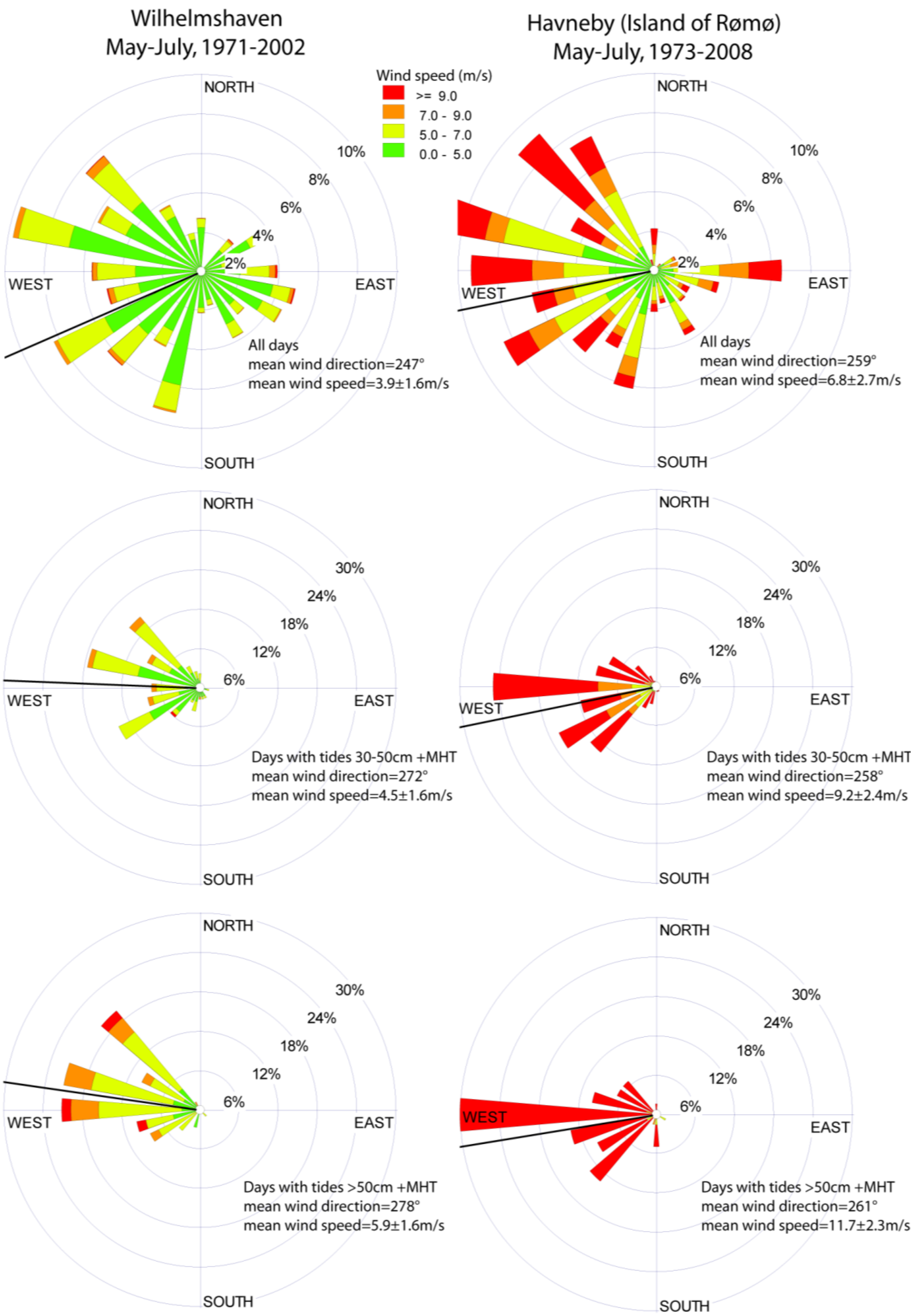


Figure 8-3 Wind roses of four weather stations nearby two mainland (Den Helder, Wilhelmshaven) and two island tidal stations (Schiermonnikoog, Havneby), see Fig. 8-1. Top panels show wind patterns during all days in May-July, while middle and lower panels present wind patterns for days with higher than normal tides (30-50cm above MHT) and extreme tides (>50cm above MHT), respectively. Solid lines in each wind rose depict the mean wind direction, while different colours represent the distribution of wind speeds. Mean wind speeds are given with ±standard deviations. Data sources: Royal Netherlands Meteorological Institute, VU University Amsterdam and German Meteorological Service

Figure 8-3 (CONTINUED)



