Grazing as a nature management tool

An experimental study of the effects of different livestock species
and stocking densities on salt-marsh birds

Freek S. Mandema

university of
groningen

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General introduction

Freek S. Mandema

Grazing management in general

Milchunas et al. (1988) hypothesized that plant diversity in grazed grassland systems is maximized at an intermediate grazing intensity. The grazing intensity at which the maximum diversity is reached varies with environmental moisture (interchangeable with aboveground net primary production) and the evolutionary history of grazing (Fig. 1.1). The Milchunas et al. (1988) hypothesis was adapted by Cingolani et al. (2005) to allow for different stable community compositions at a given grazing intensity (a possibility not explicitly allowed for in the Milchunas et al. (1988) hypothesis) (Fig. 1.1). In other words, the Milchunas et al. (1988) hypothesis implied that, for every value of grazing intensity there is a single diversity value (solid lines in Fig. 1.1). Cingolani et al. (2005) added the possibility that, after passing through a threshold triggered by past grazing management, or events such as fire, a community may have alternative stable compositions. These alternative stable compositions may have different diversity values (Cingolani et al. 2005, dashed lines in Fig. 1.1).

The Milchunas et al. (1988) hypothesis and its adaptation by Cingolani et al (2005) were developed for plant communities, Van Wieren and Bakker (2008), reviewed the effects of large herbivores on the diversity of plants, invertebrates and mammals and showed that the model can be extended to include birds, mammals and some groups of invertebrates. The general pattern in the model is that biodiversity of all organisms is highest in areas with an intermediate level of grazing intensity. Intermediate in this sense is a flexible concept, where the maximum
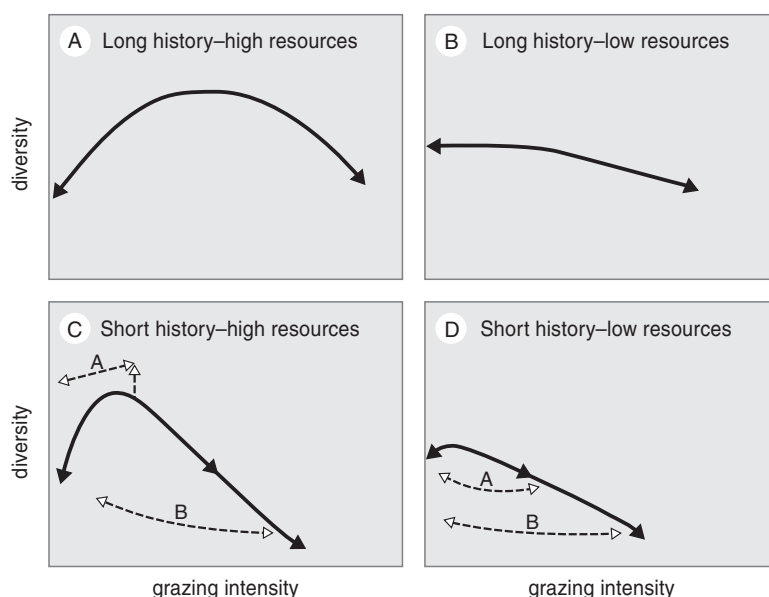

Figure 1.1 The Milchunas et al. (1988) hypothesis (solid lines) and its addition by Cingolani et al. (2005) (dashed lines).

biodiversity may depend on the productivity of a system. This has been confirmed in several studies reviewed by Van Wieren and Bakker (2008). In line with these ideas Metera et al. (2010) state that both overgrazing (resulting in bare soil or homogeneous short vegetation) and undergrazing or abandonment (resulting in homogeneous tall vegetation) of a pasture poses a threat for its biodiversity.

Where Bakker et al. (2003) still posed the question "To graze or not to graze", the question to ask now is "how to graze?" It is unlikely that one 'perfect' grazing intensity exists that maximises diversity in every system for all groups of organisms (Cingolani et al. 2005). Therefore, in this thesis, we will study the question how to graze, for birds on salt marshes.

Livestock grazing and birds

Most bird species spend a lot of time on the ground, for example, to forage or to breed. On the ground, birds are more vulnerable to predation and typically avoid predators by flight (Rogers 2003). Nests on the ground are, however, at a greater risk of being destroyed, especially in areas with human activities such as mowing or livestock grazing (Beintema and Müskens 1987, Fuller and Gough 1999).

In this thesis livestock grazing is defined as the entirety of livestock 'living' in an area. Thus, livestock grazing is not limited to biting of and eating the vegetation present, but includes: walking, standing, lying, etc. Livestock grazing has a number of effects on birds both directly and indirectly. Direct effects on breeding birds through trampling of eggs and chicks (e.g. Beintema and Müskens 1987, Pavel 2004) or disturbance of breeding adults (Hart et al. 2002, Ottvall 2005a). In rare cases, livestock have also been recorded as nest predators, probably because of a deficiency of specific nutrients in their usual diet (Pennington 1992, Fuller and Gough 1999). Indirectly, livestock grazing can affect birds, through changes in vegetation composition and structure, which in turn may alter food supplies or predation pressure (Fuller and Gough 1999, Ottvall 2005a) and consequently settling patterns of the birds. Grazing with moderate densities of livestock has been shown to lead to a higher plant diversity, on grasslands, heathland and salt marshes (Bakker 1989, Bakker et al. 2003). Grazing promotes plant diversity by inducing a more heterogeneous landscape, giving plant species opportunities to establish. Olff et al. (1997) showed that on salt marshes grazing sets back vegetational succession, preventing the vegetation from reaching a climax state of tall homogeneous vegetation dominated by a single species. However, when grazing is intensified, high densities of livestock may result in homogeneous short vegetation structure (Bakker 1989).

It has been shown that heterogeneous vegetation induced by grazing affects bird abundance. Norris et al (1997) for example found that the density of Redshanks (*Tringa totanus*) breeding on salt marshes of the Wash (UK), was highest on marshes with a heterogeneous vegetation structure. This type of vegetation structure was most abundant in marshes grazed with one head of cattle/ha. Van Dijk and Bakker (1980) found that densities of Oystercatcher (*Haematopus ostralegus*), Lapwing (*Vanellus vanellus*), Redshank, Black-tailed Godwit (*Limosa limosa*) and Skylark

(*Alauda arvensis*) breeding on a salt marsh increased with grazing by cattle with densities of 0.75 cattle/ha on a previously abandoned salt marsh.

The vegetation structure and composition of a salt marsh also affects the abundance of invertebrates and therefore also the abundance of birds feeding on invertebrates (Fuller and Gough 1999). In general Smit et al. (1981) concluded that salt-marsh management largely determines which species of birds may breed there, and Møler (1975) concluded that in order to maintain a high bird species diversity, some form of salt-marsh management is necessary. There are, however, studies that conclude the exact opposite (Thyen and Exo 2003a). They found that breeding bird density and diversity was higher on unmanaged marshes and therefore promoted a laissez faire policy for German salt marshes.

The contradicting conclusions on the effect of salt-marsh management on birds may have two likely causes. On the one hand grazing management may have different effects on the short term, compared to the long term. Bakker et al. (2003) stress the importance of long-term studies on the effects of grazing on vegetation, because they found that only after several decades of cessation of grazing of a salt marsh an equilibrium in the plant community composition was reached. Therefore, the effects of grazing through vegetation on birds can only be established fully in long-term studies. On the other hand salt-marsh management may be as diverse as grazing 0.5 cattle/ha to yearly mowing of a marsh. Drawing conclusions on the effects of management on birds is therefore only possible by comparing clearly quantified management treatments with different livestock species and different densities.

The European states signed an agreement to take all necessary measures to protect specific bird species and habitats, among which many coastal bird species and the Wadden Sea habitat (The Council of the European Communities 1992, The European Parliament and the council of the European Union 2009). Therefore, it is important to get a better understanding on the effects of different management regimes that are implemented on the salt marshes along the Wadden Sea coast. Germany, by law, states that there should be no human interference in national parks, so in 60% of salt marshes in Germany livestock grazing has ceased (Stock 2003, Esselink et al. 2009). In the Netherlands nature managers generally graze salt marshes in order to promote a higher biodiversity. The question here remains what type of grazing leads to the best results. This thesis will make recommendations on this question from the perspective of birds using salt marshes at different times of the year. For this, a large-scale grazing experiment was established on the mainland salt marshes in the North of Friesland in the Netherlands.

Study area and experimental set up

Most of the chapters in this study are based on research in a large salt-marsh area known as 'Noard-Fryslân Bûtendyks' (NFB, North-Friesland outside the dike). This in itself is part of the UNESCO Wadden Sea World Heritage Site. Chapter 2 uses data gathered on salt marshes along the entire Dutch Wadden Sea coast, but the remaining chapters focus on NFB.

Figure 1.2 Set up of the grazing experiment with five different grazing treatments in three replicates. The same five treatments were applied to all three replicates. The location of each treatment within a replicate was randomised, with the exception that two horse grazed treatments were never placed in adjacent paddocks. The location of the treatments within each replicate did not change between years. The experiment is located on salt marshes of Noord Friesland Buitendijks, in the North of the Netherlands, along the Wadden Sea coast.

NFB is located in the north of the province of Friesland in the Netherlands (53°20′N 5°43′E) and is one of the largest interconnected salt-marsh systems in Europe. It is a man-made marsh in the sense that natural sedimentation was promoted by the construction of brushwood groynes. These brushwood groynes border sedimentation fields and aid sedimentation by diminishing wave action. With every incoming tide sediment is trapped in the sedimentation fields and this accretion eventually leads to the formation of land, allowing pioneer salt-marsh vegetation to settle. Vegetation captures additional sediment, creating a positive feedback by which the salt marsh grows (Verhoeven 1980).

Historically, after accretion of sediment, a salt marsh would be embanked, creating arable land. From the 1970s onwards, this type of land reclamation was no longer economically feasible (Esselink 2000). Brushwood groynes in the area are now still maintained to avoid erosion of the marsh, and the area is managed as a nature reserve.

This type of management includes livestock grazing. Evidence shows that salt marshes in the Northern parts of the Netherlands have been grazed with livestock since 600BC (Esselink 2000). The last decades farmers have lost interest in the relatively marginal salt marsh areas (Bakker et al. 2003). However, with an increase in the appreciation of the nature conservation interest of salt marshes in the same period, livestock grazing was continued by nature conservation agencies to maintain and possibly increase plant diversity. Bakker et al. (2003) showed that grazing of a salt marsh with moderate stocking density leads to a higher plant diversity than no grazing or grazing with high livestock densities.

Within the study area a unique large-scale grazing experiment was set up over an area of 165ha of salt marsh. The experiment consisted of three 55ha replicates, each with five different grazing treatments in 11ha paddocks. The paddocks were separated by ditches or fences that were established during the grazing season from June to the end of September, and removed during the rest of the year. The summer grazing-treatments were 0.5 horses/ha, 0.5 cattle/ha, 1 horse/ha, 1 cattle/ha and a rotational treatment (Fig. 1.2). The rotational treatment alternated a year without grazing with a year with 1 cattle/ha. Livestock grazing of the experiment was initiated in 2010. Within each replicate, the grazing treatments were randomly distributed over the paddocks. However, two horse-grazed treatments were never adjacent in a replicate, because horses were believed to influence each other if placed next to each other. In addition to the five grazing treatments in each replicate, one replicate harboured an additional ungrazed treatment in an 11 ha paddock.

Before the experiment, two of the replicates had always been summer grazed with livestock, while one replicate had been long term ungrazed. In 2009 high pressure grazing was applied to the previously ungrazed replicate to create a more comparable vegetation structure and composition between the replicates.

Outline of this thesis

This thesis will cover the effects of livestock grazing on a broad range of bird species, ranging from geese in winter to breeding Redshanks in spring. Figure 1.3 shows a schematic overview of the topics addressed in this thesis. **Chapter 2** discusses the effects of grazing in contrast to long-term abandonment (>10 years) of salt marshes along the entire mainland coast of the Wadden Sea in the Netherlands on breeding bird abundances and demonstrates how changes in vegetation structure, caused by grazing has a differential effect on different groups of birds. With the insights of **chapter 2** it seems relevant to get a better understanding on the differences in effects on bird abundance and habitat of different grazing treatments. Vegetation structure of salt marshes changes with grazing (Bakker et al. 2003), but to
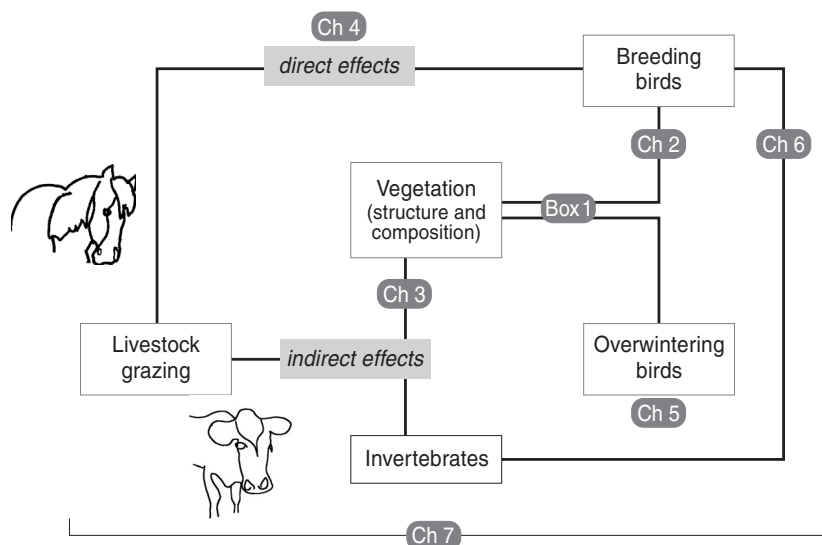
Figure 1.3 Schematic overview of the topics addressed in this thesis. Numbers in the figure refer to chapters in this thesis. The lines indicate pathways through which one component in the figure may affect other components. As such they represent topics addressed in this thesis.

what extent one grazing treatment has a different effect on bird abundance and habitat; either indirectly through the vegetation structure, or directly, is still largely unclear.

The next part of the thesis will, therefore, discuss the results of a grazing experiment with five different grazing treatments. **Box 1** will cover the distribution of birds over the five grazing treatments throughout the year.

Chapter 3 will go into more detail on the indirect effects of different grazing treatments on breeding birds. Two 'salt-marsh species', Redshank and Oystercatcher, have been chosen as study species, they are two common waders in the study area and represent two extremes in a range of nest concealment. Redshanks conceal their nests in tufts of tall vegetation and stay hidden on their nest when a threat approaches (e.g. Beintema et al. 1995, Norris et al. 1998). Oystercatchers on the other hand build relatively open nests and actively defend their nests (e.g. Green et al. 1990) Nest concealment is largely determined by the vegetation structure present. Using a method to quantify vegetation structure, this chapter will study the nest site selection of Redshanks and Oystercatchers in relation to vegetation structure and height.

Chapter 4 will explore a direct effect of livestock grazing on ground breeding birds. With artificial nests, a method adapted from previous studies (Koerth et al. 1983, Jensen et al. 1990, Paine et al. 1997, Pavel 2004, Gregory and Gamett 2009), the five grazing treatments in the experiment are compared in their trampling intensity. These results are validated with real nests from the same area and real wader nests from a previous study on grasslands by Beintema and Müskens (1987).

As the experimental area discussed in this thesis is only grazed in summer, there are no direct effects of livestock grazing on overwintering birds. Nonetheless the summer grazing does affect overwintering birds, e.g. in the available food. **Chapter 5** will show how summer grazing effects the distribution of overwintering geese, in autumn, directly after cessation of livestock grazing and in early spring, before the start of livestock grazing.

Food availability is also of vital importance for breeding birds. Meadow pipits are common breeding birds along the Dutch Wadden Sea coast. In **Chapter 6** we will show what food is taken by Meadow pipits to feed their nestlings, through an analysis of nestling droppings. Subsequently, we will quantify the food present in Meadow pipit foraging sites and random sites to gain a better understanding on the parameters of foraging sites chosen by Meadow pipits.

Finally, in the last chapter (**Chapter 7**) in this thesis, the results from the previous chapters will be integrated and general mechanisms of livestock grazing in relation to birds are discussed. Additionally, we will give general recommendations on the management of salt marshes with livestock grazing for the conservation of birds that use salt marshes throughout the year.

Livestock grazing and breeding bird numbers on marshes along the mainland coast of the Wadden Sea

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Abstract   Our study aimed to investigate how bird species richness and abundance is related to livestock grazing on salt- and brackish marshes, with an emphasis on songbirds and shorebirds.

The cover of tall vegetation was used as a proxy for the stocking density of salt marsh survey areas along the coast of the Netherlands. Survey areas with a high percentage cover of tall vegetation were assumed to have endured lower livestock grazing intensities than survey areas with a low percentage cover of tall vegetation. This relationship was verified for the tall grass Elytrigia atherica. The species richness and abundance of birds was related to the percentage cover of tall vegetation on the survey areas.

We found that the species richness was positively related to the percentage cover of tall vegetation. We also found that all of the investigated species, except Avocet showed a positive relation with the percentage cover of tall vegetation. However, the investigated songbird species only increased up to an intermediate percentage cover of tall vegetation and decreased in numbers at a higher percentage cover of tall vegetation. Redshank and Oystercatcher abundance were positively related to the percentage cover of tall vegetation on salt marshes, but negatively related to the percentage cover of tall vegetation on salt marshes.

With this type of management species number and abundance of most breeding birds can be maintained in coastal marshes. However, management of salt and brackish marshes should be tuned to the conditions of individual marshes.

Introduction

Several studies have shown the importance of moderate grazing in creating and maintaining habitat complexity for birds in different systems (e.g. Norris et al. 1997, 1998, Tichit et al. 2005, Sirami et al. 2008, Nikolov 2010). However, in the last decades livestock grazing of salt and brackish marshes was no longer economically viable in the Netherlands, leading to a decrease of livestock grazing on coastal marshes (Bakker et al. 1993, Dijkema et al. 2010). On some marshes livestock densities have decreased, while other marshes have been completely abandoned. Abandonment of salt- and brackish marshes has led to an increase in cover of tall climax plant communities such as communities dominated by *Elytrigia atherica* in salt marshes and *Phragmites australis* in brackish marshes (Bakker et al. 1993, Esselink et al. 2002, Sammul et al. 2012). Livestock grazing retards the succession of salt-marsh vegetation (Olff et al. 1997, Bakker et al. 2003). The cover of these plant communities therefore indicates to what extent a salt- or brackish marsh has been grazed where higher cover of these communities indicates a low stocking density. The cover of tall climax plant communities in a marsh can, therefore, be used as a proxy for stocking density. In the Wadden Sea area the numbers of shorebirds have been declining or have been stable (Koffijberg et al. 2006), while livestock grazing of marshes has decreased, leading to a higher percentage cover of tall vegetation on these marshes (Bakker et al. 1993, Dijkema et al. 2010).

Habitat heterogeneity is deemed an important factor in creating high levels of bird species richness (e.g. Atauri and de Lucio 2001, Cerezo et al. 2011). Thus, grazing, which changes vegetation structure (Bakker et al. 1993) is likely to lead to changes in the community composition of breeding birds (Oltmanns 2003). This will be reflected in the species richness and bird abundance. The effects of livestock grazing of salt- and brackish marshes on birds are, however, still under debate. Songbird species are generally found to benefit from an increase in tall vegetation (e.g. Oltmanns 2003, Thyen and Exo 2003b, Darnell and Smith 2004). The effect on shorebirds, however, is still unclear. Thyen and Exo (2003) state that increasing livestock grazing may lead to a lower bird diversity, because there is a decrease in breeding densities of songbirds, without a parallel increase in shorebirds. They, therefore, conclude that livestock grazing of salt marshes is unnecessary and improper for the conservation of salt-marsh breeding birds. Norris et al. (1997) found that the density of common Redshank (*Tringa totanus*) increases when larger parts of a marsh are covered with *Elytrigia atherica* dominated plant communities. Maximum densities were found at grazed sites with a high cover of *Elytrigia atherica*. However, Norris et al. (1997) investigated saltmarsh sites where up to 65% of the marsh is covered with plant communities dominated by *Elytrigia atherica*. It remains unclear what happens at sites where the percentage cover of *Elytrigia atherica* exceeds 65%. In the Northern Baltic Sea area it was found that the number of breeding shorebirds decreased with increasing cover of reeds that occurred after abandonment of coastal marshes (Helle et al. 1988). Based on the habitat requirements of several shorebird species (Beintema et al. 1995, Thyen 2000, Van de Kam et al. 2004), we expect that the highest densities of breeding pairs for many shorebird

species will be found at an intermediate percentage cover of tall vegetation, ergo at intermediate grazing intensities. If the percentage cover of tall plant communities increases over time, we expect a subsequent increase in the songbird abundance and species richness.

So, to facilitate management decisions, our study aimed to investigate how bird species richness and abundance is related to livestock grazing on salt- and brackish marshes (Bakker et al. 1993, Esselink et al. 2002). We based the livestock density of salt- and brackish marshes on the percentage cover of tall plant communities. We verified the relation between livestock density and the percentage cover of tall plant communities on salt marshes for *Elytrigia atherica*.

Methods

Study area
The study was carried out on salt- and brackish marshes located along the Dutch Wadden Sea coast (53° 23′N5° 49′E). The Wadden Sea is one of the largest and most important intertidal systems in the world (Reise 2005, Lotze 2005). The mainland salt marshes of the Netherlands Wadden Sea are largely of anthropogenic origin, because their development has been promoted by ditching and construction of sedimentation fields (Verhoeven 1980, Esselink et al. 2009). Seven of the survey areas were brackish marshes located in the Dollard-area. The marshes in the Dollard-area are inundated by a mix of fresh water from the river Ems and salt water from the Wadden Sea at high tides. Twenty-three sites were salt marshes located along the coast of the provinces of Groningen and Friesland. The survey areas ranged in size from 21ha to 447ha.

Cover percentage of tall vegetation as a proxy for stocking density
We assume that the cover of tall vegetation on salt and brackish marshes can be used to estimate the livestock grazing density in survey sites in previous years. We tested this assumption for the tall grass *Elytrigia atherica*. On salt marshes along the Wadden Sea coast we placed a total of 50 transects (different from the survey areas where birds were counted). On these transects the percentage cover of *Elytrigia atherica* was estimated visually each year from the sea wall to the intertidal flats from 1960 to 2010. The livestock grazing density of each transect was classed as ungrazed (0 livestock units/ha), intermediately grazed (≤0.7 livestock units/ha) or intensively grazed (>0.7 livestock units/ha).

The average cover of *Elytrigia atherica* for each stocking density was calculated for every year from 1960 to 2010. For each stocking density the natural log of the average cover +0.5 was used as the response variable in a linear model with year as a continuous explanatory variable to test for a relation between time and the cover of *Elytrigia atherica* at different livestock grazing intensities. Linear models were fitted using the base installation of R version 2.15.3 (R Core Team 2013).

Tall vegetation and breeding bird numbers

In order to understand the relation between numbers of breeding birds on salt- and brackish marshes and the cover of tall vegetation we estimated the percentage cover of tall vegetation and the numbers of breeding birds on 30 survey areas from 1991 to 2008.

The percentage cover of tall vegetation in each survey area was estimated from vegetation maps in Arc GIS (ArcGIS Desktop 2009). We assumed that plant communities dominated by *Elytrigia atherica* or *Atriplex portulacoides* grow tall and encroach over salt marshes without livestock grazing (Bakker et al. 1993). On brackish marshes, we selected plant communities dominated by *Phragmites australis* or *Elytrigia repens* as tall plant communities (Esselink et al. 2002, Sammul et al. 2012).

Vegetation maps for the Wadden coastline were collected from the directorate general for Public works and Water management in the Netherlands (Rijkswaterstaat). The vegetation maps followed the TMAP typology with respect to plant communities (Esselink et al. 2009). TMAP is an agreed vegetation typology used for the Wadden-Sea area in all three Wadden-Sea Countries (The Netherlands, Germany and Denmark). For the salt-marsh survey areas vegetation maps were available for the years 1992, 1996, 2002 and 2008, and for the brackish survey areas for the years 1995, 1999 and 2006.

The number of breeding pairs in each survey area was assessed annually by either territory mapping or counts of breeding pairs according to standardized methods developed for surveys of breeding birds in the Netherlands by SOVON Dutch Centre for Field Ornithology (Van Dijk and Boele 2011). With these counts, we calculated bird species richness (sum of species) and total bird abundance (sum of breeding territories) for each survey area in every year for which both breeding bird counts and vegetation maps were available. In addition, we calculated shorebird species richness and songbird species richness separately. We also calculated the abundance of the three most common shorebird species (Pied Avocet *Recurvirostra avosetta*, Eurasian Oystercatcher *Haematopus ostralegus* and Common Redshank) and the three most common songbird species (Meadow Pipit *Anthus pratensis*, Eurasian Skylark *Alauda arvensis* and Reed Bunting *Emberiza schoeniclus*).

Analysis

We used generalized estimating equations (GEE) with a log link and Poisson error structures to assess the relationship between breeding birds and the percentage cover of tall vegetation. GEEs are extensions of Generalized Linear Models that allow for modelling of correlated data, such as time series data (Hardin and Hilbe 2003). Bird counts in the same survey-area at different times are not independent of each other. The closer the two counts are together in time, the higher the higher the likelihood that similar numbers of birds are counted in the area. In this study within-survey area bird-counts can be modelled as a function of this 'time-distance' between years (Zuur et al. 2009). Hence, we used an auto-regressive correlation structure of order 1 (AR1) for the residuals to model our time series observations. An offset variable (the natural log of the surface area (ha) of each survey area) was

included in the statistical models to account for differences in size of the survey areas. Using an offset variable instead of analyzing densities has the advantage of allowing for heterogeneity within the context of a Poisson distribution (Zuur et al. 2009).

In a first series of statistical models we used bird species richness and abundance as a response variable. The percentage cover of tall vegetation and the percentage cover of tall vegetation squared were used as explanatory variables. However, as there are inherent differences in plant community types associated with salt- and brackish marshes, we made a second series of statistical models to test for differences in the relation of bird abundance and species richness with the cover of tall vegetation on salt- and brackish marshes. In this second series of models, the bird species richness and abundance were used as a response variable. The explanatory variables in these models were: percentage cover of tall vegetation, marsh type (salt or brackish marsh), and the interaction between percentage cover and marsh type. A Separate series of models was made to avoid over parameterization of the first series of models. Statistical models were reduced by backwards elimination and by an evaluation of models at every step on the basis of Wald statistics (Zuur et al. 2009). Trends in the residuals were checked for all models. GEEs were fitted using the geepack library (Højsgaard et al. 2006) in R, version 2.15.3 (R Core Team 2013).

