

# **Grazing in coastal grasslands**

Brent Geese and facilitation by herbivory

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# **Grazing in coastal grasslands**

**Brent Geese and facilitation by herbivory**

Proefschrift

ter verkrijging van het doctoraat in de  
Wiskunde en Natuurwetenschappen  
aan de Rijksuniversiteit Groningen  
op gezag van de  
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**Daniël Bos**

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te Zwolle

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# Preface

Wild enthusiasm stirred in me, when I was asked over the phone about my interest in a study on 'Moose' and 'Bear'. Wow, working on wildlife in a scenery of rugged mountain ranges and forested valleys... It took a while for me to discover that there had been a misunderstanding, since the project, in fact, dealt with 'Goose' and 'Hare'. I applied nonetheless, and found myself welcome amidst a diverse group of motivated students and fine colleagues, co-operating most closely with Maarten Loonen and Julia Stahl. One of the results of the research we were enabled to do about the geese and the hare, and their interaction with vegetation and larger herbivores, is now in your hands.

In this book, we focus on habitat use by Brent Geese, vegetation succession and facilitation, themes that have been the subject of study for many years by the departments of Plant- and Animal Ecology of the University of Groningen. It was at the initiative of Bart Ebbinghe (Alterra), Jan Bakker and Rudi Drent to bring together these separate lines of fundamental research, in order to answer an applied question: "What will happen with the Brent Geese when the management of their foraging areas is changed?".

This question is relevant, because Brent Geese spend large amounts of time on salt marshes, but also on agricultural land. There is a relationship between the attractiveness of salt-marsh habitat for Brent Geese and the degree to which farmers are bothered by them. It is an example of a very common situation, where man and nature are in potential conflict. In order to choose wisely the most suitable type of land use in such a situation, a proper ecological understanding is required. I am fascinated by these issues, and, therefore, I greatly appreciate the chance I have had to work with these people and these animals on this subject, in spite of the initial misunderstanding.

Daan Bos



CHAPTER

# 1

## General introduction

## Introduction

With increasing human population pressure, and human exploitation of resources, the existence for many other species than man has become threatened (Meffe & Carroll 1994). All around the globe, natural habitats are put to human use and this is often at the expense of natural diversity. Especially in densely populated countries such as the Netherlands, the landscape has been dramatically transformed (van Eerden 1997) and organisms that were not able to adapt to the new circumstances were forced to the margin of human society.

Where man and nature meet, there are often conflicts to be observed. Agricultural and pastoral activities may suffer from the presence of 'weed-' or 'pest' species competing for resources, transferring diseases or trampling crops (Tchamba 1996; Grootenhuis 2000). On the other hand, natural values and wild organisms are negatively affected by habitat destruction, pollution or poaching, to name a few examples. It is widely recognised that solutions to these conflicts are to be found, in order to maintain what is still left of the natural diversity. Solutions may include setting aside of essential habitat, sustainable use of natural resources or financial compensation for incurred costs suffered by individuals. In all of the cases, however, knowledge on the biology of the species concerned and the nature of the interaction with man is required to be able to find the right solution.

This thesis deals with an example of such an interaction between Brent Geese *Branta bernicla bernicla* and man in western Europe. The Brent Goose is an arctic breeding goose species, that is still largely dependent upon natural habitat. However, in winter and spring the geese also forage on improved grassland and agricultural crops, giving rise to conflicts with farmers (Vickery et al. 1994). Brent goose grazing on agricultural land results in a financial cost that is often only partly compensated for by the government in the Netherlands and Great Britain. Especially in the past decades this resulted in a negative attitude of farmers towards the geese. With the improvement of compensation schemes in the Netherlands towards the end of the 1990s this negative attitude largely disappeared, but the financial costs remained.

### *Study species*

Brent Geese are strictly coastal and more aquatic than other geese (Cramp & Simmons 1977). They breed at the Taymir peninsula in Siberia and leave there between mid-August and the 1st week of September. Some stay in Denmark and western Germany through November, before moving on in colder weather, others go straight to winter quarters in the Netherlands, southeastern England and western France (Cramp & Simmons 1977). In spring the birds gather in the Wadden Sea until main departure in mid-May (Ebbinge et al. 1999). During this period, they have to gain body mass in order to increase chances of successful reproduction (Boer & Drent 1989; Ebbinge & Spaans 1995). It is this period that we are concerned with. In late winter and early spring the majority of birds forages on agricultural land (Ebbinge et al. 1999), but in late spring salt





marshes become the key feeding areas. Nonetheless, still more than 15% of the Brent Geese in the Wadden Sea is observed at agricultural grassland by the month of May.

The population of the Brent Goose has undergone large changes in the last century. Before the 1930s wintering Brent Geese were numerous on the extensive eelgrass beds *Zostera* spp. at the coasts of western Europe. In the 1930s there was a dramatic decline in numbers (Ebbingge *et al.* 1999), simultaneously with the die-off of the eelgrass along the Atlantic coasts (Den Hartog 1994). The population recovered after 1972, when Denmark followed the Netherlands, United Kingdom and France in providing full protection from hunting for the Brent Geese (Boudewijn & Ebbingge 1994b). Until 1992 the population increased to about 300,000 birds (Figure 1.1), with large fluctuations depending upon their breeding success. Currently, however, the population is observed to decline again (Engelmoer *et al.* 2001; Ebbingge *et al.* 2002).

### Conservation management

The management of salt marshes, by livestock grazing and/or drainage, determines to a large extent which plant communities occur. Heavy livestock grazing and drainage results in a short homogeneous turf, harbouring the preferred forage species (Aerts *et al.* 1996; Kiehl 1997) for Brent Geese. Natural succession, however, results in a disappearance of the preferred food species and a decline in goose numbers (van de Koppel *et al.* 1996). By extensive grazing a vegetation mosaic is created, including short, heavily grazed sward and taller, hardly grazed patches. Most salt marshes, but especially the artificial mainland marshes have always been exploited for grazing by domestic livestock (Behre 1985; Bakker *et al.* 1997). At present, however, a trend is observed to abandon salt marshes; farmers loose interest (Dijkema 1983b) and authorities in charge of nature management opt for excluding livestock (Kempf *et al.* 1987; Stock & Kiehl 2000). This might eventually increase the problems with the farming community, if this would force geese into inland agricultural areas.

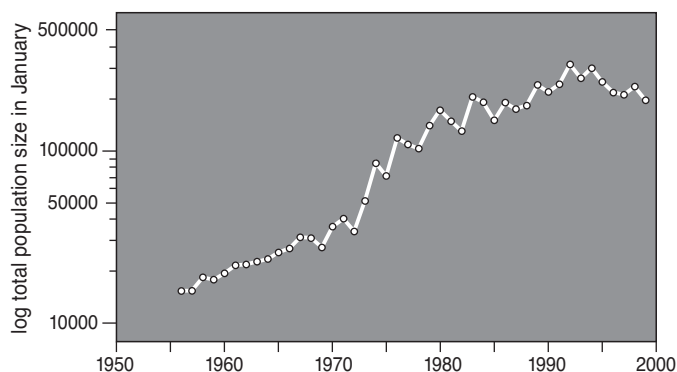


Figure 1.1 Change in the total population size of the Brent Goose. Reproduced from Ebbingge *et al.* (2002).