Wilhelmshaven
May-July, 1971-2002

Havneby (Island of Rømø)
May-July, 1973-2008

All days
mean wind direction=247°
mean wind speed=3.9±1.6m/s

All days
mean wind direction=259°
mean wind speed=6.8±2.7m/s

Days with tides 30-50cm +MHT
mean wind direction=272°
mean wind speed=4.5±1.6m/s

Days with tides 30-50cm +MHT
mean wind direction=258°
mean wind speed=9.2±2.4m/s

Days with tides >50cm +MHT
mean wind direction=278°
mean wind speed=5.9±1.6m/s

Days with tides >50cm +MHT
mean wind direction=261°
mean wind speed=11.7±2.3m/s

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Professional Appointments

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Publications

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	Maier, M., Exo, K.-M., Schlaich, A., Stahl, J. (in prep.) High plants lead to low risk: Implications of salt marsh management for ground-breeding waders.
2012	Maier, M., Exo, K.-M., Schlaich, A. & Stahl, J. (2012) Welche Faktoren beeinflussen das Prädationsrisiko? Kunstnestexperimente auf Salzwiesen. Ornithologischer Rundbrief Mecklenburg-Vorpommern 47, Sonderheft 1: 66-67.
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2011	Cervencl, A., Esser, W., Maier, M., Oberdiek, N., Thyen, S., Wellbrock, A., Exo, K.-M. (2011) Can differences in incubation patterns of Common Redshanks *Tringa totanus* be explained by variations in predation risk? Journal of Ornithology 152: 1033-1043.
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Zusammenfassung

Das Wattenmeer ist eines der wichtigsten Brutgebiete für Küstenvögel in Westeuropa. Insbesondere die Salzwiesen des Wattenmeeres haben eine herausragende Bedeutung für die Reproduktion zahlreicher Brutvogelarten. Dieser bedeutsame Lebensraum für Brutvögel unterliegt dem Schutz durch die europäische Fauna-Flora-Habitat-Richtlinie (FFH-Richtlinie) sowie durch nationale Schutzgebietsregelungen. Trotz des hohen Schutzniveaus der Salzwiesen, zeigen sich bei zahlreichen Brutvogelarten rückläufige Bestandszahlen. Um stabile Brutvogelpopulationen zu erhalten, ist neben einem strengen Gebietsschutz das Flächenmanagement von zentraler Bedeutung. Jedoch sind bis heute die Auswirkungen von unterschiedlichem Salzwiesenmanagement, beispielsweise die Effekte von Beweidung und Mahd auf die Habitatqualität für Brutvögel, nicht vollständig verstanden.

Die vorliegende Arbeit untersucht Auswirkungen von Managementmaßnahmen auf die für Brutvögel wichtigsten Habitateigenschaften von Festlandssalzwiesen. Untersucht wurden die Auswirkungen des Managements auf die Vegetationsstruktur, auf das Prädationsrisiko und auf die Verfügbarkeit von Wirbellosen als Nahrungsquelle. Darüber hinaus wurden die Veränderungen des Überflutungsrisikos für Nester verschiedener Brutvogelarten in Folge von Klimaveränderungen beurteilt.

Die Habitatqualität von Salzwiesen für Brutvögel wird stark von ihrer Vegetationsstruktur bestimmt. Die hier vorgelegten Daten bestätigen einen großen Einfluss der Nutzungsform auf die Vegetationsstruktur der Festlandssalzwiesen. Insbesondere die Vegetationshöhe und Vegetationsdichte werden durch das Management der Salzwiesen beeinflusst. Die Veränderungen in der Vegetationsstruktur wirken sich einerseits auf die Nahrungsverfügbarkeit für Brutvögel, aber auch durch die Verstecktheit der Nester auf die Prädationsraten aus. So wurde insbesondere für Nester in hoher Vegetation ein geringes Prädationsrisiko festgestellt. Zum Höhepunkt der Brutzeit, an dem eine Vielzahl von Nestern auf den Salzwiesen vorhanden ist, wurden stark erhöhte Prädationsraten ermittelt. Zeitliche Aspekte im Brutgeschehen auf Salzwiesen sind daher nicht zu vernachlässigen. Bei brütenden Rotschenkeln wurden Verhaltensanpassungen an besonders hohe Prädationsraten festgestellt: Die nächtliche Anwesenheit der Altvögel am Nest war signifikant geringer als in Gebieten mit geringem Prädationsrisiko.

Die Verfügbarkeit und Qualität von Wirbellosen als Nahrung auf Salzwiesen wurde mithilfe von Bodenfallen und durch Messungen der Energiegehalte von potenziellen Beutetieren ermittelt. Basierend auf dieser Studie konnten wir zeigen, dass Salzwiesen eine hohe räumliche Heterogenität sowohl in der Verfügbarkeit der Gesamtenergiemenge als auch in der Qualität der Nahrung für Brutvögel aufweisen. Zwischen den unterschiedlichen Standorten und Vegetationseinheiten wurden große Unterschiede in der Zusammensetzung der Wirbellosengemeinschaft festgestellt. Die Spanne reichte von Gemeinschaften, die von Insekten und Spinnen dominiert wurden, bis zu von Flohkrebsen dominierten Gemeinschaften. Die Nahrungsverfügbarkeit war stark von den Wirbellosen-Gemeinschaften der Salzwiesen abhängig, wobei die Futterqualität negativ mit der Futtermenge korreliert war. Dies bedeutet, dass entweder eine Vielzahl an potenziellen Beutetiere von geringer Qualität oder wenige Beutetiere von hoher Qualität für nahrungssuchende Brutvögel auf Salzwiesen vorhanden sind. Der Wechsel von niedrigen zu hohen Anzahlen an potenziellen Beutetieren wurde aufgrund der hohen Anzahl an Flohkrebsen in späten Sukzessionsstadien der Salzwiesenvegetation verursacht.