Results

Cover percentage of tall vegetation as a proxy for stocking density

On the ungrazed transects we found a significant relation of the natural log of the percentage cover of *Elytrigia atherica* +0.5 with time in years (F = 576.37, p < 0.0001; Fig. 2.1). On the intermediately grazed transects we also found a significant relation between the natural log of the percentage cover of *Elytrigia atherica* +0.5 and time in years (F = 237.87, p < 0.0001). However, the relation was not as strong as on the ungrazed marshes (Fig. 2.1). On intensively grazed marshes we again found a relation between the natural log of the percentage cover of *Elytrigia atherica* +0.5 and time in years (F = 25.879, p < 0.0001), but this relation again was not as strong as on the ungrazed or the intermediately grazed transects (Fig. 2.1).

After approximately 50+ years the cover of tall vegetation on an ungrazed marsh may reach 100%. On intermediately grazed marshes, the cover of tall vegetation grows less quickly and only reaches about 30% after 50+ years. Although this may grow to a higher percentage, livestock will prevent the cover of tall vegetation reaching 100%. On the intensively grazed marshes the cover of tall vegetation does grow, but to less than 10% after 50+ years (Fig. 2.1).

Tall vegetation and breeding birds

Mean bird species richness over all survey areas for all years was 12.5 ± 0.5 (mean ± SE). Bird species richness was relatively evenly distributed between shorebirds: 4.2 ± 0.3, songbirds: 4.5 ± 0.1 and the remaining birds: 3.8 ± 0.2 (Table 2.1).
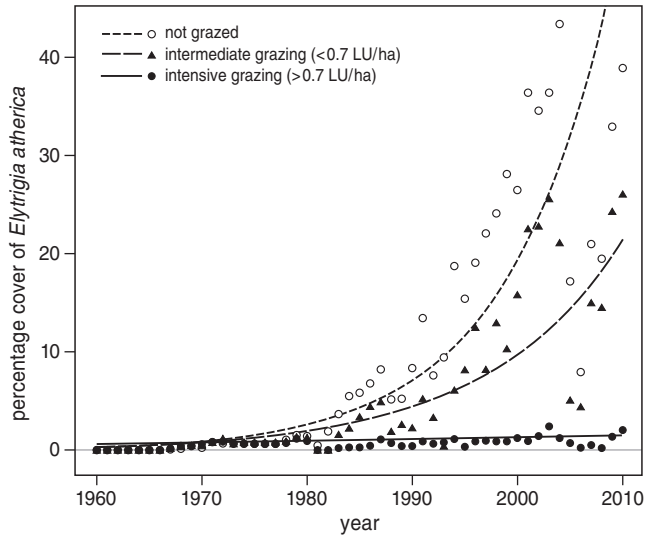
Figure 2.1 The percentage cover of sea couch *Elytrigia atherica* on salt marshes along the Dutch Wadden Sea coast from 1960 to 2010. For each year a mean cover is calculated for 15 ungrazed transects, 19 intermediately grazed transects and 16 intensively grazed transects.

Table 2.1 Mean numbers (± SE) of species and breeding bird pairs counted on all survey areas in the years that vegetation maps were available.

Species	Mean
total species richness	12.5 ± 0.5
shorebird species richness	4.2 ± 0.3
songbird species richness	4.5 ± 0.1
remaining bird species richness	3.8 ± 0.2
total bird abundance	541.0 ± 79.9
Pied Avocet abundance	69.1 ± 11.8
Eurasian Oystercatcher abundance	52.2 ± 4.9
Redshank abundance	24.2 ± 2.7
Meadow Pipit abundance	20.3 ± 3.7
Skylark abundance	5.3 ± 1.3
Reed Bunting abundance	5.0 ± 1.0

There was a significant positive relationship between total species richness and the percentage cover of tall vegetation, but the slope of this relationship decreased over time (Fig. 2.2). This positive relationship was mainly driven by the species richness of songbirds. For shorebird species richness we also found a significant positive relationship with the cover of tall vegetation in early years of this study, but no trend in the later years (Fig. 2.2, Table 2.2).

The abundance of birds was significantly positively related with the cover of tall vegetation for all investigated species except Pied Avocet. The three songbird species all showed maximum densities at an intermediate cover of tall vegetation, while Oystercatchers and Redshanks showed a general positive relation with the cover of tall vegetation (Fig. 2.3, Table 2.2).

The abundance of birds was not just explained by the cover of tall vegetation. The total bird abundance and the abundance of Avocets both declined over time, while the number of Skylarks increased with time. The relation between the cover of tall vegetation and species richness or abundance of Skylarks or Oystercatchers also weakened with time (Fig. 2.2, Fig. 2.3, Table 2.2).

Salt- and brackish marshes

For the species richness and the total species abundance we did not find that the relation with the cover of tall vegetation differed on salt- or brackish marshes. However, on brackish marshes we found that the positive relation of abundance of Meadow Pipits and Reed Buntings with the cover of tall vegetation was stronger on brackish marshes than on salt marshes. For Oystercatchers and Redshanks on the other hand, we found there was a positive relation with the cover of tall vegetation on salt marshes, but a negative relation on brackish marshes (Table 2.3).

Table 2.2 Results of a GEE for the relation between the percentage cover of tall vegetation and species richness and abundance.

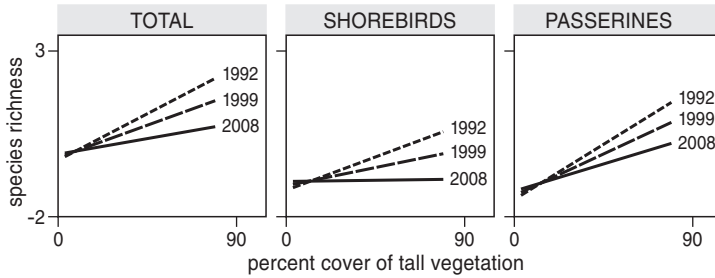|	vegetation		year		vegetation^2		vegetation:year	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p
species richness	+5.22	0.02	+0.34	0.56	0.89	0.34	−4.79	0.03
shorebird species richness	+6.73	0.01	+0.64	0.42	1.15	0.28	−6.32	0.01
songbird species richness	+4.5	0.03	+0.68	0.41	0.054	0.82	−3.94	<0.05
species abundance	+10.1	<0.01	−43.4	<0.0001	1.12	0.29	0.18	0.67
Pied Avocet	−4.24	0.04	−9.66	<0.01	0.15	0.69	1.64	0.2
Eurasian Oystercatcher	+13.9	<0.001	−1.7	0.19	1.4	0.24	−14.5	<0.001
Common Redshank	+21.1	<0.0001	0.18	0.67	2.34	0.13	3.59	0.06
Meadow Pipit	+19.1	<0.0001	0.89	0.35	−14.1	<0.001	0.06	0.79
Eurasian Skylark	+9.22	<0.01	+20	<0.0001	−6.38	0.01	−9.2	<0.01
Reed Bunting	+20	<0.0001	0.016	0.9	−4.84	0.03	0.60	0.44

Figure 2.2 Fitted lines modelling species richness as a function of cover of tall vegetation and year. On the x axes of the plots is the cover of tall vegetation as a percentage of the total vegetated area, from 0% to 90%. Note that the number of breeding pairs is offset in the model based on the size of the survey areas. When a significant year effect and/or an interaction between year and cover of tall vegetation was found in our statistical model, three years have been plotted to understand the change in intercept and/or slopes over the years of this study.
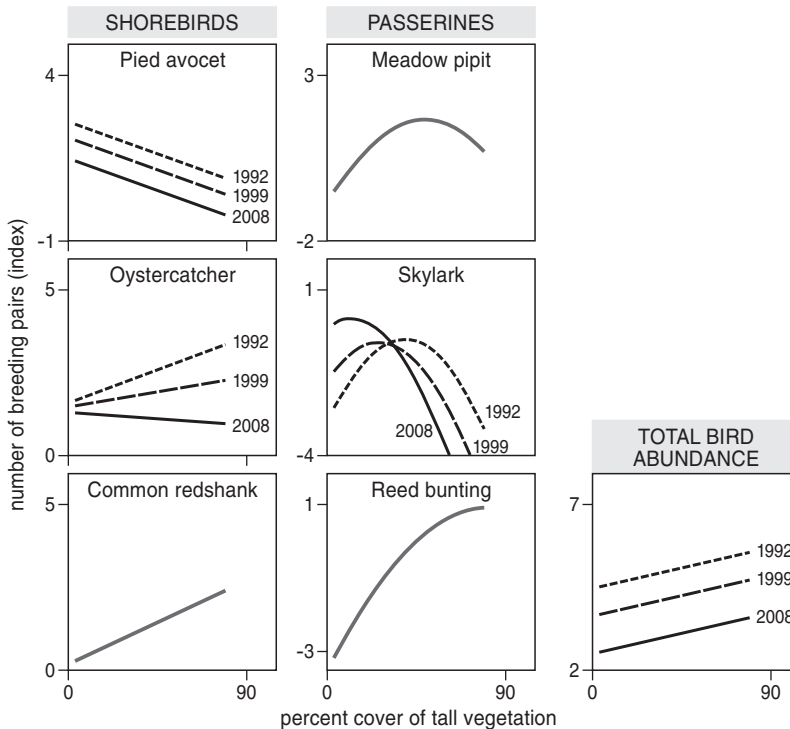
Figure 2.3 Fitted lines modelling number of birds as a function of cover of tall vegetation + cover of tall vegetation squared+year+cover of tall vegetation*year. On the x axes of the plots is the cover of tall vegetation as a percentage of the total vegetated area, from 0 to 90%. Note that the number of breeding pairs is offset in the model based on the size of the survey areas. When a significant year effect and/or an interaction between year and cover of tall vegetation was found in our statistical model, three years have been plotted to understand the change in intercept and/or slopes over the years of this study.

Table 2.3 Results of a GEE for the interaction between the percentage cover of tall vegetation with marsh type (salt marsh or brackish marsh). In the table 'vegetation' is the percentage cover of tall vegetation and 'marsh type' is a factor with two levels, salt- or brackish marsh. 'Brackish' and 'salt' indicate the direction of the relation between species richness and abundance when there was a significant difference in the relation of species richness and abundance with the percentage cover of tall vegetation between the two marsh types.

	Vegetation: marsh type		brackish	salt
	χ^2	p		
species richness	0.484	0.49		
shorebird species richness	1.59	0.21		
songbird species richness	0.518	0.47		
species abundance	0.107	0.74		
Avocet	0.11	2.58		
Oystercatcher	20.3	<0.0001	–	+
Redshank	32.3	<0.0001	–	+
Meadow Pipit	8.85	0.0029	+	+ +
Skylark	1.49	0.22		
Reed Bunting	7.7	0.0055	+	+ +

Discussion

Cover of tall vegetation as a proxy for stocking density

Our results show that the tall grass *Elytrigia atherica* increased over time on salt marshes. This increase is much more rapid on ungrazed marshes than on intermediately or intensively grazed marshes (Fig. 2.1). This confirms studies by Bakker et al. (1993) and Olff et al. (1997) who found that livestock grazing retards vegetational succession on salt marshes. We therefore conclude that the percentage cover of *Elytrigia atherica* on a salt marsh can be used as an approximation of the grazer densities of a salt marsh in previous years, provided the salt marsh has existed for several decades and tall vegetation has had the opportunity to spread over the marsh if not managed. We extend this assumption to other tall plant communities affected by livestock grazing, such as communities dominated by *Phragmites australis* on brackish marshes or *Atriplex portulacoides* on salt marshes.

The relationship between livestock grazing and the cover of tall vegetation changes over time. The longer an area has not been grazed, the faster the increase in the percentage cover of tall vegetation. Salt marshes that were intensively grazed by livestock will not be completely overgrown with tall vegetation, while marshes that are not grazed will eventually have a 100% cover of tall vegetation. In the present

study we counted birds in survey areas on existing marshes. If no grazing (or other management) had been conducted on these marshes we go by the assumption that they would be completely covered in tall vegetation. The actual percentages cover we find for the different survey areas are therefore an approximation of the grazer densities in the survey areas in previous years.

Tall vegetation and breeding birds
The total species richness as well as the shorebird species richness and the songbird species richness increased with increasing cover of tall vegetation. This confirms the study by Thyen and Exo (2003) who conclude that decreasing management of salt marshes has a positive effect on shorebirds.

Only for the abundance of Avocets did we find a negative relation with the percentage cover of tall vegetation. The abundance of all three of the investigated songbird species only increased up to an intermediate percentage cover of tall vegetation (Fig. 2.3).

The positive relation found for Reed Buntings with cover of tall vegetation may be explained by the dead stems of tall vegetation providing these birds with song perches. Additionally tall vegetation provides concealment of their nests in *Phragmites australis* tussocks or *Elytrigia atherica* (Niethammer and Von Blotzheim 1966). Survival of nests at the egg stage is positively related to the extent of concealment of nests in Reed Buntings (Brickle and Peach 2004). Maximum numbers of breeding Skylarks were reached on marshes with an intermediate percentage cover of tall vegetation. Maximum numbers of Skylarks in the survey areas were reached at lower vegetation cover in the course of the years (Fig. 2.3). Spring has commenced earlier in Europe the past decades (Sparks and Menzel 2002). The structural diversity of salt- and brackish-marsh plant communities at the time of arrival of Skylarks may therefore have changed over time. For Skylarks, this may lead to a change in the preferred plant communities to breed in and they may shift to sites with a lower cover of tall plant communities. The positive relation we found for Redshanks with the cover of tall vegetation complies with the findings by Norris et al. (1997) who found that breeding Redshanks were most abundant in grazed marshes with *Elytrigia atherica* where the vegetation was structurally diverse.

The percentage cover of tall plant communities over a marsh can be reduced with livestock grazing (Bakker et al. 1993, Fig. 2.1). Therefore, some livestock grazing of salt- and brackish marshes seems appropriate to manage the cover of tall vegetation of a marsh. This contradicts the conclusions by Thyen and Exo (2003) stating that management of salt marshes is unnecessary and improper for the conservation of salt-marsh breeding birds.

Trends in time
For two individual species we found a significant change in abundance over time (Table 2.2). Pied Avocets declined over time. This is a colonial breeding species, which is particularly vulnerable to predation. Our results suggest that apart from the cover of tall vegetation, there are other important factors determining the number of breeding pairs for these species. One possibility that has been suggested is

increased predation by foxes as a major influence on the decline of colonially breeding bird species (Van Dijk et al. 2009, Van Dijk and Oosterhuis 2010, Van Kleunen et al. 2010). For Skylarks, we found a positive trend over time on salt- and brackish marshes. For Skylarks this is especially interesting, because the total number of breeding Skylarks in the Netherlands has declined (Boele et al. 2012).

Salt- and brackish marshes
For two shorebird species (Oystercatchers and Redshanks) and two songbird species (Meadow Pipit and Reed Bunting) we found that the relation between the abundance of these species and the percentage cover of tall plant communities was significantly different on brackish marshes and salt marshes. Meadow Pipits and Reed Buntings showed a positive relationship with the percentage cover of tall vegetation, but the relation was significantly stronger on salt marshes than on brackish marshes (Table 2.3). Oystercatchers and Redshanks showed a positive relationship with the percentage cover of tall vegetation on salt marshes, but a negative relationship on brackish marshes. The preferred breeding sites of Oystercatchers are close to the intertidal flats (Ens et al. 1992). On brackish marshes tall vegetation, consisting predominantly of *Phragmites australis*, spreads from the water's edge onto the marsh. On salt marshes the predominant tall vegetation (*Elytrigia atherica*) spreads from the landward side onto the marsh. We therefore hypothesize that the tall vegetation that negatively affects Oystercatchers is more dominant at the preferred breeding sites on brackish marshes than on salt marshes.

Conclusions
We conclude that abandonment of brackish marshes and salt marshes (ceasing livestock grazing), leading to an increasing cover of tall plant communities did not cause a decline in species richness, or a decline in 'typical' marsh species such as Eurasian Oystercatcher and common Redshank. This complies with findings by Thyen and Exo (2003).

For managers of salt- and brackish marshes, not all species may have equal conservation interest (Baudry 1991, Suárez-Seoane et al. 2002). Pied Avocets, for example are listed as species to be protected by the European Natura 2000 program (European Commission 1979) and a substantial part of the world Avocet population breeds in the Wadden Sea area (Koffijberg et al. 2006). Skylark abundance decreased nationally in the Netherlands (Boele et al. 2012), while we found an increase on salt marshes.

At a high cover of tall vegetation, however, we found that several bird species are negatively affected (e.g. Pied Avocet, Meadow Pipit and Eurasian Skylark) by an increasing cover of tall vegetation. Hence, abandonment of all livestock grazing may be detrimental for some breeding bird species on a longer term.

Our results indicate that moderate livestock grazing can be used to limit the spread of tall vegetation over salt- and brackish marshes (Fig. 2.1) as well as changing the structural diversity within tall plant communities. With this type of management species number and abundance of most breeding birds can be maintained in coastal marshes.

Acknowledgements

Box

The effects of different livestock grazing-treatments on the distribution of birds – a progress report

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Abstract   The aim of this study was to gain a better understanding of the effects of five different livestock grazing treatments on bird abundances in a salt-marsh system throughout the year. We report on changes in the abundance of birds within a short timeframe (2010-2012) since the beginning (2010) of this study. The grazing treatments ranged from light grazing (0.5 cattle/ha) to intensive grazing (1 horse/ha). We counted birds every two weeks on the experimental blocks, throughout the year. A standard transect was walked and all birds that landed in, flew up from or were on the ground in a grazing treatment were counted.

The distribution of the total number of individual birds in winter (excluding flocking species) changed significantly when compared between the first and the last year of this study. In 2012, there were significantly more overwintering birds (excluding flocking species) on the 1 horse/ha treatments than on any of the other four treatments. The distribution of individual bird species and of the total number of species over grazing treatments did not significantly change over three years.

Since we expect most of the changes in the distribution of birds to occur through changes in the vegetation and since many birds breeding on salt marshes show high site fidelity, three years of experimental grazing may be too short to find clear effects of grazing treatments on the distribution of birds over a salt marsh. We recommend the continuation of this study to gain a better understanding of long term effects of livestock grazing on the abundance of birds in a salt marsh system.

Introduction

Salt marshes along the Wadden Sea coast have a long history of livestock grazing. Livestock grazing was already conducted by the first settlers in the Wadden Sea area, around 600 BC (Esselink 2000). However, in the past decades grazing management has changed along the entire Wadden Sea coast (Bakker et al. 1993). In Germany most salt marshes are part of a German national park for which a *laissez faire* policy is instituted by law. Therefore, livestock grazing is banned from up to 50% of the German salt marshes (Stock 2003). In the Netherlands livestock grazing of salt marshes by farmers was common practice. However, from the 1970s onward there has been a growing recognition that salt marshes have an important nature conservation interest (Esselink 2000). This led to a continuation of livestock grazing by nature conservation organizations with the aim to promote biodiversity of salt marshes (Bakker et al. 2003).

In a review on the impact of browsing and grazing herbivores on biodiversity, Van Wieren and Bakker (2008) mentioned that for plants, invertebrates and birds, the diversity is generally highest in moderately grazed grasslands, compared to ungrazed or heavily grazed grasslands. For many ground breeding birds it has been shown that breeding densities are highest in moderately grazed areas. Norris et al. (1997, 1998) showed that cattle-grazing promotes a heterogeneous sward that supports high densities of Redshanks. Baines (1990) showed that Lapwings (*Vanellus vanellus*) prefer to nest in short sward with many tussocks. Van Dijk and Bakker (1980) found that densities of Oystercatcher (*Haematopus ostralegus*), Lapwing, Redshank (T*ringa totanus*), Black-tailed Godwit (*Limosa limosa*) and Skylark (*Alauda arvensis*) increased on a moderately grazed salt marsh. Møller (1975) concluded that in order to maintain a high bird species diversity on a salt marsh, reed harvesting, hay production and/or livestock grazing should be conducted.

Studies describing experimental effects of grazing regimes are, however, relatively scarce. Such experiments are important because they randomly allocate grazing regimes over salt-marsh paddocks, precluding beforehand associations between grazing regimes and vegetation type. Therefore it is important to invest in large-scale experiments with grazing regimes.

For birds overwintering on salt marshes, food availability seems to be a major factor determining abundance. Granivorous passerines are suspected to be limited by food in their wintering grounds (Dunning and Brown 1982). Dierschke (2001) showed that reduced grazing leads to a higher production of profitable seeds for granivorous passerines overwintering on a salt marsh. Additionally, Twite (*Carduelis flavirostris*), Rock Pipit (*Anthus petrosus*) and Snow Bunting (*Plectrophenax nivalis*) all preferred ungrazed salt marshes (Dierschke 2001). Little is known about winter food availability for insectivorous birds, but Meyer et al. (1994) showed that in winter, generally, there are more invertebrates present on ungrazed salt marshes than on marshes grazed throughout the previous summer. However, Fuller and Gough (1999) noted that the relationship between grazing pressure and the invertebrate food of birds are likely to be complex with trade-offs between abundance and availability. Geese and other birds grazing on the vegetative parts of plants during

the autumn and winter months were found to be facilitated by intensive grazing of salt marshes during the previous spring and summer (Olff et al. 1997, Van der Graaf et al. 2002, Bos et al. 2005b)

It is not clear over what period of time livestock grazing changes the diversity and distribution of birds over a salt marsh. Birds have been found to respond mainly to vegetation structure and to a lesser extent to vegetation composition (e.g. Dallinga 1993, Norris et al. 1997, 1998, Thyen and Exo 2005). Vegetation heterogeneity, opposed to homogeneous short swards or dense tall swards, seems especially important for nest site selection (Norris et al. 1997, 1998, Mislom et al. 2010, Verhulst et al. 2011) and food availability (Fuller and Gough 1999, Vickery et al. 2001) for birds. The vegetation structure of an area can change within a few years after changes in management (Bakker 1989, Bobbink and Willems 1993). Experiments with grazing and cutting revealed that change in biomass can occur before changes in plant species composition take place (Bakker 1989, Bobbink and Willems 1993).

We expect that livestock grazing changes the vegetation structure and composition leading to a gradual change in the diversity and abundance of birds on a salt marsh. We test for the effects of livestock grazing from the first year of experimental grazing to the last year of this study (a period of three years). When an effect of livestock grazing on the abundance and/or diversity of birds was found over the three years, we additionally tested for differences in numbers of birds between the five livestock grazing treatments in just the last year of the study.

Methods

Study area
The study area (Noard Fryslân Bûtendyks) consists of 165 ha of salt marsh along the Dutch mainland Wadden Sea coast. It is located in the North of the province of Friesland in the Netherlands (53°20′N 5°43′E). The study area is part of a large interconnected salt marsh area (>4000 ha), managed as a nature reserve.

The Wadden Sea forms a central point in migratory pathways of birds (Reneerkens et al. 2005). The salt marshes along the Wadden Sea also form an important breeding habitat for many bird species, mostly waders (Van Kleunen et al. 2010). A number of bird species ranging from songbirds such as Rock Pipit and Shorelarks (*Erempohila alpestris*) to waders such as Oystercatchers also use the area as an overwintering site (e.g. Dierschke 2002). As such, the study site harbours many coastal bird species throughout the year.

Experimental design
On the salt marsh in the study area, a grazing experiment was set up with five different grazing treatments in 11 ha paddocks: 1 horse/ha, 0.5 horses/ha, 1 cattle/ha, 0.5 cattle/ha and a rotational treatment with 1 cattle/ha in one year, followed by a year without grazing and so forth. Nolte (unpublished) showed that within our study area 1 horse/ ha is the most intensively grazed treatment, while 0.5 cattle/ha is the lightest treatment. The treatments with 1 cattle/ha, 0.5 horses/ha and the rotational

treatment are each considered as different forms of moderate grazing treatments. These differences in grazing intensity are caused by the stocking densities (a higher stocking density leads to a larger proportion of short vegetation) and the livestock species. Because of the digestive system of horses (hindgut fermenters) they need to eat more than cattle (ruminants) (Arnold et al. 1984, Duncan et al. 1990, Menard et al. 2002). Additionally, horses use larger parts of the day to graze (Arnold 1984, Duncan et al. 1990, Janis et al. 2010).

The grazing experiment with five grazing treatments was replicated three times. The grazing treatments in each replicate were randomly distributed, with the exception that two horse-grazed treatments were never put next to each other, because the horses were believed to influence each other (Fig 1). The salt marsh was grazed from June to September, starting in 2010. The rotational treatments were grazed in 2009 and 2011 but not in 2010 and 2012. Freshwater was provided for the livestock in a tank located at one side of each paddock (Fig. 1.2).

Bird counts

From October 2009 to December 2012 birds were counted in the study area every two weeks, throughout the year. We walked a standard transect through each of the replicates in the experiment, starting at sunrise. All birds on the ground and those that flew up or landed within a paddock were counted and their positions drawn on a map. This method was used to make sure that only birds that could directly be linked to a specific grazing treatment were counted. This had the side effect that some bird species present in the study area did not, or in smaller numbers than expected, show up in the counts (Appendix A). For example, Twites were seen flying over the study area in small flocks, but these groups generally were not seen on the ground in the vicinity of the researchers and could therefore not be linked to a specific grazing treatment.

Analyses

The year round counts were grouped into three seasons and analysed separately. Counts from December to March were referred to as 'winter', April to July as 'spring', August to November as 'autumn'. The seasons were chosen in such a way that the months with breeding birds on the salt marsh were captured in 'spring'.

From the birds counted, six species were chosen for detailed analysis: Common Snipe (*Gallinago gallinago*), Meadow Pipit (*Anthus pratensis*), Oystercatcher, Redshank, Rock Pipit and Skylark. These species were chosen, because they were present in the study area in sufficient numbers for analysis. Additionally, the total numbers of birds and species richness were analysed. The method used to study the distribution of birds over a salt-marsh grazing experiment is not ideal for flocking birds, because high numbers of birds in a grazing treatment only indicate the preference of one flock. Analysis of dropping counts (Owen 1971) is a more appropriate method to study the distribution of Geese and other flocking birds (e.g. Wigeon (*Anas penelope*)) over a salt marsh and for this study area is discussed in Mandema et al. (unpublished, chapter 5). Therefore, from the analyses of the total number of birds flocking bird species (Barnacle Goose (*Branta leucopsis*), Brent Goose (*Branta*

bernicla), Greylag Goose (Anser anser), Wigeon and Starling (Sturnus vulgaris)) were removed.