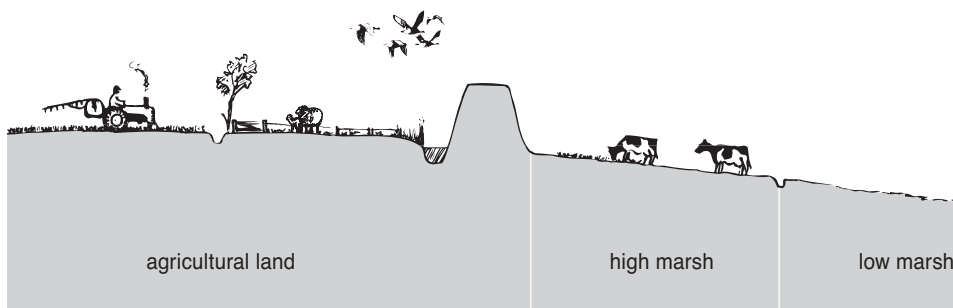
Policy plans for the Wadden Sea emphasise the diversity and natural development of salt marshes (de Jong *et al.* 1999). This includes the presence of habitats for as many plant and animal species as possible. The objective of the management of salt marshes is not based on the requirements of a single species and will, therefore, be a trade-off between maintaining a viable population of Brent Geese and other aspects of biodiversity. This thesis intends to enhance our understanding of the ecology of the Brent Goose and to provide the relevant information for this species to support such management.

## Objective

The objective of the study is to understand the patterns of habitat use by Brent Geese in spring, and the extent to which these patterns are affected by different scenarios of grazing management in agricultural grassland and salt marshes. We restrict the scope to management by livestock grazing, since this is one of the most important management activities exerted, and because at large areas of salt marsh along the Wadden Sea grazing has recently been reduced or even stopped.

## Habitat use by Brent Geese - outline of the thesis

Which factors determine the habitat use by Brent Geese in spring and the number of birds that can utilise the feeding grounds in the Wadden Sea? What is the effect of livestock grazing on habitat use by Brent Geese? In figure 1.2, some of the relations between the factors that will be taken into account are summarised in a schematic way. Two of the major habitats that are used by geese in spring are the agricultural land (pastures) and the marsh. The pastures are characterised by high primary productivity, but also by many sources of human disturbance. On the marsh there are



**Figure 1.2** The choice of feeding habitat by Brent Geese is subject of this thesis. During spring, the most important habitats used, at present, are pastures and salt marsh. Vegetation composition on the marsh is, amongst other, dependent on management by grazing with livestock and soil elevation.



many different plant communities, as a result of gradients in elevation and livestock grazing, among other things. Answering our questions requires insight in the decision rules that the geese follow to choose their foraging areas. Moreover, we need to evaluate the relationship between the management of coastal grasslands and relevant vegetation parameters, the interactions with other herbivores and potential feedback mechanisms that are operating.

### *Forage quality and quantity*

Herbivores in general are strongly tied to the quality of their food, but this feature is especially important for small waterfowl, such as the Brent Goose (Bruinzeel *et al.* 1997). The ability to fly sets a constraint on the size of the digestive tract and, therefore, Brent Geese have to select high quality forage (Sedinger 1997). Many aspects of their ecology are affected by this specialisation, such as diet composition (Prop & Deerenberg 1991; van der Wal *et al.* 2000a), choice of habitat (Prins & Ydenberg 1985) and timing of migration. Patch and habitat selection by Brent Geese were shown to correlate highly with forage quality, measured as nitrogen content (Ydenberg & Prins 1981; Teunissen *et al.* 1985; Riddington *et al.* 1997) or digestibility (Boudewijn 1984). For animal species with diets that vary less in nutrient content, such as carnivores, patch choice is assumed to be strongly dependent on resource density per se (Stephens & Krebs 1986; Sutherland 1996), but herbivores are assumed to be guided by quality and quantity (Drent *et al.* 1979; Fryxell 1991; Langvatn & Hanley 1993; Hassall *et al.* 2001). We tested the basic hypothesis that patch choice in Brent Geese is affected by quality as well as by quantity in an experiment and assessed the relative importance of each in chapter 2.

The quantity of food determines to a large extent the rate at which forage biomass can be ingested. The relationship between them is called the Functional Response. Forage quality, however, is often negatively related to forage quantity (Crawley 1983; Van Soest 1994), and the feeding areas with the highest biomass may, therefore, not yield the highest intake rate in terms of nutrients or energy. This effect may be even stronger when the functional response itself declines at high values of biomass, as has been observed in other species of wildfowl such as Wigeon *Anas penelope* (Durant 2001) and Barnacle Goose *Branta leucopsis* (van der Wal *et al.* 1998). We examined the hypotheses that the intake rate of nitrogen by Brent Geese is declining at high levels of biomass, and that this phenomenon may explain preference of Brent Geese for swards with low values of biomass (chapter 5).

### *Habitat switch*

The choice for a particular habitat by Brent Geese is depending on the season. In the Dutch Wadden Sea, Brent Geese predominantly feed on fertilised grassland in embanked polders until April. Then most of them shift their foraging activities to the newly emerging vegetation on the salt marsh (Boudewijn 1984). Barnacle Geese show a similar

switch between habitats (Prins & Ydenberg 1985), and several hypotheses have been put forward as to the causes of this switch. These hypotheses are related to forage quality (Boudewijn 1984; Prins & Ydenberg 1985), forage quantity (Vickery *et al.* 1995; Rowcliffe *et al.* 2001) and disturbance (Prins & Ydenberg 1985). Circumstantial evidence suggests that the geese prefer feeding on the marsh. In years with high world population numbers specific social categories of geese, especially young birds, that could be identified to belong to the Terschelling population, were observed on the inland feeding areas on Texel, rather than the marsh on Terschelling (Ebbinge 1992). But does that imply that inland pastures are inferior habitat? Moving from inland pasture to salt marsh implies exchanging a habitat with high levels of primary production for one with lower production. By the end of spring, the average values of

Bird's-eye view of Schiermonnikoog looking south-east. The eastern part of the Bancks' polder is visible in front, while the cattle-grazed salt marsh and the intertidal flats can be seen in the back. (photo P. Paris).





standing crop are much higher on inland pastures than on marsh habitat, and Boudewijn (1984) illustrated that this is reflected in a lower quality of the forage in the pasture. However, at some of the Wadden Sea islands, many of the Brent Geese do not switch to the salt marsh and continue grazing in the polder, until departure for the breeding grounds. At one of these islands, Ameland, sheep are grazing some of the fields in spring, while on the island of Texel, Brent Geese are almost free from human disturbance owing to the creation of a special Brent Goose reserve (Spaans & Postma 2001). We hypothesised that the spring grazing by sheep on Ameland would improve the suitability of the grass sward, enabling the geese to make use of it for a prolonged period. This process is called 'facilitation': the improvement of conditions for one organism by the other. Spaans & Postma (2001) suggested that Brent Geese themselves



could exert sufficient grazing pressure at the Brent Goose reserve on Texel to maintain a suitable grass sward in spring, since they are not disturbed there.