Der überwiegende Teil der Festlandssalzwiesen geht auf einen künstlichen Ursprung zurück. Diese vom Menschen stark überprägten Salzwiesen werden durch ein künstliches Entwässerungssystem durchzogen, das die Morphologie stark verändert. Durch die künstliche Entwässerung findet eine beschleunigte Salzwiesensukzession statt, insbesondere wenn Störungen wie durch natürliche Dynamik oder Nutzung in Form von Beweidung oder Mahd an Standorten mit hohen Sedimentationsraten fehlen. Aus dieser

beschleunigten Salzwiesensukzession resultieren großflächige Dominanzbestände weniger Pflanzenarten, die einen hochwüchsigen und dichten Bestand bilden. Innerhalb solcher hohen und dichten Vegetation sind Nester von Bodenbrütern gut versteckt und damit optimal vor Prädation geschützt. Jedoch sind in derartigen Vegetationsbeständen die Futterqualität und die Erreichbarkeit der Beute herabgesetzt, und der Bau von offenen Nestern ist nicht möglich. Beweidung oder Mahd der Salzwiesen, aber auch Wiedervernässung durch das Entfernen des künstlichen Entwässerungssystems, kann die Sukzession der Salzwiesenvegetation verlangsamen und damit eine größere Diversität der Lebensräume für Brutvögel schaffen.

Diese Studie stellt die komplexen Auswirkungen von Managementmaßnahmen auf die Lebensraumqualität der Salzwiesen für Brutvögel dar, um ein Verständnis der Wechselwirkungen zwischen Management, Abiotik, Vegetation und Fauna auf Festlandssalzwiesen zu verbessern. Dies unterstützt die Bestrebungen wissenschaftlich fundierte Management-Entscheidungen für Festlandssalzwiesen zu treffen.

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Erklärung

gemäß § 10 Abs. 2 der Promotionsordnung der Fakultät für Mathematik und Naturwissenschaften der Carl von Ossietzky Universität Oldenburg vom 26.08.2011.

Hiermit erkläre ich, dass ich eine Promotion zum Dr. rer. nat. anstrebe. Es soll der Grad eines Doktors verliehen werden.

Zudem erkläre ich, dass die vorliegende Arbeit selbständig verfasst wurde und nur die angegebenen Hilfsmittel benutzt wurden. Einzelne Kapitel wurden bereits veröffentlicht, dies ist jeweils zum Beginn der Kapitel vermerkt.

Des Weiteren erkläre ich, dass diese Dissertation weder in ihrer Gesamtheit noch in Teilen einer anderen wissenschaftlichen Hochschule zur Begutachtung vorliegt oder vorgelegen hat.

Oldenburg, 30.12.2013

(Martin Maier)

Angaben zu eigenen Anteilen:

Kapitel 1, 3, 4, 6, 7, Box A und B: Datenerhebung, Aufarbeitung der Daten, statistische und schriftliche Ausarbeitung der Manuskripte.

Kapitel 2: Datenerhebung der Geländehöhen und Nistzeitpunkte der in der Studie analysierten Rotschenkelgelege. Diskussion der Studienergebnisse und des Entwurfs des Manuskriptes mit dem Erstautor Martijn van de Pol.

Kapitel 5: Durchführung der Thermologgerstudie im Untersuchungsgebiet Beckmannsfeld im Jahr 2007. Diskussion der Studienergebnisse und des Entwurfs des Manuskriptes mit der Erstautorin Anja Cervencl.

Angeben zu Fremdbeiträgen:

Kapitel 3, 4 und 6: Hinweise und Korrekturen zu den Manuskripten durch die in den jeweiligen Kapiteln genannten Co-Autoren und Co-Autorinnen.

Kapitel 2: Statistische und schriftliche Ausarbeitung des Manuskriptes durch Martijn van de Pol, weitere Daten wurden von den Co-Autoren und Co-Autorinnen bereitgestellt.

Kapitel 4: Verwendung von Daten die durch Almut Schlaich (Co-Autorin) erhoben wurden.

Kapitel 5: Statistische und schriftliche Ausarbeitung des Manuskriptes durch Anja Cervencl, weitere Daten wurden von den Co-Autoren und Co-Autorinnen bereitgestellt.