Not all species were present in the study area year round. Detailed analyses per species were, therefore, only performed for the seasons in which a species was present each year. To test if the different grazing treatments had an effect on the distribution of birds over the study area, we compared counts from the first year of this study with counts from the last year of this study. For this we used the average counts per paddock, per season in the first and last year for each species. For each species and every season in which it was present we created a generalised linear mixed model, with the average counts as a response variable and grazing treatment (a factor with five levels, the different grazing treatments), year (a factor with two levels, first and last year) and the interaction between grazing treatment and year as explanatory variables. A significant interaction would indicate an effect of the grazing treatment, i.e. that the grazing treatments had a significant effect on the relative distribution of a bird species over the grazing treatments. The three replicates from the experiment were included as a random variable in the analyses to account for differences between the replicates. The models were generated in R (R core team 2013) using the lme4 package (Bates et al. 2011). To avoid type I errors, because of the number of analyses conducted, the p-values from the analyses were adjusted with a Bonferonni-correction, using the stats package in R (R core team 2013). If a significant interaction between grazing treatment and year was found, the counts in each grazing treatment in the last year of this study were compared using the multcomp package (Hothorn et al. 2008). These comparisons were made to understand change over the individual grazing treatments.

Results

The total number of birds (excluding flocking species) varies strongly over the seasons, with the highest numbers of birds in spring (Fig.B.1). A significant interaction between grazing treatment and year was found in winter for the total number of birds meaning that the distribution of the total number of birds over the grazing treatments changed from the first to the last year of this study. The model estimate of abundance of the total number of birds in winter increased for the rotational treatment from the first to the last year of this study, while it decreased for the four other grazing treatments (Table B.1). In the last year of the study the total number of birds in winter was significantly higher in the 1 horse/ha treatment, than in the four other grazing treatments (Fig. B.2, Table B.2)

Six species were chosen for detailed analysis, based on the available data (Appendix A). For none of these individual species, in none of the seasons we found a significant interaction between grazing treatment and year (Table B.1). This indicates that the distribution over the grazing treatments of these species did not differ significantly between the first and the last year of this study, after three years of grazing.
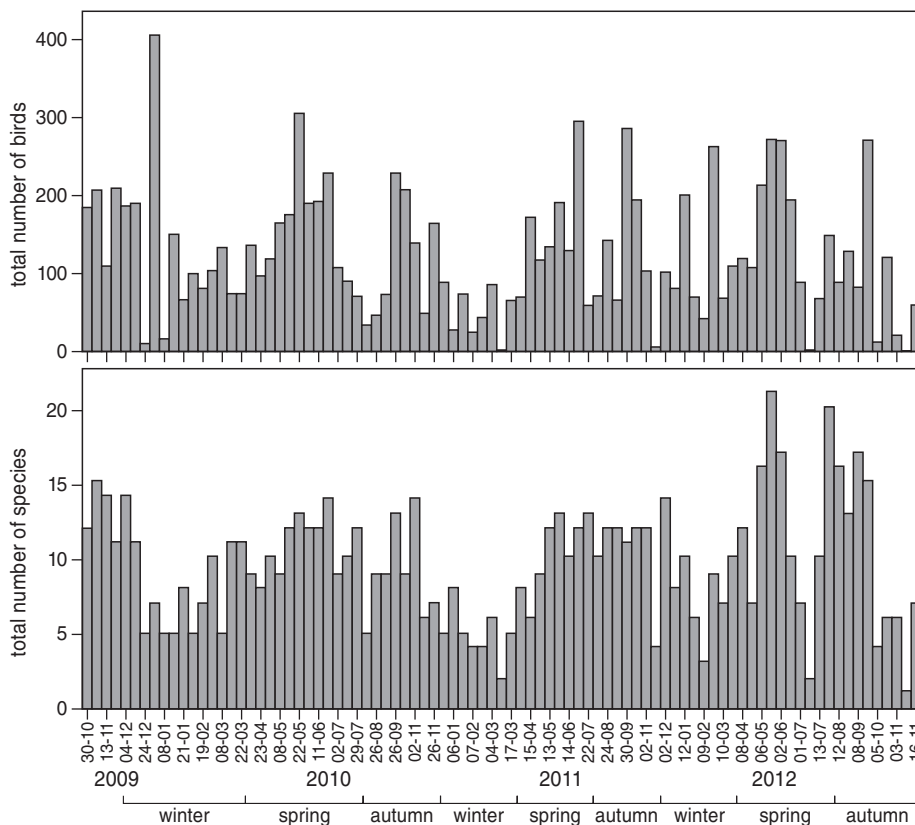
Figure B.1 Individual counts of the total number of birds (excluding flocking species) and total number of species in all experimental plots combined from October 2009 to November 2012. Figures of counts of individual species are shown in Appendix A. Numbers of birds in each season were used to determine for which bird species, in which seasons detailed analysis were conducted.

Table B.1 The grazing treatments did not significantly affect the distribution of individual birds in the study area after three years of livestock grazing. A significant interaction between grazing treatment and year (χ^2, p) in a generalised linear mixed model indicates a significant difference in the distribution of birds over the grazing treatments in the first and last year of the study. The signs (– and +) indicate how the estimates of the model for each grazing treatment change from the first to the last year of this study. Skylarks for example increase in abundance in all grazing treatments in spring (+ signs), but the distribution of the birds over the grazing treatments did not change significantly ($\chi^2 = 1.16$, p = ns).
NA indicates that insufficient data were available for analysis.

|		1 cattle/ha	1 horse/ha	0.5 cattle/ha	0.5 horses/ha	rotational	χ^2	p
all birds	spring	–	–	+	+	+	134.78	ns
	autumn	+	+	–	–	+	30.28	ns
	winter	–	–	–	–	+	413.46	<0.001
all species	spring	+	+	+	+	+	0.70	ns
	autumn	+	+	+	–	+	0.14	ns
	winter	–	–	–	–	–	0.08	ns
Redshank	spring	–	–	+	–	–	3.92	ns
	autumn	NA	NA	NA	NA	NA	NA	NA
	winter	NA	NA	NA	NA	NA	NA	NA
Rock Pipit	spring	NA	NA	NA	NA	NA	NA	NA
	autumn	–	–	–	–	–	0.07	ns
	winter	+	+	–	–	+	13.51	ns
Skylark	spring	+	+	+	+	+	1.16	ns
	autumn	+	–	–	–	–	1.55	ns
	winter	+	+	+	+	+	4.37	ns
Meadow Pipit	spring	+	–	+	+	+	5.57	ns
	autumn	+	+	+	–	+	2.46	ns
	winter	NA	NA	NA	NA	NA	NA	NA
Common Snipe	spring	NA	NA	NA	NA	NA	NA	NA
	autumn	+	+	+	+	+	2.70	ns
	winter	NA	NA	NA	NA	NA	NA	NA
Oystercatcher	spring	–	–	–	–	–	0.98	ns
	autumn	NA	NA	NA	NA	NA	NA	NA
	winter	NA	NA	NA	NA	NA	NA	NA
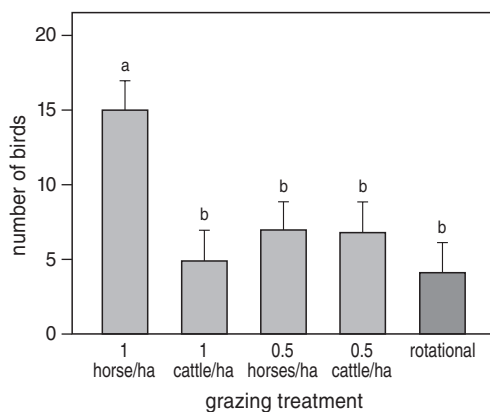
Figure B.2 The average number of birds (excluding flocking species) per two week interval.

Table B.2 Comparisons of the total number of birds between grazing treatments for the last year of the three year study in winter. The effects of grazing treatments clearly differ in each season. The signs (+ and –) indicate whether the generalised linear mixed model estimates more birds in the grazing treatment in the first column compared to the second column (+), or fewer birds (–).

		estimate	z-value	p
1 horse/ha	1 cattle/ha	+	3.722	<0.001
1 horse/ha	0.5 horses/ha	+	2.924	0.0275
1 horse/ha	0.5 cattle/ha	+	2.957	0.024
1 horse/ha	rotational	+	4.011	<0.001
1 cattle/ha	0.5 horses/ha	–	0.999	n.s.
1 cattle/ha	0.5 cattle/ha	–	0.961	n.s.
1 cattle/ha	rotational	+	0.429	n.s.
0.5 horses/ha	0.5 cattle/ha	+	0.039	n.s.
0.5 horses/ha	rotational	+	1.411	n.s.
0.5 cattle/ha	rotational	+	1.374	n.s.

Discussion

We expected that changes in the vegetation structure after three years of livestock grazing would change the distribution of birds over five livestock grazing treatments. For the total number of birds we found that experimental grazing significantly changed the distribution of the total number of birds (excluding flocking species) over a salt marsh in winter (Table B.1). The total number of birds in the winter of the last year of this study generally was higher in the more intensively grazed treatments. Possibly, food is more easily accessible in the short grazed vegetation of the intensively grazed treatments for some birds (Butler and Gillings 2004). Tall vegetation may make food items less visible (Buttler and Gillings 2004), may be harder to walk through for birds (Devereux et al. 2004) and may make it harder to detect approaching predators (Whittingham and Evans 2004).

The distribution of the total number of species and of individual bird species did not change significantly within three years of experimental grazing. We expect most of the changes in the distribution of birds to occur through changes in the structure of the vegetation. Nolte et al. (unpublished) showed that after three years of experimental grazing the canopy height in the grazing treatment with 0.5 cattle/ha was significantly higher than at the 1 cattle/ha and 1 horse/ha treatments. They also showed that the size of vegetation patches (mainly short vegetation) was significantly greater at horse grazed treatments than at cattle-grazed treatments. This suggests that within a few years of different grazing treatments, the vegetation structure did change in our study area. Nonetheless, it seems that three years of experimental grazing either is too short to find clear effects of different grazing treatments on the distribution of birds over a salt marsh or there are no effects of grazing treatments. A confounding factor may be that several of the studied species have a high breeding site fidelity (Thompson and Hale 1989, Jackson 1994, Heg et al. 2003, Bruinzeel 2006). This is likely to cause a delay in effects of grazing. We therefore recommend that large-scale grazing experiments are continued over a much longer timescale.

Spatial diversity in canopy height at Redshank and Oystercatcher nest-sites in relation to livestock grazing

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Jan P. Bakker

Abstract To understand how livestock grazing affects breeding bird numbers we need to 1) experimentally induce different grazing treatments, 2) measure breeding bird densities. In this study we did a large-scale experiment on grazing treatments and aimed to measure grazing effects on breeding bird densities. However the scale of the experiment, sufficient to establish effects on vegetation structure, was insufficient to statistically establish effects on breeding bird density. We therefore approached the problem via a different route. We measured vegetation micropatterns (mosaic of lower vegetation and taller patches at 4m × 4m) around Redshank (*Tringa totanus*) and Oystercatcher (*Haematopus ostralegus*) nests and at random sites paired with these nests sites to judge suitability of micropatterns for nest building. We also measured micropatterns at 120 permanent plots in five different experimental grazing treatments to determine how grazing affects micropatterns. We compared low stocking density of both cattle and of horses, high stocking density of cattle and of horses, and rotational grazing with a high stocking density of cattle (i.e. yearly intervals of grazing and no grazing).

   We found that Redshank and Oystercatcher nests occurred in sites with taller vegetation and more pronounced micropatterns than found at random sites. We also found that paddocks grazed with low densities of livestock or with a high density rotational grazing treatment had micropatterns as preferred by the birds. We conclude that Redshanks and Oystercatchers may benefit in terms of potential nest sites from grazing at low livestock densities or at rotational stocking densities through effects of grazing on micropatterns in the vegetation. However, this was not confirmed by direct counts of the breeding birds suggesting that limited nesting opportunity was not a very important factor. Alternatively, because both Redshank and Oystercatcher are long-living, site-faithful bird species, the duration of the experiment was too short to find effects on bird densities. We recommend a continuation of our experiment in order to study long term effects of livestock grazing on bird densities.

Introduction

Salt marshes along the Wadden Sea have a long history of livestock grazing (Bakker et al. 1993). However, in recent decades grazing of salt marshes in the northwest Europe was no longer economically feasible (Bakker et al. 1993). Therefore, many marshes were abandoned leading to tall homogeneous vegetation (Bakker et al. 1993, Esselink 2000, Esselink et al. 2002, Sammul et al. 2012). Yet, during the same period, grazing has become a common management tool in nature conservation (Ebrahimi et al. 2010) and is used as a management tool on salt marshes along the Wadden Sea coast. Grazing with high stocking densities generally leads to homogenous short vegetation (Bakker 1989), while a moderate grazing regime leads to a higher plant diversity (Bakker 1993).

The importance of spatial variation in canopy height for ground-breeding birds is well established. Norris et al. (1997, 1998) showed that the abundance of breeding Redshank on a marsh was determined by the percentage cover of sea couch *Elytrigia atherica*, the percentage cover of *Salicornia* sp. and *Suaeda maritima* and the diversity in canopy height. They also demonstrated how these parameters were related to grazing management, namely lightly grazed marshes had the highest densities of Redshanks and breeding densities of Redshanks decreased most on marshes where the grazing intensity increased from ungrazed/lightly grazed to higher grazing intensities. Milsom et al. (2000) found a positive relation of the numbers of ground-breeding birds with canopy height and the frequency and size of tussocks on coastal grazing marshes. Verhulst et al. (2011) indicate that the abundance of a number of wader species dropped with the intensification of grazing management and that the abundance of these waders is positively related to spatial variation in canopy height.

In this study we manipulated grazing intensity to causally relate breeding bird numbers to grazing regime with the aim to use this knowledge as a management tool. Because breeding bird numbers were too low for a direct approach we took an indirect approach. We related nest site selection of Redshanks and Oystercatchers to both canopy height and spatial variation in canopy height. By comparing the bird nest vegetation parameters with the vegetation parameters of different experimentally induced grazing regimes, we aim to judge what grazing regime would provide the best nesting opportunities for Oystercatchers and Redshank.

Methods

Study area

The study area (Noard Fryslân Bûtendyks) was located on the mainland coast in the north of the Netherlands (53° 20'N 5° 43'E). It is part of a large interconnected salt-marsh area (>4000 ha), managed as a nature reserve. The study area has a low salt marsh on the sea side that gradually changes halfway the distance from the edge of the salt marsh to a low summerdike in a higher salt marsh (Fig. 1.2). The area is important for a great number of breeding birds, mostly waders, in spring and thousands of geese overwinter there. In autumn, the geese in the study area prefer high

density livestock grazed sites (Mandema unpublished). Therefore, in addition to livestock grazing, grazing by geese may affect spatial variation in canopy height.

Experimental set up

The experiment consisted of three replicates (55ha/replicate) with five grazing treatments (11ha paddocks for each treatment) per replicate in a full factorial design. Before the experiment two of the replicates were long term (>10 years) grazed with approximately 1 cattle/ha and one replicate was long term ungrazed (>10 years), followed by one year of high pressure grazing to homogenise the treatments. The grazing treatments implemented in 2010 were: every year low stocking densities with 0.5 cattle/ha or 0.5 horses/ha, every year high stocking densities with 1 cattle/ha or 1 horse/ha and rotational grazing with a high stocking density of 1 cattle/ha at yearly intervals. No grazing was not added to the experiment, because 1) previous studies already established that no livestock grazing of a salt marsh is detrimental to biodiversity (Bakker et al. 2003, Norris 1997, Norris 1998) and 2) including a control area would reduce the number of grazing treatments that could be tested. We proceeded on the recommendations of Bakker et al. 2003: "The question for nature conservation in salt marshes is not: 'to graze or not to graze', but 'what are the targets and which role can grazing management play to reach these targets?'"

In this paper we focus on the type of livestock grazing that is most beneficial for the establishment of nest sites by Redshanks and Oystercatchers.

The grazing treatments were allocated randomly to each replicate; however, two horse grazed treatments were never placed next to each other, because horses were expected to influence one another if placed in adjacent paddocks. Fresh water was available for the grazing animals in each paddock (Fig. 1.2). The livestock was let into the grazing experiment in 2010, hence the paddocks with rotational grazing were not grazed in 2010 and grazed in 2011. Grazing treatments were applied in spring and summer (June to September), not in the other parts of the year.

Canopy heights were measured at nest sites and paired random sites in 2010, the first year of experimental grazing. To compare treatments, canopy heights were measured in each grazing treatment in 2011, after one year of experimental grazing.

Study organisms

We focus on the two most common ground-breeding waders in the study area, the Common Redshank (*Tringa totanus*) and the Eurasian Oystercatcher (*Haematopus ostralegus*). In the Wadden Sea area, both Redshank and Oystercatcher show a decline in breeding numbers since 1991 (Koffijberg et al. 2009). The two species represent two extremes in a range of nest concealment. Redshanks generally build concealed nests in tufts of vegetation and rely on camouflage. They only leave the nest at the very last minute upon approach of a predator (Niethammer & von Blotzheim 1966, Beintema et al 1995, Norris et al. 1998). Oystercatchers build their nests in relatively open vegetation, and rely on distraction displays and attack to deter predators (Niethammer & von Blotzheim 1966, Green et al. 1990).

Diversity in canopy heights was found to be an important factor in the nest-site choice of Redshanks (Norris et al. 1997, Verhulst et al. 2011). Tall tufts of vegetation

offer nest concealment opportunities, while surrounding, more open and short vegetation provides an escape route and better vision of approaching threats (Dallinga 1993, Whittingham & Evans 2004). Oystercatchers are active nest defenders, making nest concealment of lesser importance than for Redshanks (Green et al. 1990).

We actively searched for nests of Oystercatchers and Redshanks in the study area in the breeding season of 2010 and 2011 by visually following birds to their nest after disturbance. Nests were also found by flushing incubating birds from their nests. We searched through every treatment thoroughly and throughout the breeding season.

Edge value and canopy height

Vegetation characteristics of Redshank and Oystercatcher nest-sites were determined with a method used by (Berg et al. 1997). This method places a grid over the vegetation. The canopy height is measured in each grid cell. For each cell, the edge value can then be calculated as the average difference between the value of a cell and the values of its eight surrounding cells, weighted for the reciprocal distance to the middle cell with the formula

$$\text{Edge value (cm)} = (\sum_{i=1}^{4} |X - Y_i| + \sum_{j=1}^{4} |X - Y_j|/\sqrt{2})/(4 + 4\sqrt{2})$$

(Berg et al. 1997) (Fig. 3.1, Fig. 3.2). X is the central cell in a square of 9 cells. Y_i represent the four adjacent neighbouring cells and Z_j the four diagonal neighbouring cells. The smaller the differences between a cell and its surrounding cells, the lower the edge value for that cell.

We placed a 4 m × 4 m meter grid, consisting of 64 cells (50 cm × 50 cm) around each nest-site. Within each cell the canopy height was measured to the nearest cm using a Styrofoam drop disk (25 cm diameter, 75 g) (Holmes 1974, Stewart et al. 2001). From the canopy heights, edge values were calculated for the 36 inner cells of the grid according to (Berg et al. 1997). Subsequently, we averaged these 36 edge values to arrive at the average edge value. Additionally, the canopy heights measured at each of the 64 cells were averaged to calculate the average canopy height at each site.

A total of 29 Oystercatcher and 22 Redshank nests were paired with a random site and both were measured. The paired sites were located in the same grazing treatment (coordinates randomly generated in ArcGIS (ESRI inc. 2009) and with similar surface elevation as the nests to make sure that the nest and random site were in zones with similar inundation frequency and hence vegetation zones since vegetation composition changes strongly from low marsh to high marsh (Erchinger 1985).

To understand how livestock affects spatial variation in canopy height we compared average edge values in different grazing treatments. We placed permanent plots (four on the high marsh and four on the low marsh) within all paddocks and at similar elevation between grazing treatments within a replicate. Average edge values and average canopy height in the permanent plots were measured in 2011 (the second year of grazing in the experiment) with the same method as for the nest sites.
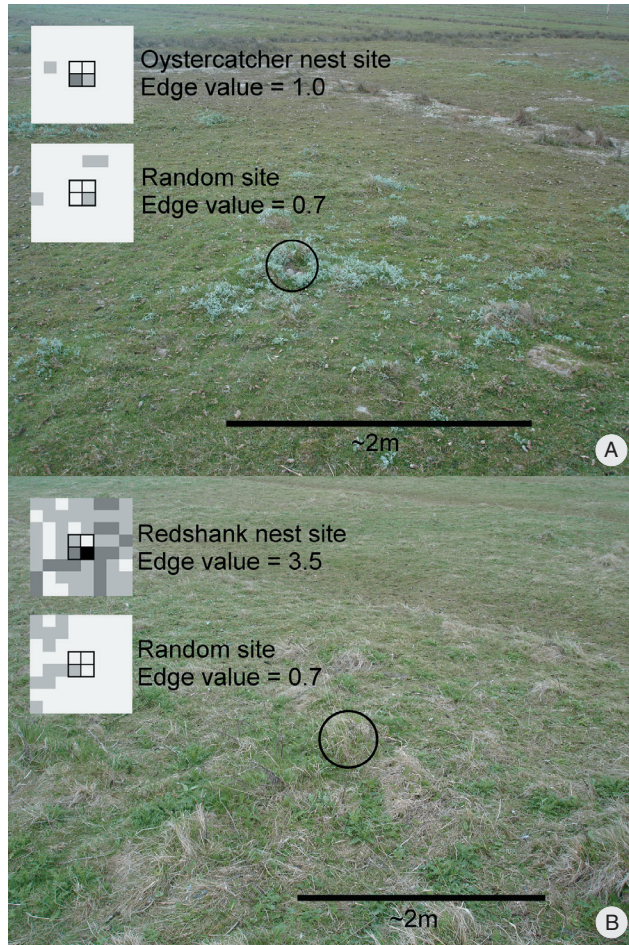
Figure 3.1 An Oystercatcher (A) and Redshank (B) nest site. The circle in each photograph indicates the position of the nest. The square grids in both photographs show the differences in canopy height between the 64 cells of the grid around a nest site and around a paired random site. The cross in the middle of the grid indicates the position of the nest or random coordinate. For the figure, the canopy height is subdivided in four classes. White is 0–5cm, light grey is 6–10cm, dark grey is 11–20cm and black is >20cm.

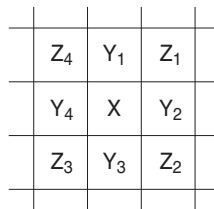|				
	Z_4	Y_1	Z_1	
	Y_4	X	Y_2	
	Z_3	Y_3	Z_2	

Figure 3.2 Diagram demonstrating how to calculate the edge value (Berg et al. 1997).

A visit to a measuring site, including setting up the grid and measuring canopy height in 64 cells lasted a maximum of 20 minutes. Measurements were not taken during rain, fog or with extreme temperatures to avoid cooling or overheating of the eggs.

Analysis

Both edge values and average canopy heights at nest sites and at random sites were compared using a Wilcoxon signed-rank test (package 'stats' in R version 2.15.0 (R Development Core Team 2012). Multiple comparisons were corrected with a Bonferroni adjustment (package stats).

To study the experimental effects of the different grazing treatments on average edge values, we created a Linear Mixed Model with the average edge values of the permanent plots as the response variable and grazing treatment as an explanatory variable. The random structure of the model was defined as a random intercept for each replicate (n = 3). To compare average edge values between different grazing treatments, we used the multcomp package (Hothorn et al. 2008) in R (R Development Core Team 2012) for simultaneous comparisons of all five factor levels. A similar model with the average canopy height instead of the average edge values was created to study the effects of grazing treatments on the average canopy height.

In all statistical models, the response variables were transformed by taking the natural log to normalise the residuals and correct for heteroscedasticity of the model. The models were fitted using the lme4 package (Bates et al. 2011) in R version 2.15.1 (R Development Core Team). Model selection was performed by backwards elimination, comparing models at every step using AIC values (Zuur et al. 2009).

Results

A comparison of Redshank and Oystercatcher nests with paired random sites showed that both Redshanks and Oystercatchers had nest sites with significantly higher edge values and taller canopy than found at random sites (Fig. 3.3). Surprisingly, we did not find significant differences in the edge values between Redshank and Oystercatcher nests, although there was a trend towards higher values at Redshank nest-sites.

From the grazing experiment, we found that the average edge values and average canopy height of lightly grazed treatments (0.5 horse/ha, 0.5 cattle/ha and rotational grazing) were significantly higher than the average edge values and average canopy height at heavily grazed treatments (1 horse/ha and 1 cattle/ha) (Fig. 3.4, Table 3.1, 3.2). Quantitatively the average edge values in low density grazed or rotationally grazed treatments were similar to the edge values around the nest sites (compare Fig. 3.3 and Fig. 3.4), suggesting that they should be preferred for nesting by waders. However, the number of nests found in 2010 and 2011 (after establishing the grazing treatments) did not differ between grazing treatments (Table 3.3). In low density and rotationally grazed paddocks we found 6.7 ± 3.9 (average ± sd) nests per paddock in
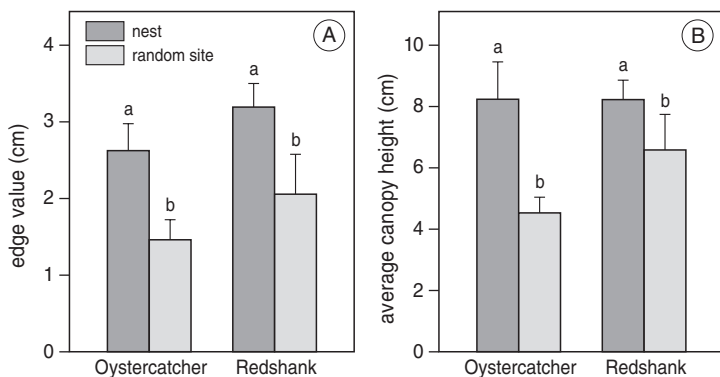
Figure 3.3 Both Oystercatchers and Redshanks choose nest sites with significantly higher average edge values (A) and a taller canopy height (B) than found at random sites as indicated by the average edge values and the average canopy height respectively. Letters denote significant differences according to a Wilcoxon signed-rank test, corrected for multiple comparisons using a Bonferonni adjustment.
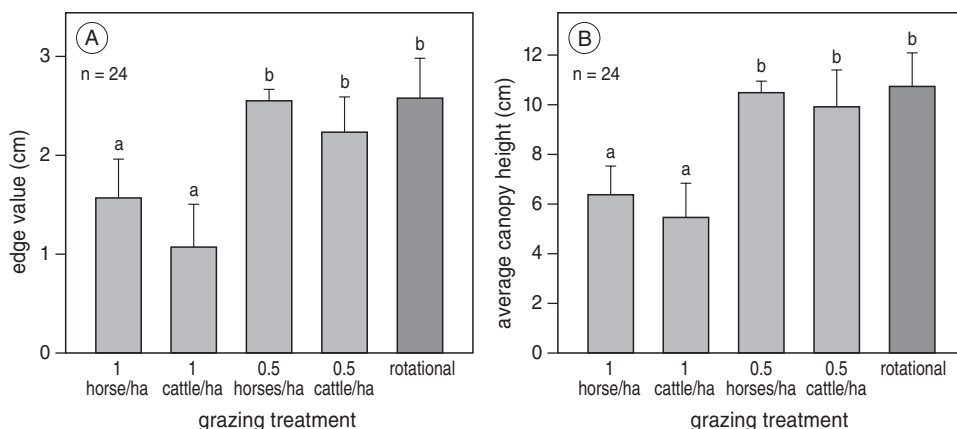

Figure 3.4 Measurements taken at permanent plots (n = 120) show that the low density grazed treatment and the rotational treatment have significantly higher average edge values (A) and a taller average canopy height (B) than high density grazed sites as indicated by the average edge values and the average canopy height respectively. Letters denote significant differences between treatments (fixed effect) as found with a Linear Mixed Effects Model. For the readability of the figures, the non-transformed edge values and canopy heights are shown.

the two years of the present study, while in high density grazed paddocks we found 6.2 ± 3.4 (average ± sd) nests per paddock of 11ha.