A proper understanding of the processes that determine the habitat switch would allow us to evaluate the value of polder habitat better and to identify the constraints that act upon the Brent Geese in spring. Why do Brent Geese move to the salt marsh, and under what conditions can polder pastures be used? What is the role of human disturbance? Do different social classes of birds make different decisions? These questions will be studied in chapter 3. Particular emphasis is laid upon the effect of scaring by farmers and the choice of individually recognisable animals. The role of the timing of livestock grazing in facilitating goose grazing in polder areas is the subject of chapter 4. In that study we test the hypothesis that livestock grazing in spring enhances the subsequent utilisation by geese. In chapter 5 we used a model simulation in combination with a field experiment to examine to what extent the geese are able to facilitate for themselves by repeatedly grazing productive agricultural grassland.

### *Vegetation succession and livestock grazing on salt marshes*

On the natural salt marsh of the island of Schiermonnikoog, Brent Geese concentrate their grazing at the early successional stages of vegetation succession (van de Koppel *et al.* 1996). The young salt marsh is characterised by low plant cover and low-statured palatable plant species such as *Plantago maritima*, *Triglochin maritima*, *Puccinellia maritima* and *Festuca rubra* (van der Wal *et al.* 2000a). With ongoing natural succession, plant cover increases, but gradually the low statured species are outcompeted by tall unpalatable plant species, such as *Elymus athericus* and *Atriplex portulacoides* (Roosen & Westhoff 1985; Olff *et al.* 1997; van Wijnen & Bakker 1997). The highest densities of geese are thus found where forage quantity is sufficient but high quality plants are not yet outcompeted by plants with less digestible components (Olff *et al.* 1997). Similar observations were made on artificial salt marshes along the mainland coast, where Barnacle Goose grazing pressure declined due to a change in the salt-marsh vegetation after the cessation of grazing with livestock (Aerts *et al.* 1996; Stock & Hofeditz 2000). Theories on vegetation succession, plant competition (Grime 1979; Tilman 1985) and plant-animal interactions (Crawley 1983) provide the theoretical frame of reference. Terrestrial plant succession refers to the dynamics of plant populations on an initially bare substrate (Tilman 1988). It is a stochastic process, but nevertheless locally often repeatable. Vegetation succession is a very important process in a dynamic environment such as the Wadden Sea, as land continually gets eroded and is formed anew due to sedimentation (Dijkema 1983a).

The geese share the marsh habitat with other herbivores, such as Barnacle Geese, European brown hare *Lepus europaeus* and livestock (cattle, sheep and sometimes horses) and Olff *et al.* (1997), van der Wal *et al.* (2000a; 2000b) and Stahl (2001) reported on the existence of facilitative and competitive effects between them. Especially livestock grazing influences the course of succession (Olff *et al.* 1997), positively affecting feeding conditions for geese (Cadwalladr *et al.* 1972; Boudewijn & Ebbinghe 1994a; Stock &





Hofeditz 2000). Livestock-grazing effects are caused by the removal of biomass, trampling, defecating and urinating, and all of these mechanisms affect plant survival and recruitment (Olff & Ritchie 1998). Some plant species tolerate grazing better than others. Heavy grazing by cattle or sheep promotes a short sward of *Puccinellia maritima* and *Festuca rubra* (Dijkema 1983a; Kiehl *et al.* 1996). Brent Geese prefer short swards with a high percentage of live grass (Summers & Critchley 1990) and thus they benefit from all grazers that keep a short sward (Bakker *et al.* 1993). Livestock grazing is also predicted to affect plant species diversity (Bakker 1989; Adam 1990), and since this is one of the parameters relevant for the management of marshes it is given some attention here.

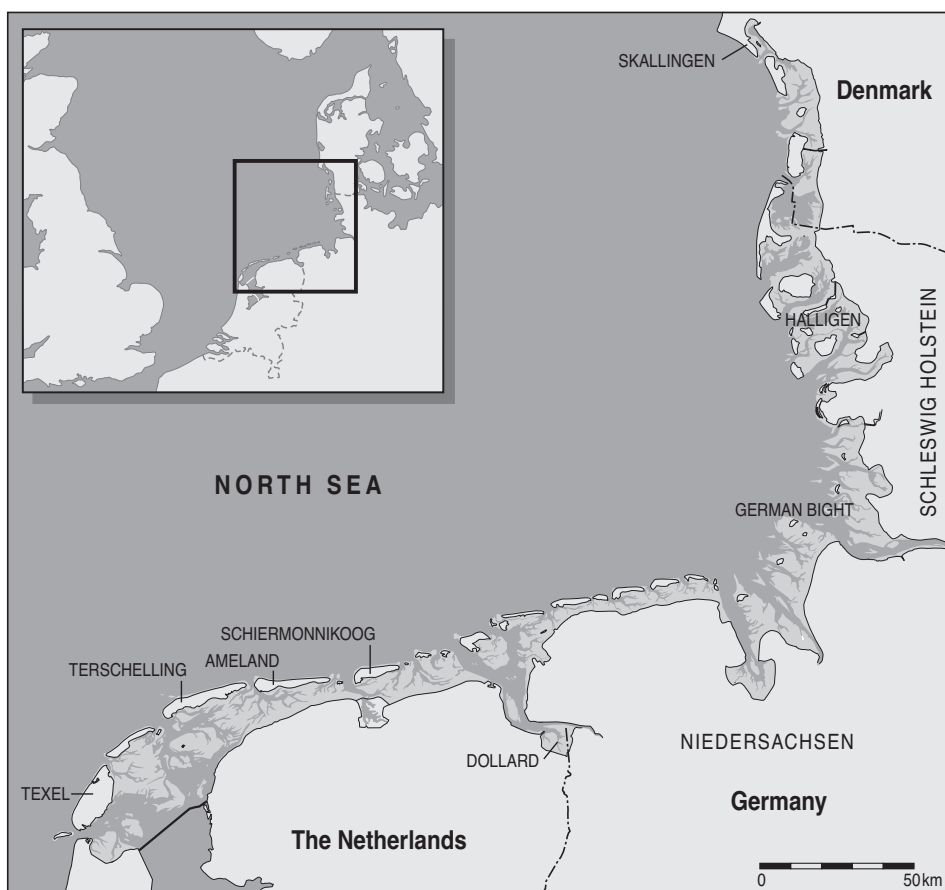
We quantified the effect of livestock grazing on vegetation composition, plant species diversity and individual forage species of geese for three barrier salt marsh systems using long term data from exclosure experiments (chapter 6). We tested the hypothesis that livestock grazing promotes the occurrence of short swards, dominated by plant species that are palatable for geese, in a transect survey along the Wadden Sea, and quantified the effect of livestock grazing on accumulated goose grazing pressure (chapter 7). In chapter 4, the use of salt marshes with different livestock-grazing regimes is compared over the entire spring, for a few sites along the Dutch Wadden Sea coast. Finally, we quantified vegetation composition of salt marshes in relation to grazing regime and soil type in chapter 8 using vegetation maps.

### *Competition and potential goose numbers*

Competitive effects can occur when organisms have to share limited resources. With increasing densities of competitors, competition for food leads to an impoverishment of the conditions and this may affect population parameters such as recruitment and mortality. Such 'density-dependent' effects (Sinclair 1989) form the feedback mechanism by which numbers of organisms are regulated (Sutherland 1996). Thus, the number of Brent Geese that can be sustained on feeding grounds along the Wadden Sea is determined by the nature of these density-dependent effects, in the long run. The potential number of birds that can graze at a particular unit of marsh in a particular period, is a function of the resource availability and the primary productivity. In chapter 8 we reviewed independent estimates of goose grazing density per plant community, grazing regime and soil type in spring. These estimates, in combination with information on the vegetation composition, were then applied to predict the mean potential numbers of geese that could forage in a particular area in May, under different scenarios of livestock grazing. These predictions were compared to observed goose numbers and distribution, to evaluate the validity of the approach and to quantify the effect of livestock grazing at the scale of the entire Wadden Sea.

## Study areas, setting the scene

All of the data were collected in agricultural grasslands and salt marshes along the international Wadden Sea (53°05'N, 4°50'E to 55°30'N, 8°20'E). The international Wadden Sea (Figure 1.3) consists of a large body of shallow salt water and intertidal flats, separated from the North Sea by a chain of 42 barrier islands, while the boundary with the mainland is almost entirely formed by coastal protection works, such as artificial marsh, barrages and different types of seawall. Important natural habitats in addition to the intertidal flats are salt marshes and dunes. The total area is 9,000 km<sup>2</sup>, including the islands, while the area of intertidal flats varies according to the tides with a maximum of 490,000 ha. The tidal amplitude ranges from 1.5 m in the West to over 4 m in the German Bight.



**Figure 1.3** Geographic map of the international Wadden Sea with the most important toponyms used in this study.





### *Major natural habitats*

On the mud flats, algae (*Ulva* spp. and *Enteromorpha* spp.) and eelgrasses occur, plant species that are exploited by Brent Geese and Wigeon. Eelgrasses have never recovered since the decline in the 1930s and still the stocks are reported to diminish (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer 1998). Salt-marsh vegetation is defined as vegetation above the low water line, that is regularly inundated by salt water. The salt marshes in the Wadden Sea can be classified in several types, according to their origin, soil composition and salinity (de Jong *et al.* 1999). The most important types considered here are barrier marshes (8,400 ha), mainland marshes (19,000 ha), Halligen (890 ha) and estuarine marshes (1,990 ha). Barrier marshes, have originated on top of a sandy substrate and have soils with a thinner layer of clay than more sheltered, artificial mainland salt marshes (Dijkema 1983a). The latter are a product of land reclamation works and feature a regular pattern of sedimentation fields and ditches. In the majority of mainland salt marshes the artificial drainage system is still maintained. Estuarine salt marshes are found at the mouth of rivers discharging into the Wadden Sea and feature plants that are less salt-tolerant, such as *Phragmites australis* and *Scirpus maritimus* (Esselink *et al.* 2000), in addition to plant species found at the other salt marshes. The Halligen are isolated pockets of salt marsh with a clayey soil in the middle of the Wadden Sea in Schleswig-Holstein (Germany). Originally they were the higher, inhabited, parts of the mainland (so-called warften), but they became islands in a period of coastal regression. The vegetation of Wadden Sea salt marshes is extensively described in Dijkema (1983a), Westhoff & van Oosten (1991) and Dierssen & Dierssen (1996). Inundation is one of the most important variables structuring the vegetation composition on salt marshes, as it is related to salinity and nutrient status of the soil (Adam 1990).

The dune systems are found on the large barrier islands in the West and North of the Wadden Sea. Large islands with dunes are lacking in the German Bight because of the higher tidal range in that area (van de Kam 1990). The vegetation ecology of Wadden Sea dune systems is, among others, given by Grootjans (1995) and Petersen (2000). Dune and salt-marsh systems are interconnected, for example by resident herbivores, such as the rabbit *Oryctolagus cuniculus* and hare, that use both habitats and locally by the flow of fresh water from reservoirs that accumulate under the dunes.

### *Predators*

The Wadden Sea serves as a habitat for many species of birds (Smit & Wolff 1981; van de Kam *et al.* 1999), mammals (van Laar 1981), fish (Dankers *et al.* 1979), insects (Dankers & Wolff 1981; Meyer *et al.* 1997), benthic invertebrate fauna (Dankers & Wolff 1981) and plants (Dijkema & Wolff 1983), some of which have already been mentioned above. However, some important vertebrates that might interact with the Brent Geese in the Wadden Sea have not been mentioned yet, and these are predatory birds such as the Goshawk *Accipiter gentilis* (Madsen 1988), or mammals such as the

fox *Vulpes vulpes* and feral cat *Felis catus*. Only three out of the 42 Wadden Sea islands are known to be occupied by foxes, while foxes are present along the entire mainland coast (van Laar 1981). Small populations of feral cat occur on some of the islands in the Wadden Sea, according to Lange *et al.* (1994).

### Human use

Many aspects of the Wadden Sea ecosystem are protected under international conventions and national regulations (de Jong *et al.* 1999; van de Kam *et al.* 1999), but human impact is clearly present in the form of tourism, shell- and shrimp fishery, gas extraction, military training and hunting (de Jong *et al.* 1999). Agricultural use is concentrated in the embanked areas, but livestock grazing is common at 60% of the salt marshes. In a few places there is mowing of grass, or even commercial goose farming out-side the dikes. In the embanked areas on the barrier islands, livestock farming is the most important agricultural activity. Large areas of land have been converted to artificial grassland, which is regularly mown and fertilised. Inside the seawalls on the mainland, soils have a high clay content, and these are often used for growing potatoes, sugar beets, cereals and other crops.

### Climate

Climatological circumstances do not vary extremely within the Wadden Sea (de Jong *et al.* 1999), as the geographical distance is less than 2.5 degrees in northerly direction. Still there are some regional differences as temperature in the coldest month is about 3 degrees lower in the north and the number of frost days doubles from 36 in Den Helder to 72 at Fanø (Bakker 1976). The average temperature in spring increases from 3°C at the beginning of March to 13.5°C by the end of May (data for Schiermonnikoog, courtesy of Free University Amsterdam). Rainfall ranges between 600 and 800 mm.yr<sup>-1</sup> (Bakker 1976) and wind speed amounts to 6 m.sec<sup>-1</sup> on average, mainly blowing from south-west and westerly directions.