Edge values generally increase with increasing canopy height and canopy height increases with time. However, the nests and paired random sites were both measured throughout the breeding season. So there is a general trend that the edge values and canopy height at nest sites are higher than at random sites throughout the season.

Table 3.1 Estimates and t-values for the fixed effects of a Linear Mixed Model for the experimental treatment effects on average edge values. The Linear Mixed Model was applied using the lme4 package (Bates et al. 2011) in R version 2.15.1 (R Development Core Team 2012). The approximation of p-values for the fixed effects of a linear mixed model is under debate (Bates 2006). Therefore, the package lme4 does not provide an approximation and we do not provide p-values here.

	Estimate	t-value
1 horse/ha	-0.071	-0.221
1 cattle/ha	-0.036	-0.098
0.5 horses/ha	0.580	3.874
0.5 cattle/ha	0.658	4.368
Rotational 1 cattle/ha	0.700	4.629

Table 3.2 Estimates and t-values for the fixed effects of a Linear Mixed Model for the experimental treatment effects on average canopy height. See Table 1 for additional details.

	Estimate	t-value
1 horse/ha	1.593	-0.310
1 cattle/ha	1.624	5.280
0.5 horses/ha	2.156	5.344
0.5 cattle/ha	2.095	4.727
Rotational 1 cattle/ha	2.219	5.971

Table 3.3 Total number of Redshank and Oystercatcher nests found in each replicate in 2010 and 2011.

	Replicate 1		Replicate 2		Replicate 3		Total
	Oysterc.	Redshank	Oysterc.	Redshank	Oysterc.	Redshank	
1 horse/ha	1	1	2	5	5	0	14
1 cattle/ha	2	5	6	6	3	1	23
0.5 horses/ha	1	0	4	3	9	1	18
0.5 cattle/ha	2	1	7	7	4	2	23
Rotational 1 cattle/ha	2	2	4	5	3	3	19
Total	8	9	23	26	24	7	97

Discussion

Redshanks and Oystercatchers built their nests in areas with relatively tall vegetation and high variation in canopy height. Such vegetation was more prominent in low livestock densities or at rotational grazing treatments than in the higher stocking density treatments suggesting that breeding opportunities were better in the low livestock treatments.

Spatial variation in canopy height and average canopy height are known to be important in the nest-site choice of waders. We found that both Redshanks and Oystercatchers choose nest sites with significantly higher average edge values than at random sites, implying a preference for spatial variation in canopy height around nest sites. Spatial variation in canopy height may provide better camouflage for the nest, while retaining an open view and escape route from the nest (Dallinga 1993, Whittingham et al. 2004). Additionally, increasing spatial diversity in canopy height may result in an increased invertebrate diversity (Olff & Ritchie 1998, Balmer & Erhardt 2000, Dennis et al. 2001, Woodcock et al. 2005, Rickert et al. 2012), providing food for chicks, once hatched.

We expected that average canopy height and spatial variation in canopy height would be more important in the nest site selection of Redshanks than of Oystercatchers on the basis of how these species differ in nest-protection strategy (see introduction). Although we found a trend towards higher edge values and canopy heights at Redshank nests, we did not find a significant difference between the two species. Both species selected nest sites with higher edge values and canopy heights than at paired random sites. Considering the different nest-defence strategies of the two species, this result is surprising. Perhaps differences between the species are more prominent on a smaller scale, e.g. the canopy height directly at the nest.

Although the data are sparse, there is no indication that breeding bird numbers differed with experimental grazing treatment. This may relate to the fact that both Redshanks and Oystercatchers are long-lived and highly site faithful (Thompson & Hale 1989, Jackson 1994, Heg et al. 2003, Bruinzeel 2006), and therefore that the effect of grazing may not yet have become evident. On the longer term, new birds settling in the study area may very well choose to breed in low density grazed sites with higher edge values.

We judge as most parsimonious explanation for the observations that 1) both species preferably nest in a vegetation structure that is most available in the low grazing treatments, yet, 2) that there is no sign that the breeding densities differ between treatments is that breeding opportunities are not limited by grazing regime through vegetation structure. Maybe, the densities of breeding Redshanks and Oystercatchers in each grazing treatment are so low, that there are enough potential nest-sites available in each of them. However, since both Redshank and Oystercatcher are long-living, site-faithful bird species (Thompson & Hale 1989, Jackson 1994, Heg et al. 2003, Bruinzeel 200). It may take several years for individual birds to adapt to changes in the vegetation structure, so the duration of the experiment may have been too short to find effects on bird densities. We recommend a continuation of our experiment in order to study long term effects of livestock grazing on bird densities.

We conclude that grazing management conducted at 0.5 cattle or horses/ha each year or at 1 cattle/ha at yearly intervals induces a vegetation structure that, in terms of canopy height and spatial variation in canopy height, is potentially better to provide nesting sites for Oystercatchers and Redshanks. Yet, grazing regime did not detectably affect breeding densities of these two species, suggesting that in the short term a lack of breeding opportunity caused by grazing regime is unlikely for these species. It remains to be shown experimentally that grazing treatments do not affect the density of breeding waders on a longer term.

Livestock grazing and trampling of birds' nests: an experiment using artificial nests

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Abstract

Purpose

The purpose of this study is to experimentally determine the differences between four grazing treatments on the trampling of nests. Additionally, we examine to what extent the trampling probability of nests is higher close to a source of fresh water.

Methods

We compare the trampling of artificial nests in five different grazing treatments in an experimental design. We use buried clay pigeon targets as artificial mimics of bird nests to obtain reliable estimates of trampling risk and compare these with real nests.

Results

We find that horses trample significantly more artificial nests than cattle resulting in lower survival rates of artificial nests under horse grazing than under cattle grazing. For both horses and cattle, we find a clear trend, approaching significance, towards more trampling at higher numbers of livestock. We found that more artificial nests are trampled closer to a freshwater tank. The survival probability of artificial nests in cattle grazed treatments in this study is found to be in the same range as real nests in the study area and very close to the survival probability of Northern Lapwing (*Vanellus vanellus*) nests under cattle grazing in a different system.

Conclusions

We recommend that horses should not be used as grazers for management purposes in areas with high densities of birds' nests in order to minimize the risk of nests being trampled. Additionally, we confirm that the location of freshwater tanks has an important effect on the distribution of livestock and hence on trampling of nests.

Introduction

Livestock grazing is commonly used as a nature management tool (Bakker 1989, Ebrahimi et al. 2010). However, a standing question in nature management is what type of livestock to use and in which densities. Trampling by livestock may result in the destruction of nests of ground-nesting birds (Fuller and Gough 1999). The risk of nests being trampled depends on the bird species as well as the type and density of livestock and time of nesting (Beintema and Müskens 1987; Green 1988; Fuller and Gough 1999). Effects of the type of livestock on trampling of birds' nests have been thoroughly studied for cattle and sheep (Beintema and Müskens 1987; Fuller and Gough 1999; Hart et al. 2002; Ottvall 2005b; Pakanen et al. 2011). Studies on trampling by horses, however, are largely absent. The digestive system of horses is different from that of cattle (Duncan et al. 1990). To obtain sufficient nutrition, horses have higher rates of food intake and consume larger quantities of food on a daily basis than cattle with similar body mass (Arnold 1984; Duncan et al. 1990; Menard et al. 2002). This leads to horses having been observed to have longer daily grazing times than cattle (Arnold 1984; Duncan et al. 1990; Janis et al. 2010). Therefore they are likely to be more active, presumably increasing the probability of trampling a nest. Additionally, horses trample with greater pressure than cattle, an effect that is strengthened by running (Liddle 1997). A possible positive effect of horse grazing is their creation of 'latrines', especially in low stocking densities. The rejection of herbage contaminated by dung (Frame and Laidlaw 2011) may lead to a higher canopy height, which is a major descriptor of canopy structure (Frame and Laidlaw 2011). Canopy structure, in turn, is important for ground nesting waders, such as Redshanks and Lapwing (Norris et al. 1997; Whittingham and Evans 2004).

Another potentially important factor on the trampling probability of nests is water availability. Water availability affects the distribution of livestock in areas where fresh water is scarce (Vallentine 1971; Holechek 1988; Ganskopp 2001). An uneven distribution of livestock can lead to several problems associated with grazing, such as damage caused by trampling (Lange 1985). We expect that the relative density of livestock is higher close to a freshwater tank, thereby increasing the trampling probability of nests near freshwater tanks. The purpose of the present study is to experimentally determine the differences between four grazing treatments (1 horse/ha, 0.5 horse/ha, 1 cattle/ha and 0.5 cattle/ha) on the trampling of nests and to assess to what extent the trampling probability of nests is affected by the proximity of a freshwater tank.

The study was carried out in a salt marsh system. Fresh water is only available at the freshwater tanks provided in the experiment. As the density of birds' nests was too low for direct comparisons of trampling risk between grazing treatments of real nests, we used artificial nests to compare treatments. Artificial nests have been used in a number of studies to assess predation of birds' nests (e.g. Martin, 1987; Picman 1987; Major 1991; Bayne and Hobson 1997; Maier and Degraaf 2001; Boulton and Cassey 2006). They have also been used successfully for studies on trampling (Koerth et al. 1983; Jensen et al. 1990; Paine et al. 1996; Pavel 2004). In

this study, we use artificial nests to assess the relative trampling risk between different grazing treatments.

In order to validate the use of artificial nests, we compare artificial nests with real wader nests by calculating trampling probabilities (Beintema and Müskens 1987) for our artificial nests and comparing them to trampling probabilities found for the small sample of real wader nests in our study area. We also compare trampling probabilities of artificial nests with trampling probabilities of real wader nests found by Beintema and Müskens (1987) in an inland grassland system.

Methods

Study site
This study was carried out on a site along the Dutch Wadden Sea coast in a mainland salt marsh (53° 20′N 5° 43′E), which is part of the UNESCO Wadden Sea World Heritage Site. It is a man-made marsh with high clay content in the soil, created with the aid of sedimentation fields. These are maintained to avoid erosion of the salt marsh. Approximately half of the study area can be considered high marsh, close to the summer dike, (Fig. 4.1) and half low marsh, close to the sea. Higher parts of the marsh are inundated less frequently with sea water than lower parts. The study site is an important breeding area for several wader species.

Experimental design
Within the study area, a grazing experiment was set up with three replicate blocks. Each replicate area of 55 ha consisted of five equally sized paddocks with different grazing treatments. We studied four grazing treatments: 0.5 cattle/ha, 0.5 horses/ha, 1 cattle/ha and 1 horse/ha (Fig. 4.1). A fifth treatment (rotational grazing with 10 cattle at yearly intervals) was not studied because it also contained 1 cattle/ha at the time of this study, providing little extra information. The different grazing treatments were allocated randomly to the paddocks in each replicate with the restriction that no two horse grazed treatments were placed next to each other, as horses were expected to influence one another if placed in adjacent paddocks. Each paddock contained a freshwater tank close to the summer dike (Fig. 4.1).

Clay pigeon targets used as artificial nests
To estimate and compare the trampling intensity between different grazing treatments, we used clay pigeon targets (fragile round discs used for shooting sports) as artificial nests.

Clay pigeon targets have been used extensively to estimate the effects of trampling by livestock (Koerth et al. 1983; Jensen et al. 1990; Paine et al. 1997; Gregory and Gamett 2009). Paine et al. (1997) found that trampling levels were similar for clay pigeon targets and simulated nests with pheasant eggs. Pavel (2004) found that artificial nests with plasticine clay in jam jar lids had similar trampling rates as natural nests of Meadow Pipit (*Anthus pratensis*) and Water Pipit (*Anthus spinoletta*). However, during a pilot study, we found that the plasticine clay was eaten by
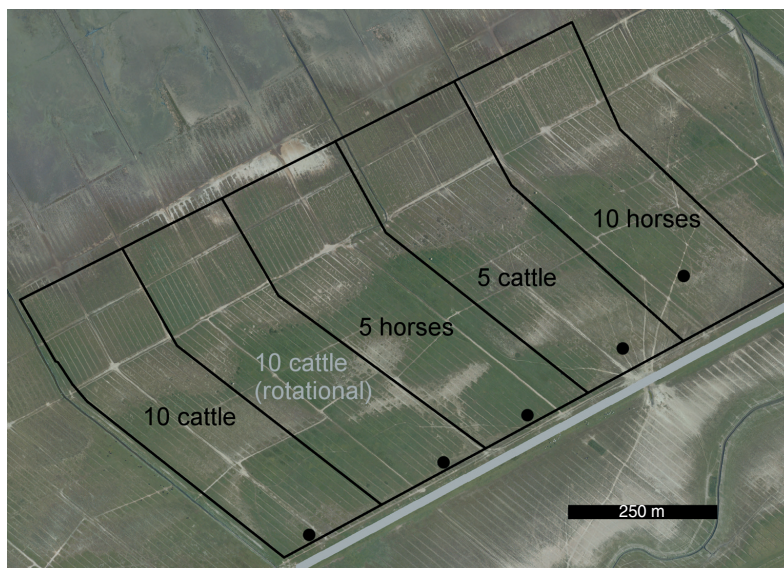
Figure 4.1 Distribution of five grazing regimes over five 11ha paddocks within one of the 55ha replicate blocks. Fifty artificial nests were randomly placed in all treatments, except for the rotational treatment. Black dots indicate the position of freshwater tanks. The grey line indicates the position of the summer dike.

the cattle in our study area, making this an unsuitable method. Instead we chose to use clay pigeon targets. The high visibility of clay pigeon targets may, however, attract livestock (Pavel 2004). Therefore, we covered the clay pigeon targets with soil to counterbalance the high visibility. For this, a soil core of 10cm diameter and 10cm depth was taken, a clay pigeon (diameter = 10 cm) was placed in the hole and the intact soil core was placed on top of the clay pigeon. The clay pigeon breaks when these soil cores are stepped on by cattle and horses. The study area was not open to the public and was fenced off with electric fence. Therefore it was not possible for large grazers other than the livestock to enter the field and breaking of artificial nests could be fully attributed to the livestock used for the experiment.

Random coordinates to place the artificial nests were generated in ArcGIS (*ArcGIS Desktop* 2010). Pavel (2004) did not find a difference in nest trampling of artificial nests placed in 'nest like locations' and artificial nests placed in a grid. This suggests that random placing of nests should provide proper estimates of trampling by livestock. In this manner, 50 clay pigeon targets were placed randomly in each of the four grazing treatments within each replicate block (total number = 600). Although 50 nests per 11 ha is a higher density than generally expected with natural nests of non-colonial bird species, Koerth et al. (1983) and Beintema and Müskens (1987) showed that relative trampling loss does not increase at higher nest densities. The artificial nests were placed on 26, 27 and 30 May 2011 respectively in each replicate and were left in the field for 21 days, which is similar to the incubation

time of a number of breeding waders (von Blotzheim, 2004). Artificial nests were checked after 7 and 21 days and recorded to be intact or trampled. A metal pin was placed in the ground next to each artificial nest and the coordinates were recorded in order to be able to find the artificial nests again with a GPS and metal detector. If artificial nests could not be found after 21 days, they were left out of the analysis. Artificial nests trampled after seven days were removed from the field.

Trampling probability in different grazing treatments
As all the artificial nests in a paddock (field within a replicate, Fig. 4.1) were pseudo-replicates, we used a linear mixed-effects model approach to analyse this data (Zuur et al. 2009). We assessed the effect of livestock species, grazing intensity and distance from the fresh water supply on trampling risk of our artificial nests. The artificial nests we could find after 21 days were used to model trampling as a binary input variable (trampled or intact), as explained by the distance of each artificial nest to the freshwater tank, the type of livestock, the density of livestock, an inter-action between distance to the freshwater tank and livestock type, an interaction between distance and livestock density and a three way interaction between distance, livestock type and livestock density. Replicate and paddock were used as random factors in the model. Models were fitted using the lme4 package (Bates et al., 2011) in R, version 2.14.1 (R Development Core Team 2011) and model selection was conducted using backward elimination, using AIC values to compare models. Using the parameters from the statistical model, pairwise comparisons between livestock types and densities were made with the multcomp package (Hothorn et al. 2008). The results for the effect of density and livestock were confirmed using an ANOVA approach on the fractions of nests trampled at different livestock types and densities. The distance from artificial nests to the fresh water supply in a paddock was calculated with ArcMap version 10.0 (*ArcGIS Desktop* 2010).

Comparison with real nests
We calculated V-values (survival rates of artificial nests per grazing animal per hectare per day) for the artificial nests in each grazing treatment as described by Beintema and Müskens (1987), using the observations after 7 and 21 days. A V-value of 1 indicates a nest survived one day with one grazer per hectare, while a value of 0 indicates a nest has been trampled after one day with one grazer per hectare. These V-values are directly comparable to V-values found for real nests. We calculated V-values for Common Redshank (*Tringa totanus*) (n = 16) and Eurasian Oystercatcher (*Haematopus ostralegus*) (n = 24) nests (two of the most common ground breeding waders in the study area). These nests were found and monitored in 2010 and 2011. Each trampling event was recorded. Additionally, Beintema and Müskens (1987) calculated V-values for several wader species under different grazing treatments in an inland grassland system. We compared V-values between cattle and horses with a Z-test as described by Johnson (1979) and applied by McGowan et al. (2005).

Results

Out of 600 artificial nests placed, 524 could be found after 21 days and of those 118 had been trampled, a fraction of 0.225 (Table 4.1). There is no reason to assume differences in the probability of finding back trampled or non-trampled artificial nests. Those nests not found back were generally located in large patches of tall vegetation, or were submerged under sea water, due to a flood of the study area just prior to the final check of the artificial nests. One paddock which combined a relatively tall canopy with a large amount of standing water due to the flood had a particularly low recovery rate (Table 4.1).

The trampling probability of artificial nests differed with grazer type. Horses trampled significantly more artificial nests than cattle as shown by pairwise comparisons of grazing treatments (Fig. 4.2) and regression analysis (Fig. 4.3). Pairwise comparison showed that 1 horse/ha trampled significantly more than 1 and 0.5 cattle/ha and that 0.5 horses/ha trampled significantly more than 0.5 cattle/ha (Fig. 4.2). Within each species of grazer, we found a clear, although non-significant ($p = 0.076$, Table 4.2), trend towards more grazers leading to more trampling of artificial nests. We did not find an interaction between grazing treatment and distance to a freshwater tank. This suggests that both for cattle and for horses, the distance to water has a similar effect.

With the linear mixed model used in this study, we found that the variance between paddocks within blocks is zero. To confirm the outcome of the model relating to differences in trampling between horses and cattle and between 0.5 and 1 animals/ha, we did an additional analysis (ANOVA) on the fractions of nests trampled per paddock (Table 4.1). In this reduced form, the data still showed a significant difference between horses and cattle and a significant difference between

Table 4.1 Numbers of artificial nests placed and the fraction trampled after 21 days.

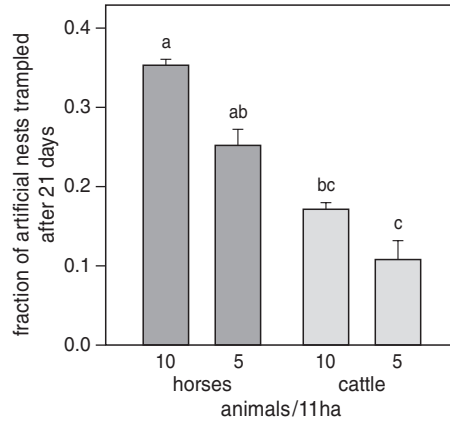| Replicate	density	species	nests placed	nests found (after 21 days)	nests trampled (21 days)	fraction
1	5	cattle	50	46	6	0.13
1	10	cattle	50	50	8	0.16
1	5	horses	50	49	14	0.286
1	10	horses	50	44	17	0.386
2	5	cattle	50	50	3	0.06
2	10	cattle	50	49	9	0.184
2	5	horses	50	48	12	0.25
2	10	horses	50	47	17	0.362
3	5	cattle	50	31	4	0.129
3	10	cattle	50	41	7	0.171
3	5	horses	50	28	6	0.214
3	10	horses	50	41	15	0.366

Figure 4.2 In horse-grazed treatments, more artificial nests were trampled after 21 days than in cattle-grazed treatments. Error bars represent standard errors of the mean, calculated over three replicates. Letters denote significant differences at 0.05% between grazing treatments in the trampling intensity of nests as found with a logistic regression model.

1 and 0.5 animals/ha was found as well (F-values of 90.58 and 26.78 and p-values of <0.001 and <0.001 respectively). The ANOVA therefore confirms the results of the more appropriate, linear mixed model.

The distance to a freshwater tank had a strong effect on the trampling probability of artificial nests. Logistic regression showed that the probability an artificial nest was trampled decreased with the distance to a freshwater tank (Fig. 4.3).

To compare artificial nests to real nests, daily survival rates of artificial nests per grazing animal per hectare (V-values, (Beintema and Müskens 1987)) were calcu-

Table 4.2 Results of a linear mixed model with distance to fresh water as a continuous explanatory variable and livestock species and livestock density as factors. Replicate and paddock were included as nested random factors in the model. The results of this model are followed by the results of a multiple comparison of all factor levels based on the model. Due to an adjustment to the p-values, because of the multiple comparisons, the difference in trampling between 10 and 5 animals is just not significant at the 5% level. However, there is a clear trend (Fig. 2).

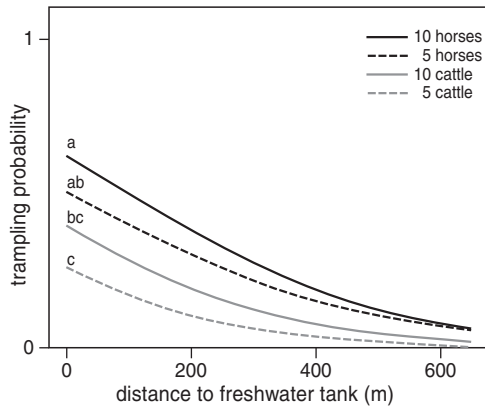|	Z-value	p-value
Intercept	-3.654	<0.001
Distance to fresh water	-5.881	<0.001
Livestock species	4.647	<0.001
Livestock density	2.067	<0.05
Results of multiple comparison of factors in the model		
Horses-cattle	4.647	<0.001
10 animals-5 animals	2.067	0.076

Figure 4.3 The probability of an artificial nest being trampled was greater closer to a freshwater tank. Letters denote significant differences between grazing treatments (shown in inset legend). Horses were more likely to trample nests than cattle. Nests were left in the study area for a maximum of 21 days.

lated. The survival rates we found for horse treatments were significantly lower than those for cattle treatments (Table 4.3). This result complies with the earlier findings on the trampling probability of artificial nests.

The V-values can be used to compare artificial nests to real nests of different bird species. With limited Eurasian Oystercatcher and Common Redshank nests exposed to livestock (14 Eurasian Oystercatcher nests and 12 Common Redshank nests exposed to cattle and 10 Eurasian Oystercatcher nests and 4 Common Redshank nests exposed to horses) and few nests trampled (0, 2, 1 and 0 respectively) in this study, we could only calculate biologically relevant V-values for Common Redshanks exposed to cattle and Eurasian Oystercatchers exposed to horses. When no nests were found trampled, the calculated survival probabilities would be 1. It is highly unlikely that this would be true in any grazed system, so a larger sample size is required in these cases. We found a V-value of 0.962 ± 0.026 for Common Redshanks under cattle grazing and a V-value of 0.971 ± 0.028 Eurasian Oystercatchers under horse grazing. We also compared V-values of artificial nests with V-values found by Beintema and Müskens (1987) in a grassland system. We found that our V-values for artificial nests under cattle grazing were very similar to V-values of Northern Lapwing nests under cattle grazing as found by Beintema and Müskens (1987) (Table 4.4). As Beintema and Müskens (1987) did not study horse grazed treatments, we could not directly compare artificial nests under horse grazing with real nests under horse grazing. However, for three of the four wader species studied by Beintema and Müskens (1987), the survival rates of nests under cattle-grazed treatments were higher than the survival rates we found for artificial nests under horse-grazed treatments (Table 4.3 and 4.4). This again suggests a higher risk of nest trampling with horses than with cattle.

Table 4.3 V-values (survival rate of artificial nests per grazing animal per hectare per day) ± standard deviations as calculated according to Beintema and Müskens (1987). A value of 1 indicates a nest definitely survives a day with one grazer per ha, a value of 0 indicates a nest is definitely trampled after one day with one grazer per ha. Survival rates over several days (t) can be calculated by V^t.

Using the average V-value for horses, we expect 29 out of 50 nests to survive a 21 day period with one horse per ha ($50*0.975^{21} = 29$ nests). V-values were calculated using data collected after 7 days and after 21 days.

treatment	cattle		horse	
	replicate	V	replicate	V
10 cattle	1	0.991 ± 0.003	1	0.978 ± 0.006
10 cattle	2	0.990 ± 0.003	2	0.978 ± 0.006
10 cattle	3	0.991 ± 0.003	3	0.978 ± 0.005
5 cattle	1	0.994 ± 0.004	1	0.979 ± 0.008
5 cattle	2	0.986 ± 0.006	2	0.966 ± 0.009
5 cattle	3	0.987 ± 0.006	3	0.970 ± 0.008
Average		0.990 ± 0.004*		0.975 ± 0.007*

* The average V-values for cattle and for horses are significantly different, p<0.05 (Z test (Johnson 1979; McGowan et al. 2005))

Table 4.4 V-values ± standard deviations from Beintema and Müskens (1987). Grazing systems: 1, dairy cattle during the day only; 2, dairy cattle day and night; 3, yearlings day and night; 4, sheep day and night.

Species	Grazing system	V
Northern Lapwing	1	0.995 ± 0.0013
	2	0.990 ± 0.0017
	3	0.984 ± 0.0024
	4	0.996 ± 0.0015
Black-tailed Godwit	1	0.988 ± 0.0027
	2	0.982 ± 0.0031
	3	0.960 ± 0.0050
	4	0.993 ± 0.0026
Common Redshank	1	0.972 ± 0.0097
	2	0.973 ± 0.0045
	3	0.964 ± 0.0045
	4	0.993 ± 0.0034
Eurasian Oystercatcher	1	0.996 ± 0.0015
	2	0.986 ± 0.0017
	3	0.991 ± 0.0011
	4	0.999 ± 0.0004

Discussion

Survival probabilities of artificial nests were significantly higher for cattle than for horses and significantly more nests were trampled by horses than by cattle in similar densities in this study. Additionally, we found a non-significant, but clear trend towards an increased trampling probability with higher grazer densities. The probability of an artificial nest being trampled was significantly greater close to a freshwater tank. The analysis did not show an interaction effect between distance to water and grazing treatment, suggesting a similar effect of distance to water for all grazing treatments.

Effect of different grazing treatments on artificial nests
The differences we found between species of livestock are likely to be explained by differences in behaviour of horses and cattle. Horses are more active than cattle (Arnold 1984; Duncan et al. 1990; Janis et al. 2010) and use longer parts of the day to graze because of their different digestive systems (Duncan et al. 1990). Studies on the behaviour of horses and cattle in our study area suggest that both livestock species prefer to graze close to the summer dike (Nolte, unpublished data). Nonetheless, horses spent more time on the low marsh, further away from the summer dike, than cattle. Cattle also spent less time per day grazing than horses. This means that horses move more than cattle, increasing the risk of trampling a nest (Nolte unpublished data).

Increasing the number of grazers per paddock is likely to increase the risk of a grazer trampling a nest (Beintema and Müskens 1987). We found such a trend, bordering significance. We did, however, not find as strong an effect as expected. One could argue that, when doubling the number of grazers, the number of nests trampled should double as well. This was clearly not the case in this study. Unpublished data showed that horses as well as cattle show a positive selection for specific plant communities (Nolte, unpublished). The positive selection for certain vegetation types would suggest that livestock are not randomly distributed over a salt marsh. Since the artificial nests in our study were randomly placed in each paddock, some artificial nests are more likely to be trampled than others. Additionally, with an increasing time interval, the chance of a nest being trampled more than once increases. We cannot distinguish this double trampling in our design. The non-random distribution of livestock over the paddocks and the relatively long time of 21 days of exposure would therefore explain why we do not find a stronger effect of livestock density, with a doubling of the number of livestock.

Although this study found an effect of distance to a freshwater tank on the number of artificial nests trampled, it should be noted that on a salt marsh, other gradients may influence the behaviour of livestock as well. Most food for livestock is available close to the summer dike and salt water inundates higher parts of the marsh (closer to the summer dike) less frequently than the lower parts. Nonetheless, although this study was conducted in a salt-marsh area, fresh water was an important and limiting resource for livestock. The only available fresh water was at the freshwater tanks supplied in each experimental paddock. Under comparable circum-

stances, livestock was shown to concentrate around freshwater tanks (Arnold 1984). This could be a partial explanation for the increased trampling with decreasing distance from a fresh water source.

Artificial nests compared to real nests

An obvious difference between real birds' nests and artificial nests is that no birds breed on and protect an artificial nest and, therefore, artificial nests will never have the same properties as real nests (Major and Kendal 1996; Wilson et al. 1998; Moore and Robinson 2004). We suggest, however, that the relative differences we found between horses and cattle and between grazers of the same type in different densities are comparable to effects on real wader nests. To study the absolute effect of livestock on ground-breeding birds using artificial nests, a correction of the V-values of artificial nests would be necessary, depending on the bird species. The behaviour of breeding birds will influence the probability of a nest getting trampled. Three factors are of particular importance: active nest defence, the effectiveness of active nest defence and the nest site choice in relation to the position of artificial nests. Using the few real nests in this study, we calculated V-values for Eurasian Oyster-catcher nests under horse grazing, which were close to V-values of artificial nests under horse grazing. Eurasian Oystercatchers show active nest defence (Beintema et al. 1995), but our results suggest that the effectiveness of this defence against horses is low. For Common Redshank nests under cattle grazing, the V-values were still in the same range but clearly lower than V-values for artificial nests. Common Redshanks do not actively defend their nest (Beintema et al. 1995), so they may choose nests sites with a relatively low trampling risk, compared to the random position of our artificial nests. When comparing our artificial nests to real nests in a much greater sample (Beintema and Müskens, 1987), we found that V-values for artificial nests were very similar to V-values found for Northern Lapwing nests in a cattle-grazed treatment. Northern Lapwings are an aggressive species which actively defend nests but active nest defence was found to have little effect on nest survival of waders in coastal meadows (Ottvall et al. 2005). This would explain why artificial nests without a defending adult have similar survival probabilities to real Northern Lapwing nests.

Apart from the described and tested direct effects of trampling by livestock on nest survival, there may also be a number of associated indirect effects. MacDonald and Bolton (2008), for example, show that Lapwings suffer from lower predation rates when nesting at high densities, possibly through a mobbing effect, deterring predators. Therefore, nest loss due to trampling may lead to lower nest densities and higher predation rates. Trampling may also lead to the destruction and loss of vege-tation or to changes in the botanical composition of grasslands (Frame and Laidlaw 2011). Since waders tend to select habitat with greater concealment than generally available (MacDonald and Bolton 2008), loss of vegetation may lead to loss of breeding habitat for waders. Changes in botanical composition may lead to changes in food availability for birds. Horses have been found to apply greater pressure to vegetation than cattle (Liddle 1997) and destruction of soils through trampling is greater with high stocking densities (Frame and Laidlaw 2011). Therefore it seems

likely that the indirect, as well as the direct effects of trampling on ground breeding birds are greatest in high density horse grazed sites.

On salt marshes and many other grassland systems, sheep are another important livestock species. Sheep were not included in this study. However, a pilot study using 15 artificial nests and two breeds of sheep (Ouessant and Texelaar) was conducted to test the suitability of our method to assess the impact of trampling by sheep. With our set-up, the clay pigeon targets did not consistently break when stepped on by sheep, most likely because of the lower body weight of sheep compared to cattle and horses. Therefore, our method in its present form would not be suitable for studies on sheep grazing.

Implications for management

We suggest that the use of horses as grazers in areas with high densities of birds' nests should be avoided to minimize the risk of nests being trampled. To further assess the impact of grazers on trampling of nests, we conclude that artificial nests, as described in this study, are a useful tool for studies on cattle and horses.

In regions with limited availability of important resources such as drinking water, livestock show distribution patterns (Valentine 1947; Bailey et al. 1996; Bailey and Brown 2011). This may create a gradient of grazing intensity by livestock. The negative impact of livestock on ground-breeding birds may be minimized by providing that resource far away from breeding colonies or areas with high densities of breeding birds. In this way, the use of fences can be largely avoided, as these might have a negative effect by acting as perches for predators (Ottvall et al. 2005; Wallander et al. 2006). Additionally, fences are largely viewed in a negative light by the general public due to the aesthetics of using fencing in natural areas (Huijser and Kociolek 2008).

Habitat preference of geese is affected by livestock grazing – seasonal variation in an experimental field evaluation

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Abstract   The number of staging geese in NW Europe has increased dramatically. Growing goose numbers put strong grazing pressure on agricultural pastures. Damage to agricultural land may be mitigated by managing nature reserves in order to optimally accommodate large numbers of grazing geese. Livestock grazing has been shown to facilitate foraging geese; we take the novel approach of determining the effects of four different livestock grazing treatments in a replicated experiment on the distribution of geese. We present experimental field evidence that livestock grazing of a salt marsh in summer affects the habitat preference of foraging geese during autumn and spring staging. In an experimental field set-up with four different livestock grazing treatments we assessed goose visitation through dropping counts, in both autumn and spring. Grazing treatments included 0.5 horse/ha, 1 horse/ha, 0.5 cattle/ha and 1 cattle/ha during the summer season. The livestock grazing regime clearly affected goose distribution in autumn, just after livestock had been removed from the salt marsh. In autumn, goose visitation was highest in the 1 head/ha grazing treatments, where grazing intensity by livestock was also highest. In line with this result, goose visitation was lowest in the 0.5 head/ha livestock grazing treatments, where the grazing intensity by livestock was lowest. The differences in goose visitation among the experimental treatments in autumn could not be explained by the canopy height. In spring we did not find any effect of livestock grazing treatment on goose visitation. Differences in the distribution of geese over the experiment between autumn and spring may be explained by changes in the availability of nutrient-rich vegetation. Livestock summer grazing with a high stocking density, especially with horses, can be used to attract geese to salt marshes in autumn and potentially reduces damage caused by geese to inland farmland. From a nature conservation point of view, however, variation in structure of the vegetation is a prerequisite for other groups of organisms. Hence, we recommend grazing of salt marshes with densities of 0.5 head/ha of livestock when goose conservation is not the only management issue.

Introduction

Over the past decades the number of staging geese in NW Europe has increased dramatically (Fox et al. 2010). An example is the almost exponential growth of the barnacle goose population (*Branta leucopsis*) from an estimated 267,000 in the 1990s to 770,000 barnacle geese in 2010 (Fox et al. 2010). Growing goose numbers put strong grazing pressure on agricultural pastures, and geese reduce grass yields originally intended for cattle (Patton & Frame 1981, Owen 1990, Vickery 1999). Farmers call for a management of nature reserves in order to optimally accommodate large numbers of grazing geese, as a measure to mitigate goose damage on agricultural land (Owen 1990, Mooij 1991, Percival 1993, Vickery et al. 1994, Vickery 1999).

Livestock grazing is a common tool in nature management (Ebrahimi et al. 2010) and it has been shown to facilitate foraging geese (Van der Graaf et al. 2002, Bos et al. 2005a). With a relatively high stocking density, grass swards are kept short and facilitate the use by grazing geese. (Van der Graaf et al. 2002, Bos et al. 2005a). A short sward enhances intake rates and young shoots are protein rich and provide food of a high nutritional value for small herbivores such as geese (Van de Koppel et al. 1996, Fox et al. 1998, Mayhew & Houston 1999). Previous studies have also shown that canopy height is an important determinant for the distribution of geese on a salt marsh (Drent & Swierstra 1977, Riddington et al. 1997, Vickery 1999), and that the highest numbers of geese will be found at a relatively low canopy height.

Livestock grazing affects canopy height and while the effects of canopy height on geese have been documented, in this study we take the novel approach of determining the effects of four different livestock grazing treatments in a replicated experiment on the distribution of staging geese. With the results from this study we make recommendations on the best management options for clayey foreland type salt marshes with regard to habitat preference of staging geese. In our recommendations we take into account the local goal of increasing biodiversity in the study area. Grazing management resulting in the highest numbers of geese may not necessarily positively affect other bird species, invertebrates or plant diversity.

Methods

Study site
The study site is part of a large connected mainland salt marsh in the north of the Netherlands along the Wadden Sea coast (53° 20′N 5° 43′E). The mainland salt marshes of the Netherlands Wadden Sea are largely of anthropogenic origin, because their development has been promoted by the construction of sedimentation fields and ditching (Verhoeven 1980; Esselink et al. 2009). These engineering works nowadays no longer aim at land claim but at conservation of the existing salt marsh. The study area and surrounding marshes are now managed as a nature reserve, with livestock grazing by cattle and horses used as a measure to increase plant diversity. The study area is an important autumn, winter and spring staging site for geese (Fig. 5.1), especially barnacle geese and, to a lesser extent, brent geese (*Branta bernicla*).
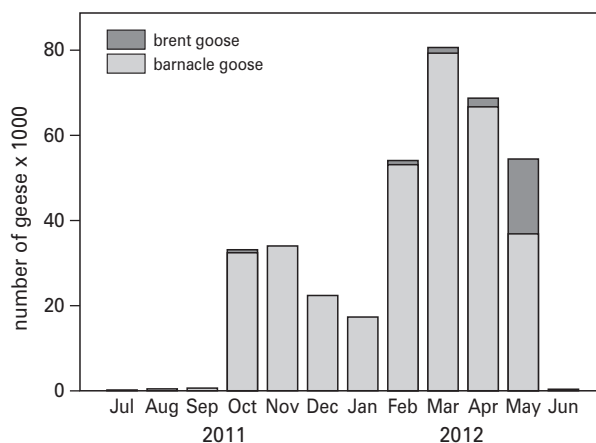
Figure 5.1 Geese numbers counted during the period of this study in the study area surrounding the experiment show that the study area is extensively used by geese in autumn and spring.

Experimental design

In spring 2010 we started a grazing experiment with three 55 ha replicates. Each replicate was divided in four equally sized paddocks with a different grazing treatment in each paddock. The grazing treatments were 1 horse/ha, 0.5 horses/ha, 1 cattle/ha and 0.5 cattle/ha. The grazing treatments were allocated to the paddocks within a replicate randomly, but we made sure not to place two horse-grazed treatments next to each other, as horses are known to be influenced in their site choice by other horses in adjacent paddocks. Livestock was present from June to October. Within each paddock, we established a transect for goose dropping counts from high to low marsh. High and low marsh were distinguished based on vegetation maps with TMAP typology (Trilateral Monitoring and Assessment Programme; Esselink et al. 2009). Four plots on each transect were placed in vegetation types classified as high marsh vegetation and four plots were placed in low marsh vegetation. The four low marsh plots were always closer to the sea edge than the four high marsh plots. In this manner eight plots per transect, a total of 96 plots, were placed in the entire study area. We marked the middle of the plots with a bamboo stick which protruded not more than 10 cm above the marsh bed.

From October to December 2011 (autumn) and from March to May 2012 (spring) we counted goose droppings and removed them from the plots at weekly intervals. For this, we used a 113 cm piece of string, which we attached to the bamboo stick at the centre of each plot. We then circled the stick, counting and removing droppings from a 4 m^2 plot with our string providing a 113-cm radius. Foraging geese defecate at regular time intervals (Owen 1971, Bruinzeel et al. 1997), so the number of goose droppings provides a sound estimate of the total grazing time by geese in a plot (Owen 1971). If the study site was flooded between the weekly dropping counts, these dropping counts were discarded from the analyses, as we could not exclude dropping removal or addition by the tidal water in the preceding interval.

In autumn, three dropping counts, one in October, one in November and one in December, were removed from the analysis, because the study area was flooded prior to the counts. In the spring period, flooding events did not interfere with the dropping counts. We calculated the average number of droppings per weekly interval for each of the 96 plots in both seasons, and used these two average values per plot in the data analyses.

Prior to the first dropping counts in both autumn and spring, the canopy height at each plot was measured to the nearest centimeter four times using a sward stick; for this a styrofoam disc was dropped down along a vertical ruler and the height above ground where it comes to rest was measured (Holmes 1974, Stewart et al. 2001). The canopy height in the plots was used as an explanatory factor for differences in goose visitation between grazing treatments. The four measurements of canopy height at each plot were averaged.

Analysis

To study the experimental effects of the grazing treatments, the dropping counts averaged over weeks were used as the response variable in a generalised linear mixed effects model with grazing treatment, season (autumn/spring), salt-marsh zone (high or low marsh, based on plant species composition), the interaction between grazing treatment and season and the interaction between grazing treatment and salt-marsh zone as the fixed explanatory variables. The three replicates of the experiment were included as a random effect. With the estimates from the model, pairwise comparisons between the treatments were made using the multcomp package (Hothorn et al. 2008) in R (R Development Core Team 2012).

We hypothesised that the possible treatment effects on goose visitation were generated by impact of livestock on canopy height. For the season with a significant treatment effect, we therefore fitted a different generalised linear mixed effects model in an attempt to explain the variation in the average number of droppings. In this model the explanatory variables were the average canopy height per plot, squared canopy height per plot, salt-marsh zone, and all two-way interactions. The three replicates of the experiment were again included as a random effect. Both statistical models were reduced by backwards elimination and by an evaluation of models at every step on the basis of AIC values (Zuur et al. 2009). The statistics were performed in R (R Development Core Team 2012), using the lme4 package (Bates et al. 2011) to create the linear mixed effects models.

Results

Overall patterns in livestock grazing

The summed numbers of goose droppings found over the entire study area are rather similar in autumn and spring (Appendix B). With the linear mixed model used in this study, we found significantly fewer goose droppings on the low marsh, than on the high marsh (Table 5.1).

Table 5.1 Significance of fixed model parameters calculated by comparing a full model with models where one of the variables was removed. DF represents the change in degrees of freedom compa`red to the best model, with 11 degrees of freedom. AIC shows the AIC values of the models without each variable. AIC value of the best model was 412.80. Models were created with the lme4 package (Bates et al. 2011) in R (R development core team 2011).

Note that the interaction between grazing treatment and marsh is significant, indicating that the effects of grazing treatment vary between the seasons.

Variable	χ^2	DF	AIC	p value
Marsh zone	14.38	1	421.70	<0.001
Grazing treatment*season	28.62	3	431.34	<0.0001

Table 5.2 Estimates and standard errors for the generalised linear mixed model showing the effects of grazing treatment on number of goose droppings. Note that the differences in the estimate for the grazing treatments in autumn are larger than the differences in the estimates for the grazing treatments in spring. This suggests that the differences between the treatments are more pronounced in autumn than in spring.

	Estimate	Standard error
1 horse/ha spring	1.83	0.65
1 cattle/ha spring	2.23	0.46
0.5 horses/ha spring	2.09	0.65
0.5 cattle/ha spring	2.06	0.65
1 horse/ha autumn	2.32	1.09
1 cattle/ha autumn	1.92	0.65
0.5 horses/ha autumn	1.65	1.09
0.5 cattle/ha autumn	1.18	1.09
low marsh v. high marsh	-0.35	0.09

Table 5.3 Canopy heights ± SE per treatment, averaged over the three replicates of the experiment.

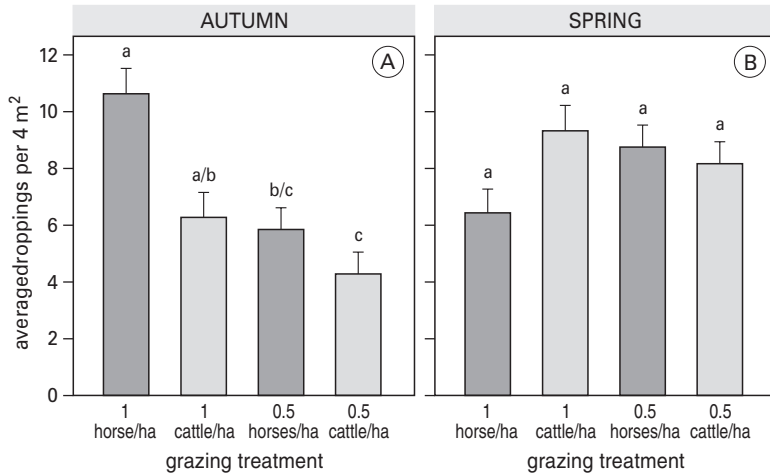| grazing treatment	average autumn	average spring
1 cattle/ha	13.8 ± 2.3	2.5 ± 0.3
1 horse/ha	8.5 ± 1.9	1.6 ± 0.3
0.5 cattle/ha	21.1 ± 4.6	3.8 ± 0.4
0.5 horses/ha	3.5 ± 2.6	3.5 ± 0.3

Figure 5.2 The average number of droppings per 4-m2 in autumn and spring in four different grazing treatments. The numbers indicate clear differences in the use of different grazing treatments by geese in autumn (A). In spring we did not find significant differences between the same grazing treatments (B). Letters above the bars indicate significant differences between the treatments in each panel.

Note that the generalised linear mixed model used to analyse the data takes into account variance between the replicates. The averages shown in the figure, therefore, are a simplification of the underlying data, which may explain why, perceived large differences between horse and cattle in the 1 head/ha treatment in both autumn and spring are not significant.

Experimental treatment effects

We found that the effects of livestock grazing treatment on the number of geese droppings differed per season (see Table 5.1). In autumn we found differences in goose droppings between treatments using pairwise comparisons (Fig. 5.2). The highest numbers of goose droppings were found in the 1 head/ha treatments, while the lowest numbers were found in the 0.5 head/ha treatments (see Fig. 5.2). In spring we did not find any significant differences in numbers of goose droppings among the treatments. Treatment effect was strongest directly after the livestock had been removed from the experiment in autumn (Table 5.2).

Does canopy height explain the treatment effects?

The differences in numbers of goose droppings in autumn between grazing treatments could not be explained through average canopy height (Table 5.3). With an additional linear mixed effects model we did not find any significant relation between average canopy height and the number of goose droppings in autumn ($\chi^2 = 1.45$, p = 0.23).

Discussion

Effects of grazing treatments

Livestock grazing treatments with high stocking densities were preferred by staging geese in autumn, while in spring grazing treatments did not seem to affect the distribution of foraging geese over the experiment. This confirms the study by Aerts et al. (1996) who found that barnacle geese were more evenly distributed over different habitat types in spring than in autumn.

At the point of completion of the growing season, at the beginning of autumn, the vegetation on a salt marsh is relatively tall and mature, and plant digestibility is low due to high fibre contents in the shoots (Demment & Van Soest 1985, Aerts et al. 1996). Summer grazing, especially in high stocking densities, keeps the vegetation short and at young growth stages. Grazing induces the growth of secondary shoots and new leaves, which are relatively nitrogen rich (Demment & Van Soest 1985, Van de Koppel et al. 1996, Fox et al. 1998, Mayhew and Houston 1999), and are high-quality food for small herbivores, such as geese (Ydenberg & Prins 1981, Summers & Critchley 1990). A preference of geese for high-quality food in short canopies (Vickery 1999, Olff et al. 1997), may explain goose preference for the 1 head/ha grazing treatments in autumn (see Fig. 5.2).

In spring new growth of vegetation occurs over the entire marsh. Previous studies have shown that geese can selectively forage on patches of high quality food in areas of lower quality food (Bos et al. 2005b). In spring geese may, therefore, spread over larger parts of the study area to forage on patches of high quality spring growth. Additionally, in autumn tall vegetation on the salt marsh may be avoided by foraging geese (Aerts et al. 1996), because predators are harder to detect (Underwood 1982, Loughry 1993, Kuijper & Bakker 2008). In winter, the salt marsh is regularly flooded during storms. These flood events destruct and flatten the vegetation and in spring, differences in vegetation structure/canopy height among habitats have become much smaller. Therefore, tall vegetation may no longer present a problem for foraging geese. This corresponds to our finding that the geese use all grazing treatments evenly in spring.

Livestock grazing may also change the plant species composition of a salt marsh (Bakker et al. 1993, Olff et al. 1997) and with that the food availability for geese (Aerts et al. 1996). Previous studies showed that the preferred food of geese differs between seasons. Brent geese prefer *Puccinellia maritima* in winter, *Salicornia* spec. leaves and seeds in autumn and *Trichlogin maritima*, *Plantago maritima* and *Aster tripolium* in spring (Prop & Deerenberg 1991, Summers et al. 1993, Rowcliffe et al. 1995, Van der Wal et al. 2000). This seasonal variation in diet preference combined with effects of livestock grazing on plant-species composition could be an alternative explanation for the effects of livestock grazing in autumn and spring found in the present study. However, Nolte (unpublished data), using data from permanent plots over three years, showed that within the study area within the timeframe of this study, plant-species composition did not change significantly in the grazing treatments. Possibly, the grazing experiment has been running too short to find effects of livestock grazing on plant-species composition (Bakker et al. 1996, Nolte unpublished).

Implications for management

Salt marshes are a natural habitat for staging geese and grazing management can be applied to conserve salt marsh habitat for geese. Succession of the salt marsh may lead to higher canopy heights and eventually the dominance of the tall grass species *Elytrigia atherica* over a salt marsh (Bakker et al. 1993). This would make salt marshes unsuitable for grazing geese. Grazing management may retard the succession of a salt marsh (Olff et al. 1997), and prevent *Elytrigia atherica* from overgrowing a marsh. In this study we show that as long as livestock grazing retards succession, the exact grazing management has little effect on the distribution of geese in spring.

The type of management recommended for an area is, however, very much dependent on the goals set for nature management. In our study area, the management goal is to increase biodiversity. Biodiversity is higher in moderately grazed areas opposed to intensively grazed areas (Bakker et al. 1993). Moderate grazing leads to a higher structural diversity in the vegetation, which in turn supports higher numbers of invertebrates than intensively grazed sites (Olff & Ritchie 1998, WallisDeVries et al. 1999, Balmer & Erhardt 2000, Dennis et al. 2001, Woodcock et al. 2005, Rickert et al. 2012). Many breeding waders in the study area, have different habitat requirements than geese, and prefer structurally diverse vegetation over short-grazed homogeneous vegetation (Norris et al. 1997, Norris et al. 1998, Milsom et al. 2000, Tichit et al. 2005, Verhulst et al. 2011). Along this line Vickery et al. (1997) describe a management conflict in grazed coastal salt marshes for staging geese and breeding waders. Some waders, such as Lapwing (*Vanellus vanellus*) or Dunlin (*Calidris alpina*), however, prefer shorter vegetation (Niethammer and Von Blotzheim 1966, Clausen and Kahlert 2010). These species may benefit from high density livestock grazing, which would present no conflict with managing a salt marsh for staging geese, although the trampling of nests is lower when an area is grazed with low stocking density (Beintema & Müskens 1987, Fuller & Gough 1999, Mandema et al. 2013). Trampling of nests may be largely prevented by postponing release dates of cattle to the end of the breeding season.