## References

- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of Greylag geese *Anser anser* and Barnacle Geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. *Z. Ökol. Natursch.* 5: 65-75
- Bakker JP (1976) Phytogeographical aspects of the vegetation of the outer dunes in the Atlantic province of Europe. *J. Biogeogr.* 3: 85-104
- Bakker JP (1989) Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht
- Bakker JP, de Leeuw J, Dijkema KS, Leendertse PC, Prins HHT, Rozema J (1993) Salt marshes along the coast of the Netherlands. *Hydrobiologia* 265: 73-95



- Bakker JP, Esselink P, van der Wal R, Dijkema KS (1997) Options for restoration and management of coastal salt marshes in Europe. In: Urbanska KM, Webb NR, Edwards PJ (eds) Restoration ecology and sustainable development. Cambridge University Press, Cambridge, pp 286-322
- Behre KE (1985) Die ursprüngliche Vegetation in den Deutschen Marschgebieten und deren Veränderung durch prähistorische Besiedlung und Meeresspiegelbewegungen. Verhandlungen der Gesellschaft für Ökologie 13: 85-95
- Boudewijn T (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. Wildfowl 35: 97-105
- Boudewijn TJ, Ebbinge BS (1994a) Dutch Wadden Sea in the past and the present. In: van Nugteren J (ed) Brent Geese in the Wadden Sea. Dutch Society for the Preservation of the Wadden Sea Harlingen, pp 51-68
- Boudewijn TJ, Ebbinge BS (1994b). General review. In: van Nugteren J (ed). Brent Geese in the Wadden Sea. Dutch society for the preservation of the Wadden Sea, Harlingen, pp 39-49
- Bruinzeel L, van Eerden MR, Drent RH, Vulink JT (1997) Scaling metabolisable energy intake and daily energy expenditure in relation to the size of herbivorous waterfowl: limits set by available foraging time and digestive performance. In: van Eerden MR (ed) Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. University of Groningen, Groningen pp 111-132
- Cadwalladr DA, Owen M, Morley JV, Cook RS (1972) Wigeon (*Anas penelope*) conservation and salting pasture management at Bridgwater Bay National Nature Reserve, Somerset. J. Appl. Ecol. 9: 417-425
- Cramp S, Simmons KEL (1977) Handbook of the birds of Europe, the Middle East and North Africa. Oxford University Press, London
- Crawley MJ (1983) Herbivory. The dynamics of animal-plant interactions. Blackwell Scientific Publications, Oxford
- Dankers NMJA, Wolff WJ (1981) Invertebrates of the Wadden Sea : final report of the 'Marine Zoology' of the Wadden Sea Working Group. Stichting Veth tot steun aan Waddenonderzoek, Leiden
- Dankers NMJA, Wolff WJ, Zijlstra JJ (1979) Fishes and fisheries of the Wadden Sea: final report of the section 'Fishes and fisheries' of the Wadden Sea Working Group. Stichting Veth tot steun aan Waddenonderzoek, Leiden
- de Boer WF, Drent RH (1989) A matter of eating or being eaten? The breeding performance of Arctic geese and its implications for waders. WSG Bull. 55: 11-17
- de Jong F, Bakker JF, van Berkel CJM, Dankers NMJA, Dahl K, Gätje C, Marencic H, Potel P (1999) Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group, Wilhelmshaven
- den Hartog C (1994) The dieback of *Zostera marina* in the 1930's in the Waddensea; An eye witness account by A. Van der Werff. Neth. J. Aquat. Ecol. 28: 54
- Dierssen K, Dierssen B (1996) Vegetation Nordeuropas. Ulmer, Stuttgart
- Dijkema KS (1983a) The saltmarsh vegetation of the mainland coast, estuaries and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 185-269
- Dijkema KS (1983b) Use and management of mainland salt marshes and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 303-312
- Dijkema KS, Wolff WJ (1983) Flora and vegetation of the Wadden Sea islands and coastal areas: final report of the section Flora and vegetation of the islands of the Wadden Sea Working Group. Stichting Veth tot steun aan Waddenonderzoek, Leiden
- Drent R, Ebbinge B, Weyand B (1979) Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. Orn. Ges. Bayern 23: 239-264
- Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anatidae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle
- Ebbinge BS (1992) Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla bernicla* on spring staging sites. Ardea 80: 203-228

- Ebbinge BS, Berrevoets C, Clausen P, Ganter B, Guenther K, Koffijberg K, Mahéo M, Rowcliffe JM, St.Joseph A, Süßbeck P, Syroechkovski EE, Jr. (1999) Dark-bellied Brent Goose *Branta bernicla bernicla*. In: Madsen J, Cracknell G, Fox AD (eds) Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International, Wageningen, National Environmental Research Institute, Rønde, pp 284-297
- Ebbinge BS, Heesterbeek JAP, Ens BJ, Goedhart PW (2002) Density dependent population limitation in dark-bellied brent geese. *Avian Sci.* (in press)
- Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26: 105-113
- Engelmoer M, Taal J, Wymenga E, Kuipers R (2001) Aantalsafname bij de Rotgans *Branta bernicla* langs de Friese waddenkust. *Limosa* 74: 41-56
- Esselink P, Zijlstra W, Dijkema KS, van Diggelen R (2000) The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. *Biol. Conserv.* 93: 61-76
- Fryxell JM (1991) Forage quality and aggregation by large herbivores. *Am. Nat.* 138: 478-498
- Grime JP (1979) Plant strategies and vegetation processes. John Wiley, Chichester
- Grootenhuis JG (2000) Wildlife, Livestock and Animal Disease Reservoirs. In: Prins HHT, Grootenhuis JG, Dolan T (eds) Wildlife Conservation by Sustainable Use. Kluwer Academic Publishers, Boston, pp 81-114
- Grootjans AP, Lammerts EJ, van Beusekom F (1995) Kalkrijke duinvalleien op de Wadden eilanden. Stichting Uitgeverij van de Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* 127: 97-104
- Kempf NJL, Lamp J, Prokosch P (1987). Salzwiesen: geformt vom Küstenschutz, Landwirtschaft oder Natur? Internationale Fachtagung zu Perspektiven für Schutz und Pflege von Salzwiesen im Wattenmeer. Umweltstiftung WWF-Deutschland, Husum
- Kiehl K (1997) Vegetationsmuster in Vorlandsalzwiesen in Abhängigkeit von Beweidung und abiotischen Standortfaktoren. Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg e.V., Kiel
- Kiehl K, Eischeid I, Gettner S, Walter J (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. *J. Veg. Sci.* 7: 99-106
- Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (1998) Umweltatlas Wattenmeer. Bd. 1 Nordfriesisches und Dithmarscher Wattenmeer. Ulmer, Stuttgart
- Lange R, Twisk P, van Dijk W (1994) Zoogdieren van West-Europa. Stichting Uitgeverij van de Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency: An experiment. *Oecologia* 95: 164-170
- Madsen J (1988) Duehøg Accipiter gentilis forstyrret og dræber Knortegaes *Branta bernicla* ved specialiseret jagtteknik. *Dansk Orn. Foren. Tidsskr.* 82: 57-58
- Meffe GK, Carroll CR (1994) Principles of conservation biology. Sinauer Associates, Inc., Sunderland
- Meyer H, Reinke H-D, Irmeler U (1997) The arthropod fauna of different Wadden Sea salt marshes in Schleswig-Holstein and Lower Saxony. *Faunistisch-Ökologische Mitteilungen* 7: 267-284
- Off H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814
- Off H, Ritchie ME (1998) Effects of herbivores on grassland plant diversity. *Tree* 13: 261-265
- Petersen J (2000) Die Dünenalvegetation der Wattenmeer-Inseln in der südlichen Nordsee. Eine pflanzensoziologische und ökologische Vergleichsuntersuchung unter Berücksichtigung von Nutzung und Naturschutz. Husum Druck- und Verlagsgesellschaft mbH u. Co. KG, Husum
- Prins HHT, Ydenberg RC (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). *Oecologia* 66: 122-125
- Prop J, Deerenberg C (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28



- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153-160
- Roozen AJM, Westhoff V (1985) A study on long-term salt marsh succession using permanent plots. *Vegetatio* 61: 23-32
- Rowcliffe JM, Watkinson AR, Sutherland WJ (2001) The depletion of algal beds by geese: a predictive model and test. *Oecologia* 127: 361-371
- Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and water fowl. *Condor* 99: 314-326
- Sinclair ARE (1989) Population regulation in animals. In: Cherret JM, Bradshaw AD, Goldsmith FB, Grubb PJ (eds) *Ecological Concepts*. Blackwell, Oxford, pp 197-241
- Smit CJ, Wolff WJ (1981) Birds of the Wadden Sea : final report of the section 'Birds' of the Wadden Sea Working Group. Stichting Veth tot steun aan Waddenonderzoek, Leiden
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Stahl J (2001) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD thesis University of Groningen,
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton,
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitates durch Nonnen- und Ringelgänse. In: Stock M, Kiehl K (eds) *Die Salzwiesen der Hamburger Hallig.* Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 43-55
- Stock M, Kiehl K (2000) Empfehlungen zum Salzwiesenmanagement im Nationalpark Schleswig Holsteinisches Wattenmeer. In: Stock M, Kiehl K (eds) *Die Salzwiesen der Hamburger Hallig.* Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 74-77
- Summers RW, Critchley CNR (1990) Use of grassland and field selection by Brent Geese *Branta bernicla*. *J. Appl. Ecol.* 27: 834-846
- Sutherland WJ (1996) *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford
- Tchamba MN (1996) Elephants and their interactions with people and vegetation in the Waza Logone Region, Cameroon. PhD thesis University of Leiden, Leiden
- Teunissen W, Spaans B, Drent R (1985) Breeding succes in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea* 73: 109-120
- Tilman D (1985) The resource ratio hypothesis of plant succession. *Am. Nat.* 125: 827-852
- Tilman D (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, N. J.
- van de Kam J (1990) *De wadden, wereld tussen eb en vloed*. Terra, Landelijke Vereniging tot behoud van de Waddenzee, Zutphen
- van de Kam J, Ens BJ, Piersma T, Zwarts L (1999) *Ecologische atlas van de Nederlandse wadvogels*. Schuyt & Co, Haarlem
- van de Koppel J, Huisman J, van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745
- van der Wal R, van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos* 82: 123-130
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000a) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D (2000b) On facilitation between herbivores: How Brent Geese profit from brown hares. *Ecology* 81: 969-980
- van Eerden MR (1997) *Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands*. PhD thesis University of Groningen
- van Laar V (1981) The Wadden Sea as a zoogeographical barrier to the dispersal of terrestrial mammals. In: Smit CJ, den Hollander J, van Wingerden WKRE, Wolff WJ (eds) *Terrestrial and freshwater fauna of the Wadden Sea area*. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 231-266
- van Soest PJ (1994) *Nutritional Ecology of the ruminant*. Cornell University Press, Ithaca (NY)
- van Wijnen H, Bakker JP (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. *J. Coast. Cons.* 3: 19-26

- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499-508
- Vickery JA, Watkinson AR, Sutherland WJ (1994) The solutions to the brent goose problem: a economic analysis. *J. Appl. Ecol.* 31: 371-382
- Westhoff V, van Oosten MF (1991) *De Plantengroei van de Wadden eilanden*. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Ydenberg RC, Prins HHT (1981) Spring grazing and the manipulation of food quality by Barnacle Geese. *J. Appl. Ecol.* 18: 443-453

Foraging Brent Geese (photo J. Stahl)







## CHAPTER 2

# The relative importance of food biomass and quality for patch and habitat choice in Brent Geese

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### Abstract

We have studied the relative importance of food biomass and food quality for habitat preference in Brent Geese by manipulating these parameters. Levels of biomass and food quality, measured as nitrogen content, were independently enhanced by temporary enclosure from grazing and addition of artificial fertiliser in a full-factorial experiment. Instantaneous intake rate increased linearly with sward height, over the range of values studied. Patch preference, as determined from the number of aggressive interactions and bird density for wild Brent Geese, was however highest for plots with the highest nitrogen content. Grazing pressure, measured as dropping density, showed the same pattern. Only the number of interactions was measurably affected by sward height in addition to the effect of nitrogen content. These results complement earlier work (Riddington *et al.* 1997; Hassall *et al.* 2001) by demonstrating that, even at low values of sward height, food quality is an important parameter determining patch choice. Our results are consistent with the expectation that patch choice is influenced by nitrogen intake rates and they provide an explanation for distribution patterns of Brent Geese on agricultural grasslands and the sequence in which pasture and marsh habitats are utilised in spring.

## Introduction

Models of patch choice in herbivores are in most cases based upon a relationship between intake rate and biomass of food (Turner *et al.* 1993; Percival *et al.* 1996; Percival *et al.* 1998; Pettifor *et al.* 2000). Often, the shape of this functional response is assumed to decelerate towards a plateau according to the disc-equation (Holling 1959; Spalinger & Hobbs 1992; Gross *et al.* 1993; Ginnett & Demment 1995). Under this assumption, classical theory predicts that herbivore density will reach its maximum at the highest standing biomass (Oksanen *et al.* 1981). This generalisation however does not fit the empirical facts. Accordingly, Fryxell (1991), corroborated by van de Koppel *et al.* (1996), provided a theoretical framework to account for the effect of food quality on resource acquisition in herbivores. He showed that aggregation of ruminants at intermediate levels of biomass can result from spatial variation in food quality and from forage maturation effects, under the assumption that food quality declines with increasing biomass. Experimental work by Langvatn & Hanley (1993) and Wilmshurst *et al.* (1995) on red deer *Cervus elaphus* support the model prediction that intermediate levels of biomass will be preferred over patches with high biomass, if the intake rate of energy or protein is higher in these patches.

The average quality of the diet is negatively related to body size in mammalian (Prins & Olff 1999) and avian (van Eerden 1997) herbivores. Small herbivores, such as lagomorphs and herbivorous waterfowl, are therefore even more likely to be influenced by differences in food quality than the large ruminants. In waterfowl, the digestion of food is poor due to a relatively short digestive tract and high passage rates (Prop & Vulink 1992). This makes them more sensitive to food quality than expected according to body size (Sedinger 1997). Geese, for example, typically feed on high quality food (Owen 1980). Indeed, many field studies show relationships between foraging decisions of waterfowl and food quality: At the diet level, geese are observed to choose those components that yield the highest energy and protein intake rate (Prop & Deerenberg 1991). At the patch level grazing pressure and nitrogen content of food are highly correlated (Ydenberg & Prins 1981; Teunissen *et al.* 1985; Vickery *et al.* 1994). And also at the scale of staging sites, e.g. the island of Schiermonnikoog, could the habitat choice be related to protein content (Prins & Ydenberg 1985) and to digestibility (Boudewijn 1984). In many of these examples, however, the analysis is confounded by differences in plant production, standing biomass and presumably, the intake rate of food. It is, therefore, difficult to determine to what extent foraging decisions are affected by intake rate of food and food quality.