In those areas where geese themselves are of conservation concern e.g. Light-bellied Brent Geese *Branta bernicla hrota* in Denmark (Clausen et al. 2013), our results show that geese in autumn benefit most from high density livestock grazing by horses. Benefits for geese with a conservation concern should in these areas be carefully weighed against detrimental effects of high density horse grazing for other groups of organisms.

Lastly, livestock grazing may be used to keep geese on salt marshes instead of inland agricultural fields. This will most likely be of little effect; we only found a significant difference between livestock grazing treatments in autumn. The geese inflict most damage to farmland in spring when the grass is growing fastest and is harvested as food for livestock (Mayes 1991, Vickery 1999). Additionally, managing nature areas for geese will, at best, temporarily remove the pressure from agricultural fields. Considering the strong increase in goose numbers over the past decades (Fox et al. 2010), it seems likely that increasing the amount of land that is suitable as foraging habitat for geese will eventually lead to an increase in the number of geese

and renewed pressure on farmland. Nonetheless, providing areas of high-quality foraging grounds for geese in autumn may attract geese to salt marshes, at least temporarily relieving some of the stress created by geese on farmland.

Chapter 6

Foraging site choice and diet selection of meadow pipits *Anthus pratensis* breeding on grazed salt marshes

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Abstract

Capsule
Breeding Meadow Pipits foraged in vegetation than at random locations for caterpillars and large spiders.

Aims
To gain better understanding of the foraging ecology of breeding Meadow Pipits on grazed coastal salt marshes regarding food availability, choice of foraging location, and diet selection. We specifically tested the hypothesis that adult birds would prefer to forage in patchy vegetation of mixed short and tall stands, thereby maximizing food abundance and accessibility.

Methods
 We measured food availability in relation to vegetation structure, Pipits habitat use and nestling diet for six individual pairs. Nestling diet was determined by microscopic analysis of nestling faeces while food availability over different vegetation heights was estimated by suction sampling. Information on habitat use was gathered by direct observation.

Results
We found the highest abundance of food items in tall vegetation. Contrary to our expectations, vegetation at Pipit foraging locations was less patchy than at random locations, yet we found no evidence for a preference for short or tall vegetation. Concerning diet we found strong evidence for selective foraging for larger prey, since the relative abundance of especially large spiders (>5mm) and caterpillars (±2cm) (together comprising >80% of nestling diet) was much higher in the faecal samples than in the field. This diet differed considerably from Meadow Pipit diet reported from other habitats.

Conclusions
These findings suggest that the creation of patchy vegetation by grazing or otherwise may not be invariably beneficial to breeding Meadow Pipits.

Introduction

Meadow Pipits (*Anthus pratensis*) are common birds in the Netherlands with relatively stable numbers of breeding pairs since 1990 (Boele et al. 2013). They form an important food source for red-listed Harriers (*Circus cyaneus*, *C. pyrargus*, *C. aeruginosus*) (Redpath 1992, Koks et al. 2007), and have been suggested to be good bioindicators of habitat quality for grassland birds (Vanhinsberg & Chamberlain 2001). Also on salt marshes along the Dutch Wadden Sea coast Meadow Pipits are a common breeding bird, suggesting that these provide adequate habitat. Recent changes in the grazing management on salt marshes may pose a threat to Meadow Pipits and other insectivorous passerines, however, little is known about their habitat requirements in this ecosystem. Historically, salt marshes in the Netherlands were grazed with livestock. During the past decades, however, livestock grazing was no longer economically feasible, and many sites were abandoned (Bakker et al. 1993). Abandonment of salt marshes generally leads to a homogeneous tall vegetation structure (Bakker et al. 1993, Sammul et al. 2012), which is unattractive to many ground-breeding bird species (Norris et al. 1997, Norris et al. 1998, Milsom et al. 2000). The purpose of this study, therefore, is to gain a better understanding of the foraging ecology of breeding Meadow Pipits on salt marshes, particularly in relation to food availability and vegetation structure.

Previous studies on foraging passerines on inland grasslands generally suggest a trade-off between the accessibility and the abundance of food items (e.g. Fuller and Gough 1999, Devereux et al. 2004, Butler & Gillings 2004, Atkinson et al. 2004). Birds that visually hunt for ground-dwelling invertebrates, such as Meadow Pipits, can easily manoeuvre through short vegetation. Moreover, prey detectability in short vegetation is higher, because larger distances can be overseen without interfering vegetation (Butler & Gillings 2004). Yet, the abundance of most invertebrate groups, including important food sources for Meadow Pipits is higher in tall vegetation (e.g. Luff 1966, Dennis et al. 2008).

As foraging habitat, heterogeneous grasslands combining tall vegetation with patches of bare ground and short vegetation, are therefore likely to provide the highest food availability for Meadow Pipits and other grassland birds (Vickery et al. 2001, Atkinson et al. 2005, Evans et al. 2006). Moderate livestock grazing can increase the structural vegetation heterogeneity (Adler et al. 2001), and may therefore be an adequate management option for optimizing availability and accessibility of food for Meadow Pipits and other typical grassland birds, like Skylarks, Lapwings and Starlings (Devereux et al. 2004, Evans et al. 2005, Vandenberghe et al. 2009). So far, however, experimental evidence showing selection of patchy vegetation for foraging is limited.

The diet of Meadow Pipits known from inland populations mainly consists of flies (Diptera), beetles (Coleoptera), spiders (Araneae), bugs (Hemiptera), wasps (Hymenoptera) and moth larvae (Lepidoptera) (Wilson et al. 1996), and Meadow Pipits generally select for the larger of the available prey (Hågvar et al. 2011). For salt-marsh breeding populations, the diet is currently unknown, and might differ from inland populations due to the habitat specific fauna of salt marshes. The inver-

tebrate fauna of grazed salt marshes is dominated by spiders and beetles, as well as springtails, flies and leafhoppers (Irmler & Heydemann 1986, Ford et al., 2013). In tall, ungrazed salt-marsh vegetation, however, abundance and biomass of invertebrates is higher than on grazed salt marshes with short vegetation (Ford et al. 2013). This is mostly attributable to the high abundance of larger spiders (Pétillon et al. 2007), and the semi-terrestrial crustacean *Orchestia gammarellus* (Ford et al. 2013), known to be an important food item for fish foraging on salt marshes during inundations (Laffaille et al. 2005). We expect the diet of Meadow Pipit nestlings on salt marshes to reflect the locally available prey items, but we also expect selective foraging for larger items.

We hypothesize that breeding Meadow Pipits foraging on salt marshes will select foraging locations that have a higher number of transitions from tall to short vegetation than random locations, exploiting the food spill-over from the high vegetation into the low vegetation.

Methods

Study site
This study was conducted on a mainland salt marsh along the Dutch Wadden Sea Coast (53° 20' N, 5° 44' E). The salt marsh was developed by promoting sedimentation with construction of sedimentation fields and ditches during the early 20th century (Verhoeven 1980, Esselink et al. 2009). Although the study area has a history of agriculture, it is now managed as nature reserve. Cattle grazing, with a stocking density of 1 animal ha^{-1}, has been employed over at least ten years preceding this investigation in order to maintain high levels of plant diversity. The area is important for a number of breeding wader- and passerine species, and for foraging raptors and short-eared owls.

Experimental design
To determine the diet of nestling Meadow Pipits at the study site, we collected and analysed droppings during the breeding seasons of 2009-2011. Furthermore, we tested whether prey items were more abundant in tall vegetation than in short vegetation by sampling invertebrates at locations independent of Meadow Pipit nests over the complete range of vegetation heights present at the site. We did this in a stratified random sampling design, taking samples at six locations with short vegetation (<10cm), six locations with vegetation of intermediate height (10-20cm) and six locations with tall vegetation (>20cm) (for details on the sampling protocol see below). Tall vegetation accounted for approximately 20% of the site during the time of sampling (pers. obs.).

To determine where adult Meadow Pipits forage during the breeding season we adapted the method of Vandenberghe et al. (2009). Observation towers (height 3m) were erected at the centre of the study site to provide a good overview over the entire salt marsh used by Meadow Pipits. Nests were located by visual observations of adult Meadow Pipits carrying food. For each Meadow Pipit nest, three one-hour

observations were conducted. The observations were started when a Meadow Pipit was seen leaving its nest. The most visited foraging location per observation round was later visited for sampling vegetation height patchiness and prey abundance. In this way, we located a total of six nests, with three foraging locations per nest.

Using measuring tape, the distance from a nest to each of the three foraging locations was determined when the nestlings had fledged (maximum one week after determining foraging locations). At the same distance from the nest, but in a random direction, a paired random location was established for comparisons of vegetation parameters and availability of food for Meadow Pipit nestlings. The direction was randomised by throwing a wooden stick straight up and using the direction indicated by the stick once on the ground.

Diet composition of meadow pipit nestlings

To determine the diet composition of Meadow Pipit nestlings, we collected faecal samples of nestlings from each of the nests observed in 2011. We supplemented these with samples collected from different nests over 2009 and 2010, and two samples from nests that were predated before observations of foraging behaviour could be done, adding up to a total of 23 samples from 13 nests. Nestlings (age 1–7 days) were shortly handled, which would generally result in a dropping being produced. If no droppings were produced within 10 minutes, no faecal samples were collected from the nest. Faecal samples were stored in 70% ethanol until identification.

We identified all parts of invertebrates present in a faecal sample to the highest taxonomic level possible. This was often class or order level for the very fragmented remains of adult insects, whereas spiders could generally be identified to species level, based on their genitalia (using a private reference collection from the same area, identified using Roberts (1987)), but were later grouped as large (body length >5mm) or small (<5mm). Parts of most invertebrate groups were well preserved. A comparison of neck collars of nestlings and faecal analyses of three passerine species has shown that the relative abundance of spiders, caterpillars and flies are approximated well by faecal samples, while beetle abundance was generally overestimated (Moreby & Stoate 2000). All of these taxa have hard parts that are well preserved (Ralph et al. 1985). Soft bodied taxa, like springtails, however may be underestimated using this method (Moreby & Stoate 2000).

For every sample (one dropping) we determined the minimum number of prey items of each (group of) species by matching the parts found. We assumed that unidentifiable parts belonged to an individual of which other parts were identified. Individual invertebrates possess two or more of many parts (e.g. jaws, legs, wings or pedipalps (male genitalia of spiders)), hence if matching left- and right-hand parts were present, we assumed these to belong to the same individual. Therefore, the numbers counted should be seen as the minimum number of individual invertebrates eaten.

Parts of spider legs were omitted from the counts because they were often numerous and not attributable to any number of individuals, unless no other spider parts were present in the sample. Jaws of insect larvae and spiders were matched based on size, saw pattern and coloration. The size of the caterpillars was estimated

based on the size of the jaw parts by M.G.M. Jansen using a private collection. Species or groups present in the faeces (>2%) were considered to be "actual prey", whereas all invertebrates occurring on the salt marsh were defined as "potential prey".

Sampling protocol
We sampled vegetation parameters and invertebrates at all locations (foraging locations n = 18), random locations (n = 18), and the independent locations measured for the range of vegetation height) following a standardized sampling protocol: At each location (from here onwards called a "square" *sensu* VandenBerghe et al. (2009)) we laid out four ropes of 6m length, in a crosswise fashion, so that a central area of 2m x 2m was bordered by the ropes. Along the four ropes we counted the number of transitions between short and tall vegetation (as defined by Bakker et al. (1984): tall vegetation >10cm, with a distinct litter layer, short vegetation <10cm, no litter layer) as a measure for patchiness of the vegetation.

At each of the four corners of the central area we first estimated vegetation height by lowering a ø 25 cm, 75 g Styrofoam drop disk onto the vegetation along a calibrated stick (Holmes 1974), and applied suction sampling for invertebrates. Suction sampling was done using an inverted leaf blower (Echo Shred 'n' Vac, ø 15 cm, maximum air velocity 73 ms^{-1}) equipped with a 1mm mesh net. Because tall vegetation is well known to inhibit efficient suction sampling (Brook et al. 2008), we used a two-stage suction protocol. First we applied suction to the vegetation layer in a ø 50cm sampling ring for 30 seconds, after which we clipped all biomass from the ring and applied suction to the litter layer for another 30 seconds (see Van Klink et al. 2013). In this way we sampled ($4 \times 0.196 \, \text{m}^2 =$) $\pm 0.75 \, \text{m}^2$ per square. All invertebrates were collected by manually sorting the yield from the net in the field. Invertebrates were identified in the field to the same taxonomic groupings revealed by faecal analysis. The groups collected could therefore be classified as actual prey (also present in faecal samples) or potential prey (present in the field, but not found in faecal samples).

Statistical analyses
All statistical tests were conducted with R.15.3 (R Core Team 2013). We tested for differences in the number of individuals between groups in the faecal samples using Poisson-distributed generalized linear mixed models (GLMM) from the lme4 R-package (Bates et al. 2012). We used 'sample' nested in 'nest' as random factors, prey number as dependent and prey group as explanatory variable. Similarly, we tested for differences in the frequency of occurrence (proportion of samples in which a group was present) of the different groups over the samples were tested by binomial GLMM with sample nested in nest as random factors.

The relationships between vegetation height and abundances of all invertebrates combined and of actual prey groups at the independent squares, were assessed by regressing abundance per square (0.75 m^2) against mean vegetation height using Poisson distributed general linear models (GLM). The relation between vegetation height and the fraction actual prey items of all invertebrates was tested using bino-

mial GLM. Differences between the observed foraging squares and paired random squares were assessed using GLMM, using pairs nested in nest as random variables. Differences in vegetation height were log-transformed before analysis, and patchiness (number of transitions between short and tall vegetation) and prey abundance were assessed with Poisson-distributed models.

The relation between relative abundance of the different prey groups in the faecal samples (n = 13) and at the foraging and random squares (n = 36) was assessed for all invertebrate groups making up more than 2% in either the faeces or the field (97% of the individuals). We tested for significance using Mann-Whitney U-tests. All non-parametric tests were available in the STATS package for R.15.3.

Results

Diet composition
We obtained 23 samples of faeces from 13 nests over the period 2009-2011, from which we identified 214 individual prey items. Almost 40% of the prey items were spiders and caterpillars made up another 40% (Fig. 6.1A). There was a significant difference in the abundances of the different groups per sample (GLMM: $\chi^2 = 89.18$, $p < 0.001$, Fig. 6.1B). Spiders and caterpillars were equally abundant, but were significantly more abundant than any of the other groups, while beetles were least abundant (Fig. 6.1B). Spider parts were present in every sample we analysed and all but one of the individuals belonged to species >5 mm body length (according to Roberts (1987)). The smallest species, *Pachygnatha degeeri*, which has a body length of ±4 mm was found only once (Appendix C). The caterpillars were, based on the size of the jaws (±0.425 mm) approximately 2 cm in length (M.G.M. Jansen pers. comm.), and were present in over 90% of the samples. Remains of insect adults (flies (Diptera) and (parasitic) wasps (Hymenoptera)) were present in about 65% of the samples, but always in low numbers (Fig. 6.1B & C, appendix C). Molluscs, both bivalves and gastropods, were also found in several samples. Beetles were only found in three samples and only made up less than 2% of the prey items found. The parts found belonged to smaller species, although a definite identification could not be made. Composition of all samples can be found in appendix C.

Relation of prey abundance and vegetation height
Mean vegetation height at the independent squares ranged from 5 to 46 cm, with 21 to 101 invertebrate individuals per sampled square. Based on the faecal analysis we consider the following arthropod groups to be actual prey for Meadow Pipit nestlings: spiders (body size >5 mm) (*Pardosa purbeckensis*, *Enoplognatha mordax*, *Clubiona stagnatilis*, *Pachygnatha clercki*, *Stemonyphantes lineatus* and *Trochosa ruricola)*, caterpillars (body size ±2 cm), other insect larvae, flies and wasps, pupae, and molluscs. All other groups found (small spiders, small beetles, cicadellid leaf-hoppers, spittlebugs, true bugs, adult soldier beetles and ladybirds) were not considered to be important prey items, as they were very rare or not present in the faecal samples.
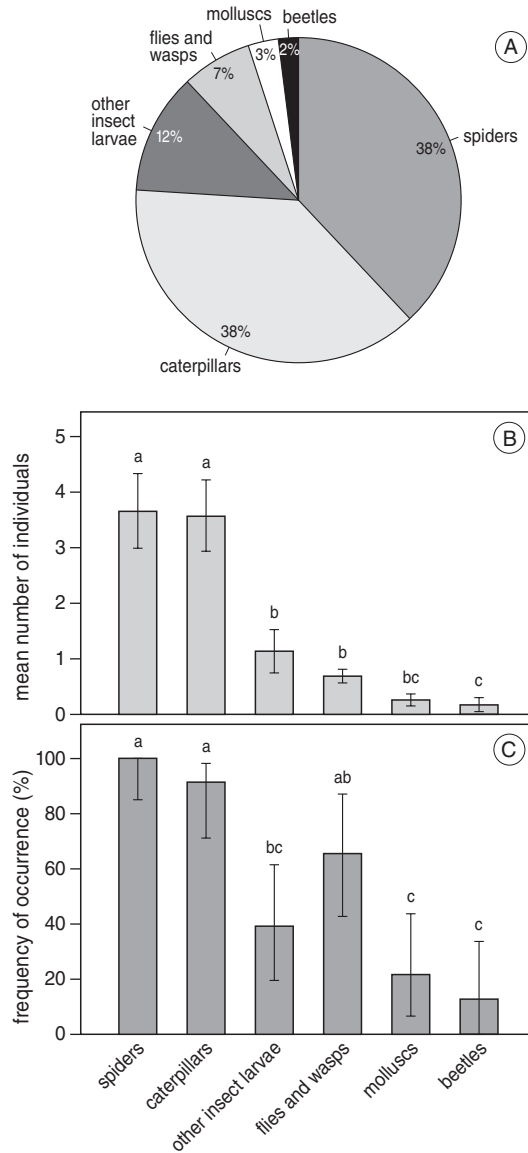
Figure 6.1 Diet composition of Meadow Pipit nestlings based on 23 faecal samples from 13 different nests, collected 2009-2011 at a mainland salt marsh at the Dutch Wadden Sea coast. A) diet composition of all samples combined, B) mean number of invertebrate individuals per sample (mean ±se), C) frequency of occurrence of the different invertebrate groups over all samples (% ± 95% CI). Different letters denote significant differences (P < 0.05).
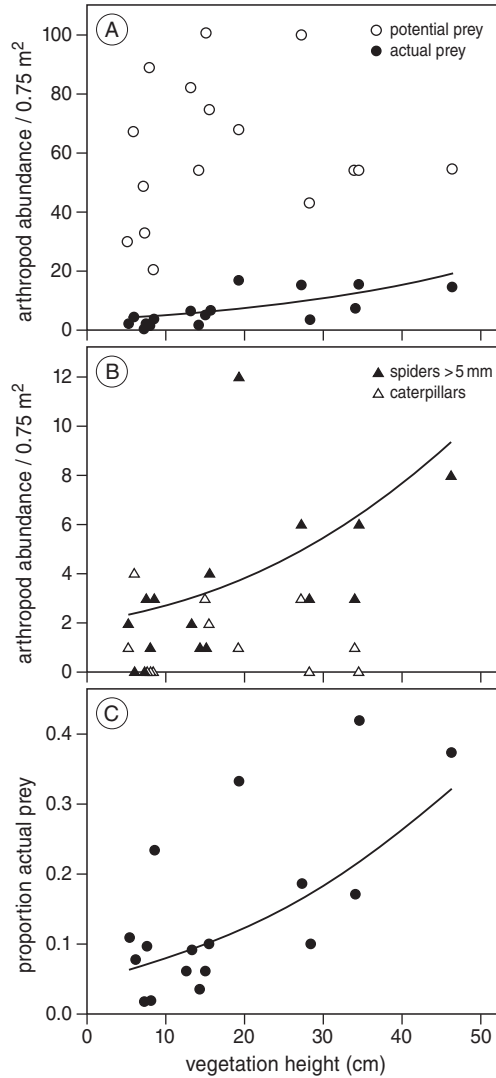
Figure 6.2 Relationships between vegetation height and invertebrate abundance. A) abundance of potential prey (all invertebrates in the vegetation) and actual prey (invertebrate groups also present in the faecal samples), B) abundance of the most important actual prey groups (large spiders (body length >5mm) and caterpillars (± 2 cm)), C) percentage actual prey items of all invertebrates. Fitted curves according to GLM are only shown for significant relationships.

There was a strong relationship between vegetation height and abundance of actual prey (GLM: $\chi^2 = 28.29$, P < 0.001), but no relationship between total invertebrate abundance (potential prey) and vegetation height (GLM: $\chi^2 = 0.3$, P = 0.58, Fig. 6.2A). Of the main food items only spiders and caterpillars were abundant enough to allow statistical inference. Spider abundance showed a positive relation with vegetation height (GLM: $\chi^2 = 183.9$, P < 0.001, Fig. 6.2b), but caterpillar numbers were not related to vegetation height (GLM: $\chi^2 = 0.1$, P = 0.75). There was a significant positive linear relationship between percentage of actual prey items (actual prey/potential prey) and vegetation height (GLM: z = 6.1, P < 0.001; Fig. 6.2C).

Foraging locations
There was no significant difference between the foraging squares and the paired random squares in abundance of actual prey (GLMM: $\chi^2 = 2.33$, P = 0.13, Fig. 6.3A) or vegetation height (GLMM: $\chi^2 = 0.69$, P = 0.4, Fig. 6.3B). Patchiness of the vegetation, based on the number of transitions between high and low vegetation, was significantly lower at the foraging squares than at the random squares (GLMM: $\chi^2 = 20.12$, P < 0.001, Fig. 6.3C).

Comparing the relative abundance of the different invertebrate groups found in the faecal samples and in the field revealed strong selective behaviour of foraging Meadow Pipits (Fig. 6.4). Large spider species (>5mm), caterpillars (2 cm), molluscs and other insect larvae were more often found in faeces than would have been expected based on their relative abundance in the field. Conversely, small spiders (< 5mm) and beetles (<5mm), as well as the larger soldier beetles were rare in faecal samples, but were abundant in the field. Only flies and wasps were as abundant in the field as in the diet (Fig. 6.4).
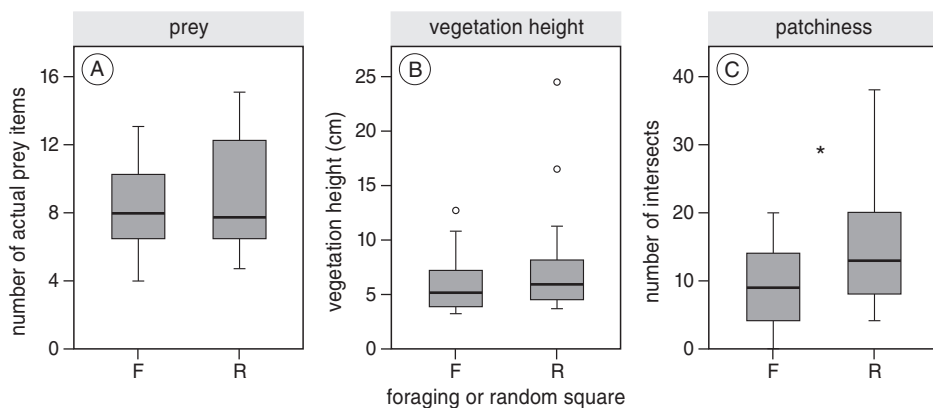

Figure 6.3 Differences between foraging squares and random squares A) number of actual prey items, B) vegetation height, and C) patchiness (measured as number of transitions of short and tall vegetation along four 6m ropes). Patchiness was significantly higher in random squares than in foraging squares (* denotes significant difference at P<0.05 according to GLMM).
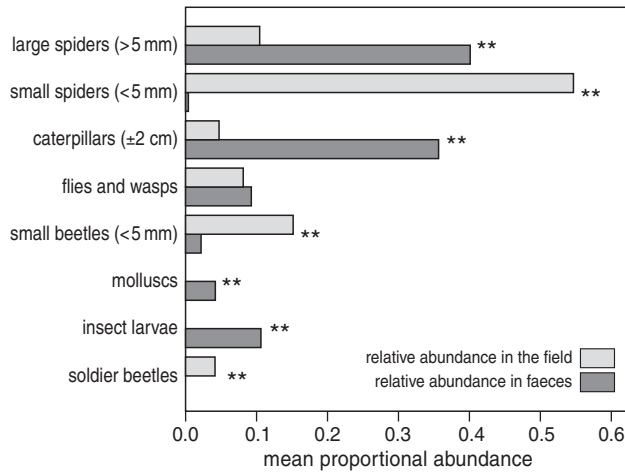
Figure 6.4 Difference in relative abundance of all invertebrate groups present in faecal samples (n = 23) and in field samples (n = 36). Groups making up less than 2% of both pools were omitted. *P < 0.05, **P < 0.001 according to Mann-Witney U tests.

Discussion

Our field measurements confirmed the positive relation between vegetation height and abundance of invertebrate prey (e.g. Luff 1966, Dennis et al. 2008), and we found strong evidence for selectivity of Meadow Pipits in prey choice. We did not find a preference for foraging in short vegetation as was found in other habitats (Douglas et al. 2008, Vandenberghe et al. 2009). Furthermore, contrary to our expectations we found Meadow pipits to forage preferentially in less patchy vegetation. This contradicts the suggestion that heterogeneity in vegetation height is an important characteristic of Meadow Pipit foraging-habitat (Atkinson et al. 2005, Vickary et al. 2001).

In our measurements, both the foraging squares and the random squares exhibited some patchiness, but the number of transitions between tall and short vegetation was lower at foraging squares. Therefore we conclude that Meadow Pipits on salt marshes had a preference for more homogeneous vegetation. Fine grained patchiness, characterised by a high number of transitions between short and tall vegetation, appears to be unattractive to foraging Meadow Pipits. Perhaps in highly patchy vegetation overview of the foraging location and predators is impaired. Whatever the reason, our results suggest that livestock grazing may decrease preferred foraging habitat for meadow pipits if a too fine-grained mosaic of short and tall stands develops.

We did not find a difference in mean vegetation height of the foraging and the random squares. There seems to be disagreement in literature regarding foraging preferences of Meadow Pipits. Some studies have found this species to preferably

forage in short vegetation (Douglas et al 2008, Vandenberghe et al. 2009), while other studies report Meadow Pipits to be generally associated with taller vegetation (Atkinson et al. 2005). Our results suggest that structure of the vegetation patchiness rather than vegetation height might better describe Meadow Pipit foraging habitat. Diet composition of nestling Meadow Pipits breeding on salt marshes differed from compositions reported from other habitats. We found a dominance of spiders and Lepidoptera larvae, whereas in the Scottish uplands, leatherjackets (Tipulidae larvae) were reported to comprise 70% of the diet of nestling Meadow Pipits (Evans et al. 2005), but these were not found during sampling. Apart from Tipulidae larvae and adults, also spiders and Lepidoptera larvae were selected more than their relative abundance predicted, in this habitat (Douglas et al. 2008). Conversely, in mountainous areas of Wales, diet of nestling Meadow Pipits mainly consisted of adult Diptera and larvae of both Lepidoptera and saw flies, whereas spiders were absent (Walton 1979). In the alpine tundra of Norway, tipulid adults were also found to form a large part of the diet, combined with Plecoptera and insect pupae (Hågvar et al. 2011). Furthermore, the importance of rove beetles (Staphylinidae) in the diet of Meadow Pipits (Wilson et al. 1996) was not supported by our findings, despite the high abundance of this beetle family at our study area (R. van Klink unpublished data). Meadow Pipit diet clearly varies among habitats probably in part because these birds adjust their diet to the locally available food.

We found strong evidence for selectivity in prey choice. The diet of nestlings was highly consistent over the faecal samples we analysed and matched with species present on salt marshes (Irmler & Heydemann 1986, Ford et al. 2013, Van Klink et al. 2013). However, large groups of invertebrates found in the field were not found back in the faeces, most notably small spiders (<5mm) (mostly of the family Linyphiidae) and small beetles (of the genera *Ochtebius*, *Helophorus* and *Bembidion*). Beetle and spider parts are generally well preserved (Ralph et al. 1985), and if the smaller species had been part of the diet, their remains should have been apparent in our samples. Moreover, in a study comparing diet estimated with neck-collars on the chicks or faecal analysis (Moreby & Stoate 2000), it was found that with faecal analysis the abundance of beetles in bird diets is rather overestimated than underestimated. This strongly suggests that these species are selected against by Meadow Pipits. The energetic costs of catching and providing these small invertebrates to nestlings may outweigh the energetic gain for nestlings (Kacelnik 1984, Wright et al. 1998). Conversely, Collembola and other soft bodied taxa are known to be badly preserved in faeces (Moreby & Stoate 2000), and may therefore have been missed in our analysis. The mollusc shells found in the faeces may have had a role as gastroliths rather than as actual prey. Therefore, molluscs may be of importance for Meadow Pipits on salt marshes, since small stones, as found in the stomachs of both adult and nestling Meadow Pipits by Hågvar et al. (2011) are scarce in the heavy salt marsh clay.

Our measurements suggest that Meadow Pipits do not always select high vegetation patchiness for foraging. Livestock grazing at intermediate densities can create considerable patchiness (Adler et al. 2001), which is expected to benefit plant and animal diversity. Evidence is, however, that fine grained heterogeneity created by

grazing may not be beneficial for all plant and animal species occurring in an ecosystem (e.g. Van Klink et al. 2013, Dennis et al 1997). This illustrates a need for more insight in the effects of small-scale vegetation heterogeneity for populations of insectivorous birds and their prey.

Synthesis

Freek S. Mandema

Introduction

The core question posed in this thesis is how to apply grazing as a tool for nature management for birds both in terms of the choice of livestock species and in the choice of stocking densities. Livestock grazing induces structural diversity in vegetation (Berg et al. 1997, Bakker et al. 2003). Stocking densities of livestock for a large part determine whether a salt marsh becomes a homogeneous short sward, or whether heterogeneous structured vegetation is induced (Bakker 1989). The livestock species used is also of importance; through differences in behaviour between livestock species, their effect on salt-marsh vegetation may vary (Olff and Ritchie 1998, Loucougaray et al. 2004). Such differences in vegetation structure have been shown to be important for birds (e.g. Dallinga 1993, Norris et al. 1997, Norris et al. 1998, Whittingham et al. 2004). In order to answer the question 'how to graze' a unique experiment was established on paddocks of 11 ha each in three replicates. The experiment was conducted on a salt marsh in the Netherlands and applied both cattle and horses in two densities (0.5 and 1 head/ha). Additionally a rotational grazing treatment (yearly alternating no grazing with grazing with 1 cattle/ha) was applied. Most studies until now described bird diversity and abundance in existing management regimes. In this study we created the management regimes experimentally. Two of the replicates in this study were grazed with differing densities of livestock before the experiment. One of the replicates had not been grazed for more than 20 years before the experiment. In order to create similar starting conditions with respect to vegetation height and vegetation structure high densities of livestock (>1 head/ha) were applied to the previously ungrazed replicate one year before the start of the experiment. This enabled us to test for effects of grazing regime on bird abundance and bird distribution throughout the year. We used the experiment to determine to what extent there are differences in vegetation micropatterns between the grazing treatments and studied vegetation micropatterns at Redshank (*Tringa totanus*) and Oystercatcher (*Haematopus ostralegus*) nests to infer effects of grazing on the abundance of potential nest sites. Subsequently we tested whether the grazing treatments differed in the likelihood of nest trampling between cattle or horses. Since salt marshes are used extensively by geese from autumn to early spring, we also tested whether the use of salt marsh by geese differed with the grazing treatments. Lastly, we studied Meadow Pipit nestling (*Anthus pratensis*) diets to determine which invertebrates were fed to Meadow Pipit nestlings and whether the availability of these food items differed between foraging sites and random sites, again to infer potential effects of grazing on the suitability for pipit breeding.

The effects of grazing in this thesis could only be determined over the short timescale that the experiment lasted. We were therefore forced to study the long-term relation between livestock grazing and the abundance and diversity of birds on the basis of a non-experimental dataset.

Here I will present the most important findings and show how our study relates to previous studies on the effects of livestock grazing. Based on this integration we will make recommendations for management of salt marshes.

Integration of results

In **chapter 2** we showed that an increase of tall vegetation on a salt marsh on a long-term (50 years) abandonment of salt marshes did not necessarily lead to a reduction of bird species richness, yet individual species may experience detrimental effects of abandonment of grazing on abundance. We also showed that the local conditions on a marsh may be an important factor in the distribution of birds over salt marshes and should, therefore, be taken into account when deciding on a management regime for a salt marsh. In **chapter 2** we confirm that some form of livestock grazing is beneficial for birds in general, as is also suggested in the introduction (Milchunas et al. 1988), but in **chapter 2** we cannot provide data on the effect of different livestock grazing treatments, because there is no clear data available on the exact stocking densities and livestock species used on all salt marshes along the Dutch Wadden Sea Coast.

In the box we demonstrated that after two years of grazing the total number of birds was affected by livestock grazing. Livestock grazing has been shown to retard vegetation succession of salt marshes (Olff et al. 1997). Our results show that the most intensively grazed paddocks had the highest numbers of birds (disregarding flocking bird species) in all seasons. This is in agreement with Reif et al. (2013) who suggested that it is important to maintain areas open and at early successional stages to aid specialist bird species.

The distribution of individual bird species, throughout the year, did not change by experimental livestock grazing. However, our experiment did not include a replicated ungrazed treatment, so we could not make statistical comparisons between the grazing treatments and an ungrazed control. One of the replicate blocks did, however, contain an ungrazed treatment (ungrazed >20 years). Birds in this treatment have been counted biweekly, as were all the other treatments. Interestingly, the total number of Reed Buntings (*Emberiza schoeniclus*) counted from October 2009 to December 2011 was greater in this treatment than in the other treatments (Fig. 7.1 A). Oystercatchers on the other hand were clearly underrepresented in the counts of the ungrazed treatment (Fig. 7.1 B). This fits the results from **chapter 2** where Reed Buntings increased in numbers with increasing cover of tall vegetation.

In **chapter 3** we found that both Oystercatchers and Redshanks place their nests on parts of the salt marsh with more pronounced vegetation patterns than found at random sites. Additionally we found that the treatments grazed with the highest stocking densities (1 horse/ha and 1 cattle/ha) had significantly less pronounced vegetation patterns than the other treatments (Fig. 7.2). These findings confirm studies by Norris et al. (1997, 1998) who found the highest densities of Redshanks on grazed salt marshes where grazing induced structural heterogeneity in the vegetation.

Most of the chapters in this thesis discuss the indirect effects of grazing on bird abundance and diversity through vegetation structure. However, a grazing treatment resulting in the highest adult bird abundance or the highest vegetation heterogeneity is not necessarily the grazing treatment with the highest reproductive success of the birds. For Black-tailed Godwits (*Limosa limosa*) high production grassland may act as an ecological trap, if breeding success in these areas is lower
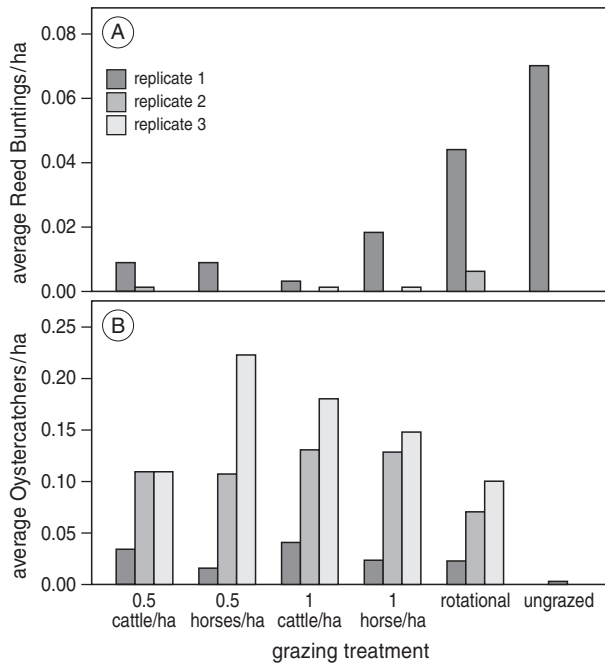
Figure 7.1 The average number of Reed Buntings (A) and Oystercatchers (B) per hectare, counted from October 30, 2009 to December 16, 2011. Each replicate and each grazing treatment has been counted an equal number of times. The counts of the grazing treatments were all conducted on the same day. Reed buntings are overrepresented in the ungrazed treatment in replicate 1, while Oystercatchers are underrepresented. Additionally it should be noted that replicate 1 had a history of no grazing before the experiment, while replicate 2 and 3 had a history of cattle grazing.
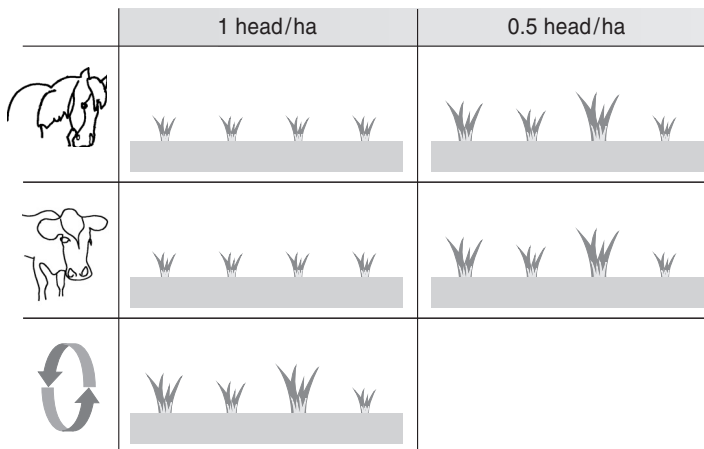
Figure 7.2 Grazing with low densities of livestock (0.5 head/ha) or rotational grazing with cattle (in a year with grazing) leads to more pronounced micropatterns in the vegetation in the breeding season than livestock grazing with 1 head/ha every year.
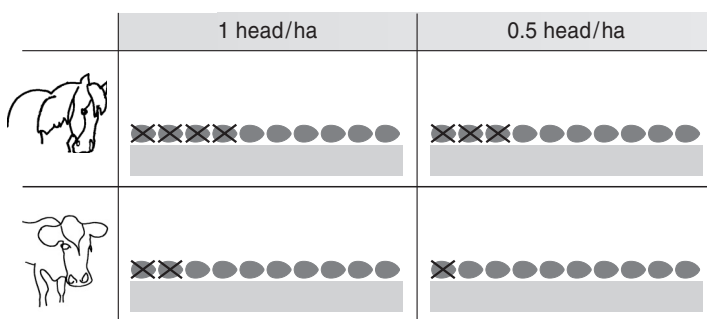
Figure 7.3 With grazing by horses significantly more nests are trampled than with grazing by cattle, even at lower densities of horses. The figure is based on the fraction of artificial nests trampled after 21 days (**chapter 4**). Each egg represents 10%. The number of trampled nests was rounded to the nearest 10%.

than needed for a viable population and godwits continue to breed in these areas (Groen et al. 2012). Our study area is not mown; however, the survival of nests differs between the grazing treatments.

In **chapter 4** we showed that nests are more likely to be trampled in horse-grazed treatments than in cattle-grazed treatments. Additionally, nests were more likely to be trampled with livestock densities of 1 cattle/ha or 1 horse/ha, than with livestock densities of 0.5 cattle/ha or 0.5 horses/ha (Fig. 7.3). We also showed that the trampling rates found in our study area are similar to trampling rates found by Beintema and Müskens (1987) on inland grasslands. In a study by Pakanen et al. (2011) conducted on coastal grazing meadows in Finland it was found that livestock grazing with 1.47 cattle/ha (including calves) led to relatively high trampling rates. Based on a literature review, these authors also showed that high stocking densities of cattle (>3 head/ha) generally lead to much higher trampling rates than with lower stocking densities (<1 head/ha). This is in accordance with our findings in **chapter 4**. Pakanen et al. (2011) additionally note that trampling rates are highest in the week after the onset of grazing.

In general nature management with livestock bears with it the risk of nest trampling. This risk can be strongly reduced by postponing the onset of grazing to late summer when most birds have finished breeding. It should be avoided that salt marshes become ecological traps where livestock grazing induces preferred nest site characteristics, only to negatively affect the reproductive output of birds by trampling of nests (Schlaepfer et al. 2002)

In **chapter 5** the distribution of geese over the experiment was determined by dropping counts. The horse-grazed treatments of 1 horse/ha were most used by geese in autumn (Fig. 7.4).

Our results in **chapter 5**, based on an experiment with cattle and horses are largely in agreement with a study by Stock and Hofeditz (2003) on the Hamburger Hallig (Germany) using a different livestock species. They showed that after a change in management from intensive sheep grazing (9 sheep/ha) to either intensive

	autumn 2011		spring 2012	
	1 head/ha	0.5 head/ha	1 head/ha	0.5 head/ha
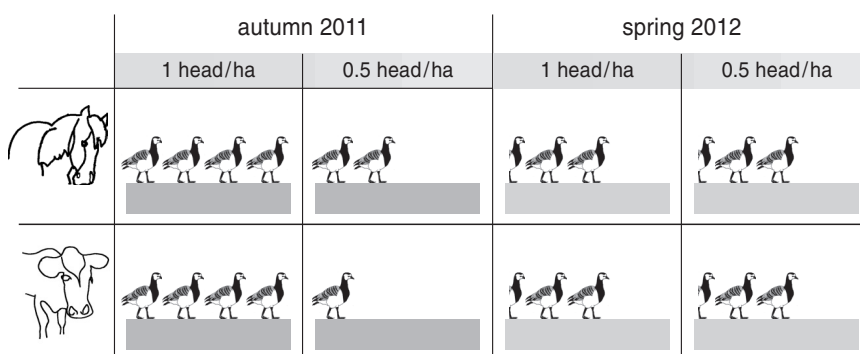
Figure 7.4 Schematic overview of goose use of different grazing treatments in autumn and spring. In autumn the 1 horse/ha treatment was used the most by geese, while in spring the geese used all treatments equally.
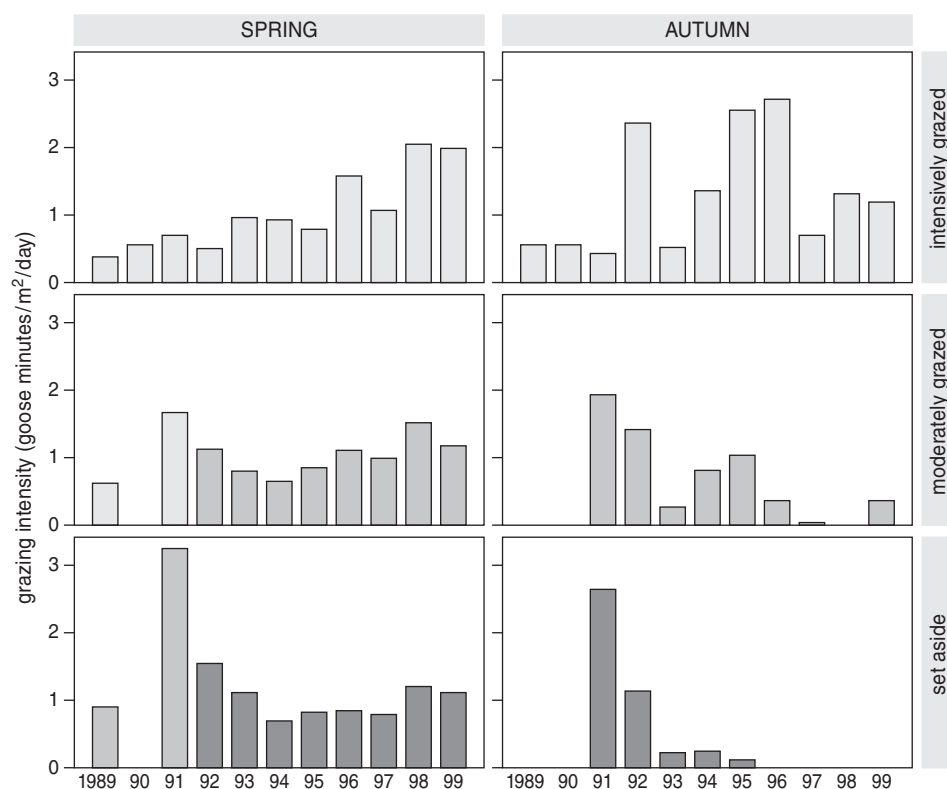
Figure 7.5 Grazing intensity of Barnacle goose (goose minutes m^{-2} day^{-1}) after a change in management in the summer of 1991 on the Hamburger Hallig in spring and autumn. Light grey bars = grazed intensively by sheep (9 sheep/ha); middle grey bars = moderate sheep grazing (0.7 sheep/ha); dark grey bars = not grazed by sheep. From Stock and Hofeditz (2003)..

(9 sheep/ha), moderate (0.7 sheep/ha) or no sheep grazing goose numbers declined steeply on ungrazed and moderately grazed marshes, especially in autumn (Fig. 7.5). On the intensively sheep grazed marshes, goose numbers increased.

The results from Stock and Hofeditz (2003) combined with our results from **chapter 5** strongly suggest that to promote the use of salt marshes by geese any grazing resulting in a homogeneous short sward with livestock is appropriate. However, Stock and Hofeditz (2003), too, concluded that the type of management appropriate for geese is disadvantageous for many other bird species and opposes local goals of increasing diversity of other organisms. Micropatterns (Fig. 7.2) in the vegetation as well as vegetation structure on a scale of 25 metres (Nolte unpublished), for example, are more pronounced in the grazing treatments with 0.5 head/ha than in grazing treatments with 1 head/ha. Vegetation structure on different scales is important for a number of breeding bird species (e.g. Dallinga 1993, Norris et al. 1997, Norris et al. 1998, Whittingham et al. 2004).

In addition to providing food for overwintering birds, salt marshes also provide food for chicks of birds breeding on salt marshes. Food provisioning of the parents is an important factor determining the survival of nestlings and thus reproductive success. Parents should maximise the amount of food brought to the young (Kacelnik 1984, Wright et al. 1998). This can be achieved by selecting the larger prey items in order to minimize the number of flights between foraging grounds and the nest (Wright et al. 1998) while, the distance from the nest to foraging grounds should be taken into account (Wright et al. 1998). In **chapter 6** we showed that Meadow Pipit nestlings were fed mostly large spiders and caterpillars (Fig. 6.1) even though many small prey items were abundantly available on the salt marsh. This is in accordance with a report by Wilson et al (1996).

Interactions between birds, invertebrates and plants

The study on birds discussed in this thesis was part of a larger study incorporating the effects of grazing on plants, and invertebrates. These groups of organisms all interact on a salt marsh. Increasing the diversity of birds as well as increasing the diversity of plants and invertebrates are management goals for the salt marshes along the Wadden Sea coast (Esselink et al. 2009). As with the vegetation structure around Oystercatcher and Redshank nests, it was found that structure (variation in height) in the vegetation on a slightly larger scale (25 m) was lowest with 1 horse/ha and highest with 0.5 cattle/ha (Nolte unpublished). Partially this may be caused by the fact that a horse generally eats more than a cow due to differences in their digestive systems (Duncan et al. 1990). Horses also eat more low quality vegetation, such as the tall grass *Elytrigia atherica*. This grass species tends to overgrow the salt marsh when left ungrazed (Bakker et al. 2003). When *E. atherica* already covers a marsh, horse grazing may be a suitable management tool to remove it to facilitate a more heterogeneous salt-marsh vegetation. However, the number of flowering plants is lower when grazing with 1 horse/ha than when grazing with other grazing treatments (Nolte et al. 2013).

The negative effect of horse grazing on plants described in the previous paragraph is also visible in the abundance and diversity of invertebrates. High stocking density on salt marshes and most other habitats is detrimental to the abundance of most invertebrate species (Van Klink unpublished). High stocking densities of sheep on German salt marshes, for example, affected total invertebrate species richness negatively (Van Klink et al. 2013), and especially of specialist moth species (Rickert et al 2012, Van Klink et al 2013). In the experimental setup described in this thesis, the abundances of flower visiting insects were lowest with 1 horse/ha (Van Klink unpublished). Since invertebrates are an important food source for many birds, a decrease in invertebrates in the 1 horse/ha grazing treatment may also be detrimental for bird diversity and/or abundance.

The rotational grazing treatment on the other hand seems to offer interesting perspectives for the conservation of invertebrate species. Flower visiting insects were found to be most abundant in years without grazing in the rotational grazing treatment (Van Klink unpublished). In general, years without grazing lead to an increase in species richness of invertebrates (Morris 2000).

The integral study on birds, invertebrates and plants described in this paragraph allowed us to study interactions between different groups of organisms. However, questions on the effects of livestock grazing for each of the groups differed and often measurements were taken at different times during the year to gain specific data for that group. For example, measurements at birds' nests were mostly taken during the breeding season from approximately April to the end of June, while measurements on plants were often taken in July and September, when plants were fully grown and bloomed. Studies on interactions between plants, invertebrates and birds could be further improved by studying these groups simultaneously during the year.

Future studies

For research on birds we recommend continuation of the grazing experiment as it was presented in this thesis, especially to gain more knowledge on the effects of the rotational grazing treatment, which seems promising for the conservation of salt-marsh birds. Continuation of the experiment started in this thesis will allow studies on long-term effects of grazing on different aspects of bird life histories, for example by monitoring the breeding success of birds in different grazing treatments. A longer-term study will also allow direct comparisons of number of nests of different bird species in each grazing treatment to gain more knowledge on the actual nest-site preferences of, for example, Redshanks and Oystercatchers.

Thus far with the grazing experiment we gained knowledge on the, mainly short-term, effects of grazing on plants, invertebrates and birds, but for future studies we also recommend more focus on the interactions between these groups and the ecosystem as a whole.

The observation that Reed Buntings were overrepresented and Oystercatchers underrepresented in one ungrazed treatment (Fig. 7.1 A) suggests that effects of

grazing on birds lag behind the actual grazing, i.e. it takes time for birds to respond to changed management, and changes in the species composition of birds on a salt marsh may take more time than the duration of this study. This suggestion is also supported by the observation that the replicate which was ungrazed before the experiment harboured more Reed buntings than the other two treatments, which were grazed before the experiment (Fig. 7.1 A). We stress that longer-term studies on grazing are crucial to understand effects of livestock grazing on birds.

The study on the distribution of geese on the salt marsh should be continued to understand how geese respond to the rotational grazing treatment after a year without livestock grazing. To improve decisions on livestock grazing as a management tool, future research should help to find the latest possible date to initiate grazing in a given season that maximizes the long term bird diversity by maximising the settling chance in spring while keeping the nest trampling risk low enough. Again the rotational grazing treatment offers interesting perspectives. In years without grazing no nests will be trampled, plants flower and attract pollinating invertebrates and set seed which is beneficial for birds, while in years with trampling cattle trample relatively few nests, compared to horses.

Implications for management

This thesis aimed to gain a better understanding on applied questions regarding the effects of livestock grazing on birds on salt marshes. Based on this aim and the results in the previous chapters a number of general recommendations can be made to aid salt-marsh managers in their decisions on nature management of salt marshes with respect to birds (table 7.1). Livestock grazing can indeed be used as a tool to manage salt marshes. In the Wadden Sea area a general goal is increasing biodiversity (Esselink 2009), and bird diversity may be an important part of this. Other goals for nature conservation may be the conservation of specific species thus maximising their abundance. For example Lesser White Fronted Geese (*Anser erythropus*) on the Baltic coast are a species of conservation concern.

Different grazing treatments may aid in reaching different management goals. Grazing with high densities of livestock, such as with 1 horse/ha may lead to a homogeneous short sward (Bakker 1989). This type of sward is suitable for geese and may attract larger numbers of geese to salt marshes in autumn (**Chapter 5**). Grazing with 1 cattle/ha is not likely to lead to the same short sward, attractive for geese, as grazing with 1 horse/ha. Grazing a salt marsh with 1 horse/ha, however, increases the risk of trampling birds nests in spring (**Chapter 4**). Additionally, grazing a salt marsh with 1 horse or cattle/ha leads to less pronounced micropatterns in the vegetation (**Chapter 3**). These micropatterns are small-scale vegetation heterogeneity that is preferred by Redshanks and Oystercatchers for nesting.

With 0.5 horses/ha the risk of nests being trampled is reduced compared to grazing with 1 horse/ha, but is still larger than with grazing with 0.5 cattle/ha. Micropatterns in the vegetation are significantly more pronounced when grazing with 0.5 horses or cattle/ha than with 1 horse or cattle/ha. The more heterogeneous

vegetation with 0.5 horses or cattle/ha is not as attractive for geese as the homogeneous sward created by grazing with 1 horse/ha.