Recent work by Riddington *et al.* (1997) and Hassall *et al.* (2001) showed the importance of nitrogen constraints for patch choice in Brent Geese *Branta bernicla bernicla*. In their study with wintering Brent Geese on coastal grasslands in Britain, birds preferred short swards over tall swards under unfertilised conditions, due to a negative correlation between nitrogen content and sward height. The lifting of this constraint by fertilisation resulted in a preference for tall swards. They formulate their findings in relation to the forage maturation hypothesis, by arguing that swards of intermediate





length are preferred due to opposing constraints associated with sward height. At low sward heights intake rate forms an important constraint, while nitrogen content and digestive constraints become important at taller swards.

We quantitatively elaborate upon their concept by manipulating the same parameters under different circumstances. Our study focuses on the spring situation, where levels of sward height are generally low. The birds are also in a different physiological state, as they have to acquire fat reserves for spring migration and breeding (Ebbinge & Spaans 1995). Following Riddington *et al.* (1997) and Hassall *et al.* (2001), we started from the premise that both food quality and biomass will affect patch choice and that intake rate will be positively related to biomass. We studied the relative importance of these variables at a low range of sward heights by experimentally manipulating them within a single plant community. The preference for patches was estimated from behavioural measures as well as from grazing pressure for wild Brent Geese, and we established the relationship between biomass and intake rate of food using captive animals. After McKay *et al.* (1994) and Hassall *et al.* (2001) who stressed the importance of protein acquisition for Brent Geese, we will use nitrogen content as a measure of quality throughout the present paper. The relationship between nitrogen content and other measures of food quality will later be discussed.

## Study area

The experiment was carried out at the cattle-grazed salt marsh (400 ha) of Schiermonnikoog (53°30'N, 6°10'E), a barrier island in the Dutch Wadden Sea. Numbers of Brent Geese staging on Schiermonnikoog range between 2,000 and 4,000 during spring (van der Wal *et al.* 2000b). For a detailed description of the salt marsh see Olff *et al.* (1997). In early spring the geese spend most of the time foraging in the embanked polder (270 ha), but towards May a gradual shift to the salt marsh is observed. Barnacle Geese *Branta leucopsis* (Prins & Ydenberg 1985) are also important herbivores utilising the marsh, leaving the island around mid April (Stahl 2001). Although European brown hares *Lepus europaeus* are abundant at some of the ungrazed sites, their density at the cattle-grazed salt marsh was relatively low when the experiment was performed. The grazed salt marsh is grazed with cattle from the end of May until November at a stocking rate of 0.5 cow.ha<sup>-1</sup> and harbours a mosaic of plant communities (van Wijnen *et al.* 1997). The plant communities here, that are characterised by *Festuca rubra* and *Puccinellia maritima*, experience the highest grazing pressure of the whole island by Brent Geese in May (unpublished data).

## Methods

Twenty-eight plots of 2m by 6m were selected within the *Juncetum gerardi* and the *Puccinellietum maritimae* plant communities, in areas on the cattle-grazed salt marsh. The communities were dominated by short *Festuca rubra* (41%), *Juncus gerardi* (20%) and *Puccinellia maritima* (15%), and known to be frequently visited by Brent Geese. The plots were homogenous with respect to vegetation composition and height. Subdivision into 7 replicate blocks of 4 plots each was made, where plots within a block were nearer to each other than to plots in adjacent blocks. Average distance between plots in a block was approximately 4 m. Four different treatments were assigned randomly to these plots, within a block. These treatments included fertiliser application and temporary herbivore exclosure in a full factorial way. This resulted in plots of high biomass with high quality (fertilised & excluded, FE), high biomass and low quality (unfertilised & excluded, UE), low biomass and high quality (fertilised & grazed, FG) and finally low biomass with low quality (unfertilised & grazed, UG). Fertilisation was accomplished using a commercial fertiliser ( $\text{CaCO}_3\cdot\text{NH}_4\text{NO}_3$ , 27%), dissolved in 0.5-liter water and sprayed over the vegetation, resulting in a net addition of 25 g of  $\text{N}\cdot\text{m}^{-2}$ . Geese and hares were excluded for 3 - 4 weeks using chicken wire (5 cm meshwidth, 50 cm high). The experiment was carried out in two series. The first 3 complete blocks (12 plots) received the treatments April 1st 1998. The second series of 4 blocks (16 plots) was treated April 5<sup>th</sup>. An observation tower was placed within a distance of 100 m from the plots and behavioural data of the geese were recorded, starting from the moment that the exclosures were removed. Observations started April 22<sup>nd</sup> and May 5<sup>th</sup> for the first and second series, respectively.

### *Vegetation analysis*

The day before the exclosures were removed, the available biomass and the sward height were measured. Aboveground biomass was estimated by randomly taking one sod of 10 cm x 10 cm per plot and cutting it to ground level. The material was sorted to live and dead material, washed, dried at 60°C for 48 hours and weighed. Using a PSII field spectrometer (ASD, Boulder), reflectance values were measured for red and infra red light, and an index of green biomass was calculated (Normalised Difference Vegetation Index, NDVI, Esselink & van Gils 1985). The development of live standing biomass over time was monitored by measuring the green biomass-index at weekly intervals. Live biomass was positively correlated to the green biomass-index (Pearson  $r^2 = 0.46$ ,  $P < 0.01$ ,  $n = 28$ ). Sward height was measured with a 24 g, 20 cm diameter polystyrene disc that was dropped on the vegetation, sliding along a calibrated stick that rested on the ground. Sward height was linearly related to biomass of live leaves ( $\text{g dry mass}\cdot\text{m}^{-2}$ ) ( $y = 0.099 + 0.32x$ ,  $r^2 = 0.84$ ,  $P < 0.001$ ) and to the green biomass-index (value) ( $y = 0.68 + 0.048x$ ,  $r^2 = 0.42$ ,  $P < 0.001$ ). In most analyses, sward height is therefore used as an index of the quantity of food available. On a more detailed level, growth and depletion were measured using the leaf-length of individually marked



*F. rubra* or *P. maritima* tillers following Bakker & Loonen (1998). For this purpose 18 tillers were selected per plot in 4 of the blocks and their leaf-lengths measured approximately once every six days. Leaf elongation was estimated from ungrazed tillers only. Vegetation composition was recorded for entire plots by visually estimating the cover of plant species using the decimal scale (Londo 1976).