The rotational grazing treatment offers interesting perspectives to combine salt-marsh management goals in a single grazing treatment. The years with grazing help in the creation of in field heterogeneity i.e. vegetation structure, while the years without grazing provide disturbance-free habitat in which no bird's nests will be trampled by livestock. For goose species it is too early to make clear predictions on the effects of rotational grazing, because thus far goose numbers in winter on the rotational grazing treatment have only been determined after a year with grazing.

The rotational grazing treatment also offers interesting perspectives for additional studies on the nest-site choice of Meadow Pipits on salt marshes. In 2011 the majority of Meadow Pipit nests were found in the rotational grazing treatment and none in the 1 horse/ha treatment. Although this observation cannot be used to determine a preference of Meadow Pipits for any specific grazing treatment to breed in, we hypothesize that livestock grazing affects the nest site choice of Meadow Pipits, and possibly other bird species. The rotational grazing treatment offers interesting perspectives for additional studies on the nest site choice of Meadow Pipits on salt marshes.

To protect birds' nests from being trampled, livestock grazing can be postponed to as late in the year as possible (end of June). Any problems that arise from livestock trampling nests may be avoided by postponing livestock grazing until after the peak breeding season.

Table 9.1 Effects of five different grazing treatments on bird diversity and abundance for different groups of birds, based on the results from the chapters in this thesis. Plus (+) signs can be read as an effect going up and minus (-) signs as an effect going down compared to the opposite signs in each row. Plus signs between brackets ((+)) are expected effects that we cannot directly show. Question marks (?) indicate that we do not have data to make recommendations. For example, with grazing with 0.5 horses/ha trampling of nests goes up compared to grazing with 0.5 cattle/ha while exploitation by geese goes down compared to grazing with 1 horse/ha. The colours are an advice to nature managers. Green indicates a recommendation to use a grazing regime in order to achieve the effects in each row, while red indicates a recommendation not to use a grazing regime. Orange indicates that the effect of the grazing treatment differs between a year with and without grazing in the rotational grazing treatment.
Note that nests are not trampled by livestock in the rotational treatment in the years without livestock grazing, while it has 1 cattle/ha in the years with grazing and hence nest trampling.

| | Chapter | Horses | | Cattle | | 1/ha rotational |
		0.5/ha	1/ha	0.5/ha	1/ha	
Micropatterns in vegetation	3	+	-	+	-	+
Nest trampling	4	+	+	-	+	-/+
Exploitation by geese	5	-	++	-	+	?
Food for songbirds	6	?	(-)	?	?	(+)

It may be clear that different management goals lead to different recommendations on grazing management. In general however, we recommend to apply different grazing treatments to different salt marshes simultaneously. This will lead to large scale heterogeneity (Benton et al. 2003). These large scale mosaics of grazing treatments have previously been recommended for salt marshes by Bos et al. (2005). In this manner some areas can be managed for, for example, geese, while others are managed to create structural diversity in the vegetation for other groups of birds. In our experiment, flocks of geese rarely spread out over just one grazing treatment. We therefore recommend that variation in management of salt marshes should be conducted over areas larger than 11 ha in size.

Conclusions and relevance for other systems

Salt marshes are unique systems in many ways, but many of the results presented in this thesis can be applied to other grazed grassland systems as well. Trampling of nests of ground-breeding birds is a common problem on American rangelands as it is on grazed salt marshes. Management recommendations from **chapter 5**, such as using fresh water tanks to draw livestock away from areas with high densities of breeding birds (**chapter 5**, Primrose and Delaney 2007) may be applicable on rangelands, too. The importance of vegetation structure has been recognized on salt marshes (e.g. Norris et al. 1997, Milsom et al. 2000) as well as in other grassland systems (e.g. Fuhlendorf and Engle 2001, Verhulst et al. 2011). Many waders, such as Redshanks and Oystercatchers are not exclusively linked to coastal areas. These birds also commonly breed on agricultural land (Beintema et al. 1995). Our results from **chapter 4** on vegetation micropatterns around nests of Oystercatchers and Redshanks can be used for the conservation of these species breeding inland as well.

In The Netherlands Brent geese (*Branta bernicla*) and Barnacle geese (*Branta leucopsis*) are increasing rapidly in numbers (Fox et al. 2010). This may be different for other goose species. For example Lesser White-fronted Geese on the Baltic coast are a threatened species. The results from **chapter 6** could be used to aid the conservation of this species.

In conclusion we stress that the application of a grazing treatment should always be considered in light of a specific target. Any grazing treatment may have beneficial effects for one group of organisms, while it negatively affects another group. Local conservation concerns can be used as a basis to decide on the management of any system with livestock grazing.

Appendix A. Average numbers of all bird species per season counted from 2009 to 2012 at two week intervals within the livestock grazing experiment.

date	arctic tern	avocet	barn swallow	barnacle geese	black headed gull	black tailed godwit	brent goose	buzzard	carrion crow	common gull	common kestrel	common quail	common sandpiper	common snipe	common tern	curlew	dunlin
autumn 2009				19.3			2.5	0.3	1.5		0.3			45.5		0.8	7.5
winter 2009-2010				37.5	0.8		6.7	0.2	1.4		0.2			7.2		0.5	0.2
spring 2001		5.8		2396.9	0.3	1.3	124.2	0.8	0.3		0.2				1.3	0.2	
autumn 2001				58.5				0.4	0.3		0.5			9.5		0.3	0.5
winter 2001-2011				0.1				0.1	0.1					0.1			
spring 2011	0.1	1.1		2552.3		2.9	5.4	0.3	0.7	0.1	0.3			0.1	0.3	0.3	
autumn 2011				39.9		0.6		0.3	0.3		0.1			7.0		0.1	1.6
winter 2011-2012				61.6			0.8	0.3	0.3	2.6				7.8		0.6	1.6
spring 2012	0.5	6.7	0.6	0.3	0.6	1.1	37.3	0.1				2.0		0.2	0.1	0.2	0.3
autumn 2012								1.3	1.0		2.0	0.3	0.1	15.0			1.0

date	eurasian dotterel	eurasian wigeon	eurasian woodcock	european goldfinch	european greenfinch	fieldfare	gadwal	golden plover	great egret	green sandpiper	greenshank	grey heron	greylag goose	hen harrier	herring gull	house martin	jack snipe
autumn 2009		125.0									3.8		2.3				0.8
winter 2009-2010						0.4					0.2				0.8		
spring 2010	0.2			1.2				0.8			0.2					16.5	
autumn 2010					0.1						0.4		0.5		0.3		
winter 2010-2011															0.1		
spring 2011								1.5								0.3	
autumn 2011										0.9	2.7	1.0	8.4	0.6	0.3	0.3	
winter 2011-2012											0.5		8.4				
spring 2012								0.2		1.1	0.1		2.0		0.1	3.1	0.1
autumn 2012			0.1	16.8						0.6	1.6	0.1	0.1	0.2	0.1	0.1	
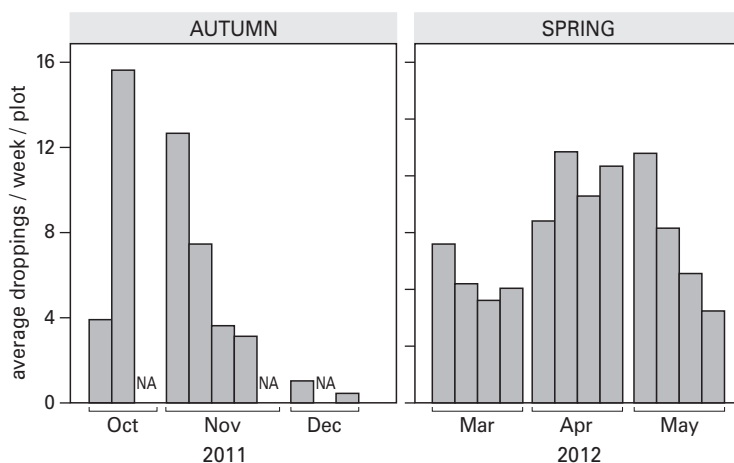
Appendix B. The average number of droppings per week per 4 m^2 plot in the whole experiment. Note that in autumn three counts were removed from the analysis, because the study area was flooded in the period prior to the weekly count (NA).

Appendix C. Diet composition of Meadow Pipit nestlings: all 23 samples, identified to the highest taxonomic level possible.

nest	year	*Clubiona stagnatilis*	*Enoplognatha mordax*	*Pachygnatha clercki*	*Pachygnatha degeeri*	*Pardosa purbeckensis*	*Stemonyphantes lineatus*	*Trochosa ruricola*	**total spiders**	bivalves	gastropods	beetles	ants	ants	**total adult insects**	caterpillars	insect larvae	grass
1	2011	-	-	-	-	-	-	1	1	-	-	-	-	-	1	7	-	-
1	2011	-	1	1	-	1	-	-	3	-	-	-	-	1	1	2	2	-
1	2011	1	1	-	-	1	-	-	3	-	-	-	-	-	1	6	-	-
2	2011	-	-	-	-	-	-	-	2	-	-	-	-	-	-	3	-	-
3	2011	-	-	1	-	-	-	-	1	-	1	-	-	-	-	2	-	-
4	2011	1	1	-	-	-	-	-	2	-	-	-	-	-	1	2	-	-
5	2011	-	1	1	1	1	-	-	4	-	-	-	-	-	1	8	1	-
5	2011	-	-	-	-	2	-	-	2	-	-	-	-	-	1	9	-	-
6	2010	-	-	1	-	-	-	-	1	-	-	-	-	-	-	9	2	-
7	2010	-	-	-	-	2	-	-	2	1	-	-	-	-	1	1	-	1
8	2011	1	1	3	-	3	-	-	8	-	-	-	-	-	-	2	1	-
8	2011	-	2	1	-	1	-	-	4	-	-	-	-	1	1	1	-	-
8	2011	-	-	-	-	-	-	-	1	-	-	-	-	1	1	1	-	-
8	2011	-	1	-	-	3	-	-	4	-	-	-	-	-	-	-	-	-
9	2011	-	1	-	-	-	1	-	3	-	-	-	-	-	-	3	6	-
9	2011	-	-	-	-	-	1	-	1	-	-	1	-	-	1	1	2	-
9	2011	-	-	-	-	-	-	-	1	-	-	2	-	-	1	7	6	-
10	2011	-	-	3	-	2	-	-	5	1	-	-	-	-	1	4	4	-
11	2010	-	-	-	-	2	-	-	3	-	2	-	-	-	1	1	-	-
11	2010	-	-	-	-	1	-	-	2	1	-	1	-	-	1	1	2	-
11	2010	-	-	-	-	13	-	-	13	-	-	-	1	1	1	4	-	-
12	2009	-	-	-	-	10	-	-	10	-	-	-	-	1	-	8	-	-
13	2010	1	-	-	-	7	-	-	8	-	-	-	-	-	-	-	-	-
TOTAL		**4**	**9**	**11**	**1**	**49**	**2**	**1**	**84**	**3**	**3**	**4**	**1**	**3**	**15**	**82**	**26**	**1**

Cited literature

A

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Summary
Samenvatting

Summary

How to graze?

Bakker et al. (2003) posed the question "to graze or not to graze". This question related to the management of salt marshes for nature conservation. Ten years later there is general consensus in the Netherlands that livestock grazing on a salt marsh can be beneficial for the biodiversity of a salt marsh. The question remains, however, how to graze? It is unlikely that one 'perfect' grazing regime exists that maximizes diversity in every system for all groups of organisms. To shed light on this we studied effects of grazing treatments on bird abundance and diversity on salt marshes where we experimentally manipulated the grazing regime.

Livestock grazing has direct and indirect effects on birds. Direct, by e.g. trampling nests or disturbance of breeding birds. Indirect by e.g. changing the vegetation structure. In the Netherlands nature managers generally graze salt marshes in order to promote a higher biodiversity and birds are often a focal point. In this thesis we make recommendations on how the direct and indirect effects of livestock grazing can be used to promote bird diversity and abundance.

The study was conducted on a large salt-marsh area in the north of the Netherlands, Noard Fryslân Bûtendyks. Within the study area a unique large-scale experiment was set up over an area of 165ha. The experiment consisted of three 55ha replicates, each with five different grazing treatments in 11ha paddocks. The grazing treatments were: 1 horse/ha, 0.5 horses/ha, 1 cattle/ha, 0.5 cattle/ha and a rotational treatment, yearly alternating grazing with 1 cattle/ha with a year without grazing. The effects of these treatments were recorded during the first three years of the experiment

Distribution of birds over grazed salt marshes

We studied the diversity and abundance of birds on salt marshes both on a large scale on marshes along the Wadden Sea coast using descriptive data as well as on a smaller scale in our grazing experiment. On the large scale we used the cover of tall vegetation as a proxy for grazing intensity, while on the small scale we ourselves determined the exact stocking densities. On the large scale we found that moderate livestock grazing can be used as a tool to limit the spread of tall vegetation over a salt marsh, as well as to change the structural diversity within tall plant communities. With this type of management, the number of species and the abundance of most breeding birds can be maintained in coastal marshes.

On the smaller scale we found that there were more overwintering birds (excluding flocking species such as geese) on the 1 horse/ha treatment than on any of the other grazing treatments. A longer term experiment is however required to gain more detailed insights in the distribution of birds over different grazing treatments throughout the year.

To understand how geese are affected by different grazing treatments, we conducted a different study. In this study dropping counts were used to calculate which grazing treatments were used the most by geese. We found that in autumn goose visitation was highest in the 1 head/ha grazing treatments and lowest in the 0.5 head/ha grazing treatments. In spring on the other hand we found no difference in goose visitation between the five grazing treatments.

Direct and indirect effects of livestock grazing on birds

Livestock grazing affects the distribution of birds over a salt marsh, but it also affects individual birds both directly and indirectly. We studied the potential trampling intensity of nests by using clay discs laid out in the field and found that horses trample significantly more than cattle, likely resulting in lower survival rates of nests under horse grazing than under cattle grazing.

Indirectly, livestock grazing affects birds through the vegetation structure. We found that both Redshank and Oystercatchers choose nest sites with significantly more pronounced micropatterns (a measure of vegetation heterogeneity) than found at random sites. We also found that these micropatterns were found mostly in paddocks grazed with low densities of horses and cattle or in the rotational treatment.

Grazing may also affect the availability of food for birds. We studied the foraging site choice and diet selection of Meadow Pipit nestlings and found that breeding Meadow Pipits foraged for caterpillars and large spiders in vegetation that was less heterogeneous than vegetation at random locations. The highest abundance of food items was found in tall vegetation. These findings suggest that the creation of patchy vegetation by grazing or otherwise may not be invariably beneficial to breeding Meadow Pipits.

Conclusions

The core question posed in this thesis is how to apply grazing as a tool for nature management for birds both in terms of the choice of livestock species and in the choice of stocking densities. Grazing with high densities of livestock, such as with 1 horse/ha may lead to a homogeneous short sward (Bakker 1989). This type of sward is suitable for geese and may attract larger numbers of geese to salt marshes in autumn. Grazing a salt marsh with a high stocking density (1 horse/ha), however, increases the risk of trampling birds nests in spring and leads to less pronounced micropatterns in the vegetation. The latter is also true for 1 cattle/ha.

The rotational grazing treatment offers interesting perspectives to combine salt-marsh management goals in a single grazing treatment. The years with grazing help in the creation of in field heterogeneity i.e. vegetation structure, while the years without grazing provide disturbance-free habitat in which no bird's nests will be trampled by livestock. In general however, we recommend to apply different grazing

treatments to different salt marshes simultaneously. This will lead to large scale heterogeneity. Each grazing regime has its specific effects leading to the suggestion that a combination of different grazing regimes in one conservation area may give the best opportunities for nature management of birds in salt marshes.

Future studies

To rigorously answer how grazing regimes affects bird diversity and abundance we recommend continuation of the grazing experiment resulting in this thesis, to gain more knowledge on the effects of the rotational grazing treatment, which seems promising for the conservation of salt-marsh birds. Moreover, long-term effects of grazing can be important, because some of the birds studied have a life cycle of many years, precluding perhaps direct adaptation to our experimental change in grazing treatment. Monitoring the settlement patterns of young entering in the population and their breeding success in relation to experimental grazing treatment should deliver us long-term effects of grazing on important aspects of bird life histories and bird diversity, both crucial parameters in salt-marsh management.

Samenvatting

Hoe te beweiden?

Bakker et al. (2003) stelden de vraag: "beweiden of niet beweiden". Deze vraag was gerelateerd aan het beheer van kwelders ten behoeve van natuurbescherming. Tien jaar later is er in Nederland overeenstemming dat beweiding van kwelders met vee gunstig kan zijn voor de biodiversiteit van een kwelder. De vraag blijft echter: hoe te beweiden? Het is onwaarschijnlijk dat er een enkel 'perfect' beweidingsregime bestaat waarmee de diversiteit van alle groepen organismen in alle systemen gemaximaliseerd kan worden. Om hier meer duidelijkheid over te geven, hebben we de effecten van beweidingsregimes op vogelaantallen en vogeldiversiteit op kwelders met experimentele beweidingsregimes bestudeerd.

Beweiding met vee heeft direct en indirecte effecten op vogels. Direct, door, bijvoorbeeld, het vertrappen van nesten of het verstoren van broedende vogels. Indirect, door, bijvoorbeeld, het veranderen van de vegetatiestructuur. In Nederland worden kwelders meestal beweid om een hogere biodiversiteit te bewerkstelligen. Vogels zijn hierbij vaak een prioriteit. In dit proefschrift doen wij aanbevelingen over hoe de directe en indirecte effecten van beweiding met vee gebruikt kunnen worden om hogere vogelaantallen en een hogere vogeldiversiteit te bewerkstelligen.

De studie is uitgevoerd in een groot kweldergebied in het noorden van Nederland, Noard Fryslân Bûtendyks. In dit gebied is een uniek grootschalig experiment opgezet met een oppervlakte van 165 ha. Het experiment bestond uit drie replica's van 55 ha, elk met vijf verschillende beweidingsregimes in proefvakken van 11 ha. De beweidingsregimes waren: 1 paard/ha, 0,5 paarden/ha, 1 koe/ha, 0,5 koeien/ha en een rotatiebeheer waarin een jaar beweiden met 1 koe/ha wordt afgewisseld met een jaar zonder beweiding. De effecten van deze beweidingsregimes werden geregistreerd gedurende de eerste drie jaar van het experiment.

Verspreiding van vogels over beweide kwelders

We hebben de aantallen van vogels en de diversiteit van vogels op kwelders bestudeerd op zowel een grote schaal, met gebruikmaking van beschrijvende data, als op een kleine schaal, in ons beweidingsexperiment. Op de grote schaal gebruikten we de bedekking van hoge vegetatie als een maat voor de intensiteit van beweiding. Op de kleine schaal bepaalden we zelf de veedichtheden. Op de grote schaal vonden we dat beweiding met lage veedichtheden gebruikt kan worden om de verspreiding van hoge vegetatie over een kwelder te beperken en om de diversiteit in de vegetatiestructuur van hoge plantgemeenschappen te veranderen. Met behulp van dit type beheer kan het aantal soorten en de aantallen vogels van de meeste broedvogels op kwelders behouden worden.

Op de kleinere schaal vonden we dat er meer overwinterende vogels (zonder vogels die zich in groepen ophouden, zoals ganzen) zaten op de proefvakken met 1

paard/ha dan op elk van de andere proefvakken. Een experiment op langere termijn is echter nodig om een gedetailleerder beeld van de verspreiding van vogels gedurende het jaar over de beweidingsregimes te krijgen.

Om te begrijpen hoe ganzen beïnvloed worden door verschillende beweidingsregimes hebben we een andere studie uitgevoerd. In deze studie hebben we tellingen van ganzenkeutels gebruikt om te berekenen welke beweidingsregimes het meeste gebruikt werden door ganzen. We vonden dat het bezoek van ganzen in de herfst het hoogste was in de beweidingsregimes met 1 dier/ha. In de lente vonden we echter geen verschil in het bezoek door ganzen tussen de vijf beweidingsregimes.

Directe en indirecte effecten van beweiding met vee op vogels

Beweiding met vee beïnvloedt de verspreiding van vogels over een kwelder, maar het beïnvloedt ook individuele vogels, zowel direct als indirect. We bestudeerden de potentiele vertrappingsintensiteit van nesten door gebruik te maken van kleiduiven die we over de kwelder verspreid hadden en vonden dat paarden significant meer vertrappen dan koeien. Dit resulteert waarschijnlijk in lagere overlevingskansen van nesten onder paardenbeweiding dan onder koeienbeweiding.

Indirect beïnvloedt beweiding vogels via de vegetatiestructuur. We vonden dat zowel Tureluurs als Scholeksters nestplekken kiezen met significant duidelijkere micropatronen (een maat voor heterogeniteit in de vegetatie) dan op willekeurige plekken. We vonden ook dat deze micropatronen vooral te vinden waren in proefvakken met lage dichtheden van paarden en koeien of in het rotatiebeheer.

Beweiding kan ook de beschikbaarheid van voedsel voor vogels beïnvloeden. We bestudeerden de keus van foerageerplekken en de voedselkeuze van graspieperkuikens en vonden dat broedende graspiepers foerageerden voor rupsen en grote spinnen in vegetatie met minder heterogeniteit dan vegetatie op willekeurig gekozen plekken. De hoogste aantallen insecten die als voedsel konden dienen werd gevonden in hoge vegetatie. Deze bevindingen suggereren dat het creëren van heterogene vegetatie, met beweiding, of op een andere manier, is niet per definitie voordelig voor graspiepers.

Conclusies

De kernvraag die gesteld wordt in dit proefschrift is hoe we beweiding kunnen gebruiken in het natuurbeheer van vogels in termen van de keus voor het soort vee en de keus van veedichtheden. Beweiding met hoge dichtheden van vee, zoals met 1 paard/ha kan leiden tot homogene korte vegetatie (Bakker 1989). Dit type vegetatie is geschikt voor ganzen en kan, in de herfst, grotere hoeveelheden ganzen naar een kwelder lokken. Het beweiden van een kwelder met hoge veedichtheden (1 paard/ha) vergroot echter de kans op vertrapping van nesten in de lente en leidt tot minder duidelijke micropatronen in de vegetatie. Het laatste geldt ook voor beweiding met 1 koe/ha.

Het rotatiebeheer biedt interessante perspectieven om verschillende kwelderbeheerdoelen te combineren in een enkel beweidingsregime. De jaren met beweiding helpen bij het creëren van vegetatiestructuur terwijl de jaren zonder beweiding een verstoringsvrije habitat leveren waarin geen nesten worden vertrapt door vee. In het algemeen raden wij echter aan om tegelijkertijd verschillende beweidingsregimes te bewerkstelligen op verschillende kwelders in het zelfde gebied. Dit leidt tot heterogeniteit op grote schaal. Elk beweidingsregime heeft zijn eigen specifieke effecten, wat leidt tot de suggestie dat een combinatie van verschillende regimes in één natuurgebied de beste kansen voor natuurbeheer van vogels op kwelders kan bieden.

Toekomstige studies

Om de vraag hoe beweidingsregimes aantallen vogels en de diversiteit aan vogels beïnvloeden grondig te beantwoorden raden wij aan om het experiment dat heeft geresulteerd in dit proefschrift, voort te zetten. Op deze manier kan meer kennis over het rotatiebeheer, dat veelbelovend lijkt voor het behoud van kweldervogels, verkregen worden. Daarnaast kunnen lange-termijn effecten van beweiding belangrijk zijn, omdat een aantal van de bestudeerde vogels een levenscyclus van vele jaren hebben, waardoor ze zich mogelijk niet direct aanpassen aan onze experimentele verandering van beweiding in het studiegebied. Het monitoren van vestigingspatronen van jonge vogels die de populatie binnen komen en hun broedsucces in relatie tot de experimentele beweidingsregimes zou ons lange-termijn effecten van beweiding op belangrijke aspecten van de levensgeschiedenis van vogels en de diversiteit van vogels, beide belangrijke parameters in kwelderbeheer, op moeten leveren.

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Mijn promotoren Jan en Joost wil ik bedanken voor de tijd en moeite die zij in mij hebben gestoken. Jan die, ondanks dat hij al met pensioen was, altijd zeer snel reageerde op alle stukken die ik hem zond. Ook wil ik Jan bedanken voor de mooie excursies naar verschillende kwelders met de coastal ecology expeditie. Om op zo'n manier in korte tijd allerlei verschillende kweldergebieden te zien heeft mij heel erg geholpen om mijn eigen werk in het grotere perspectief van de gehele Waddenzee te plaatsen. Joost wil ik speciaal bedanken voor de uren op zijn kantoor waarbij mijn resultaten en plannen uitgebreid werden besproken. Soms miste er van mijn kant zaken in de voorbereiding van deze gesprekken, waardoor we meer tijd kwijt waren dan misschien nodig was geweest. Joost heeft dit altijd geduldig opgepakt. Zonder de kritische noten van Joost zou ik het niet gered hebben om een aantal van mijn hoofdstukken gepubliceerd te krijgen.

Naast mijn promotoren ben ik ook bijgestaan door een co-promotor en verschei-dene andere begeleiders. Bruno was voor mij als co-promotor een belangrijke link met SOVON en heeft altijd waardevolle opmerkingen gemaakt bij verschillende hoofdstukken. Ook bij Kees K. en Julia Stahl, beide tevens werkzaam bij SOVON, kon ik altijd terecht om resultaten door te spreken. Naast mijn eigen begeleiders wil ik ook de andere leden van de begeleidingscommissie hartelijk bedanken voor hun

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In de vier jaar van mijn promotie heb ik ook uitgebreid ondersteuning gehad van studenten, met name studenten die de cursus Community Ecology Research volgden. Vermoedelijk ben ik niet altijd de beste begeleider geweest, omdat ik zelf ook nogal is moest zoeken hoe ik problemen in mijn dataverzameling op ging lossen. Dankzij het eigen initiatief en de bereidwilligheid om mee te denken hebben Jeroen, Maite, Frank, Jelle, Emma, Mo, Pieter-Wytze en Annemarie mij bijzonder geholpen. Nu waren het niet alleen studenten die mij hebben geholpen, ook heel wat anderen hebben mij op verschillende momenten geholpen met allerlei zaken: Corinna, Judith, Katherina, Elske, José, Piet, Crijn, Maarten, Adrienne, Joy, Jos, Arne, Daan, Remco, Roos, Kelly bedankt!

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