A mixed sample of the green leaf-tips of *F. rubra* and *P. maritima*, and a sample of *J. gerardi* was taken, weighted and stored in a box containing ice in which they were transported to the laboratory. Samples were stored at  $-80^{\circ}\text{C}$  within 12 hours until later analysis of food quality parameters. Total nitrogen concentration was determined with a modified Kjeldahl method. For this purpose dry material was digested with concentrated  $\text{H}_2\text{SO}_4$  containing 0.2 M Na-salicylate at  $360^{\circ}\text{C}$  in the presence of a catalyst containing  $\text{K}_2\text{SO}_4\text{:CuSO}_4\text{:Na}_2\text{SeO}_3$  15:5:0.085 (w:w:w) and 16.5% Na-thiosulfate. Ammonia was then determined colorimetrically (Starrcol spectrophotometer, SC-60-S, R&R Mechatronics, The Netherlands) at 415 nm using Nessler's reagent A (Merck, Germany) mixed 1:1 (v:v) with 9 N NaOH. Reduced nitrogen compounds were determined according to Bailey (1967). Fresh material, stored at  $-80^{\circ}\text{C}$ , was ground in liquid nitrogen, incubated in 3% HCl (v:v) for 2 hours in order to precipitate the insoluble fraction (mainly proteins). The insoluble fraction was separated from the soluble fraction (containing mainly ammonium and amino acids), by filtration through a black ribbon filter. Each fraction was digested in  $\text{H}_2\text{SO}_4$  at  $360^{\circ}\text{C}$  in the presence of a catalyst containing  $\text{K}_2\text{SO}_4\text{:CuSO}_4$  3:1 (w:w). Ammonia was then determined as described for total nitrogen.

Nitrate levels were determined using an HPLC according to Maas *et al.* (1986). The non-structural carbohydrates and hemicellulose were extracted from dry material in 80% ethanol and determined colorimetrically according to Fales (1951) with a spectrophotometer (Starrcol, SC-60-S, R&R Mechatronics, The Netherlands). Water content was determined from the difference between fresh- and dryweight. The acid detergent fibre content (ADF, Robbins 1993) was assessed for samples that were pooled per treatment, as a measure for digestibility.

### *Foraging behaviour of Brent*

From dawn to dusk, the experimental site was observed. Goose density and number of agonistic interactions were recorded at regular intervals by sequentially scanning each plot and observing it for ten seconds (see Teunissen *et al.* 1985). An agonistic interaction was defined as a sudden interruption of the current behaviour of an individual to try and chase another until the previous behaviour is resumed. Interaction frequency was assessed by dividing the number of interactions by the number of birds present in the plot. Average bird density was calculated by dividing the total number of birds observed in each plot by the total number of times that at least one goose in the plot was counted. Visit time (bird minutes) was calculated by multiplying the amount of time that geese were present at individual plots with the average bird density in the plot, per hourly interval. We collected data on step and peck rates per plot at regular

intervals, for as many individual animals as possible. Step and peck rates were determined by measuring the time required for 10 steps and 50 pecks, respectively, using a chronometer. We were able to observe the second series of the experiment for 15 days, but practical reasons limited the observation period for the first series to three subsequent days. At the end of each day, droppings were counted on the entire experimental plots and removed. Grazing pressure was defined as the rate of accumulation of droppings per unit area per day.

Instantaneous intake rate of food was estimated, using a pair of captive Brent Geese, brought into an experimental chamber for the measurements. These geese were allowed to eat 50 pecks from a sod of 10 cm x 20 cm, taken from the field plots, that was weighed before and after the trial to the nearest 10 mg (Sartorius pro 32/34F). Removed biomass ( $W_r$ , g fresh weight) was measured as the weight loss of the sod (g) during the trial, corrected for spilled food (g) and evaporation (g). Evaporation rate ( $\text{g.s}^{-1}$ ) was estimated from the weight loss of the same sod in the same room, during five minutes prior to the trial, and multiplied by the duration of the trial (s) to obtain an estimate of evaporation (g). Time spent pecking per individual was carefully estimated using video recordings of the feeding trials and summed to obtain an estimate of total pecking time ( $T_p$ , s). The intake rate ( $\text{g fresh.s}^{-1}$ ) was calculated by dividing removed biomass ( $W_r$ ) by total pecking time ( $T_p$ ). Sodds were provided to the geese in random order, with a constant interval of 20 min. During the experimental trials and the 8 weeks before, the geese were housed in a 2 m x 2 m indoor facility and additionally fed with dried food pellets and grass presented as sods. Light followed a diurnal cycle mimicking outside circumstances. The geese had been captured from the wild in 1996 and had been housed in a large open aviary until 8 weeks before the experimental trials. All catching, handling and non-invasive experimentation with captive geese in this study was conducted under a permit from the Dutch Ministry of Agriculture, Nature Management and Fisheries and a DEC permit of the Commission for the use of Animals in Experimental trials of the University of Groningen. (DEC No BG07696).

### *Data analyses*

Data were averaged per plot to avoid pseudo-replication and analysed using a Randomised Block ANOVA (Zar 1996). In this analysis 'fertilisation' and 'grazing' were entered as fixed factors and 'block' was entered as a random factor. When appropriate, data were square root transformed ( $y' = \sqrt{y+0.5}$ ), to obtain normality and homogeneity of variances. Percentage values routinely were Arcsine transformed. Post-hoc comparisons between the four treatments were carried out using Tukey's honestly significant difference test. When the assumptions of parametric ANOVA could not be met, a non parametric Friedman ANOVA and associated post hoc comparisons (Zar 1996) were used instead. Changes in peck and step rate over time were investigated to study depletion effects. For this, a multiple linear regression was carried out, with treatment as a factor and time (cumulative hours of observation after start of the experiment) as a covariate. The foraging parameters peck rate, step rate



and intake rate were related to vegetation height, nitrogen content and the interaction between them, using backward multiple regression, eliminating variables when they were not significant at the 0.05 level. Finally, we used the number of interactions, bird density and the grazing pressure as parameters of preference and tested for the effect of vegetation height, nitrogen content and the interaction between them, using backward multiple regression. In these regression analyses we corrected for differences between the two series by incorporating series as a fixed factor. Statistical analyses were carried out with SPSS 8.0 (SPSS Inc.).

## Results

### *Treatment effect on the vegetation*

At the onset of observations, after removal of the exclosures, a significant difference in total live biomass was found between excluded plots (UE,FE) and those that received continuous grazing (UG,FG;  $F_{1,18} = 12.4$ ,  $P < 0.05$ , see Table 2.1). Both other indices of food biomass, the green biomass-index and sward height revealed the same pattern. Parameters of food quality were also strongly related to the treatments. Foodplants in fertilised plots (FG,FE) had a higher nitrogen ( $F_{1,18} = 130$ ,  $P < 0.001$ ) and water content ( $F_{1,18} = 154$ ,  $P < 0.001$ ) than plants in unfertilised plots (UG,UE). A significant interaction ( $F_{1,18} = 10.7$ ,  $P < 0.05$ ) between fertilisation and grazing arose as the nitrogen content was enhanced by grazing in unfertilised plots. The distribution of nitrogen over the different chemical compounds was hardly affected by the treatments, although unfertilised plots had a slightly enhanced proportion of insoluble nitrogen. Nitrate was virtually absent in all of the samples, averaging 0.3% on dry weight basis. The content of non-structural carbohydrates (starch and soluble sugars) and hemicellulose was lower in the fertilised & grazed treatment (FG, Tukey,  $P < 0.05$ ), but the other treatments were not significantly different. No differences in plant species abundance were observed between the treatments.

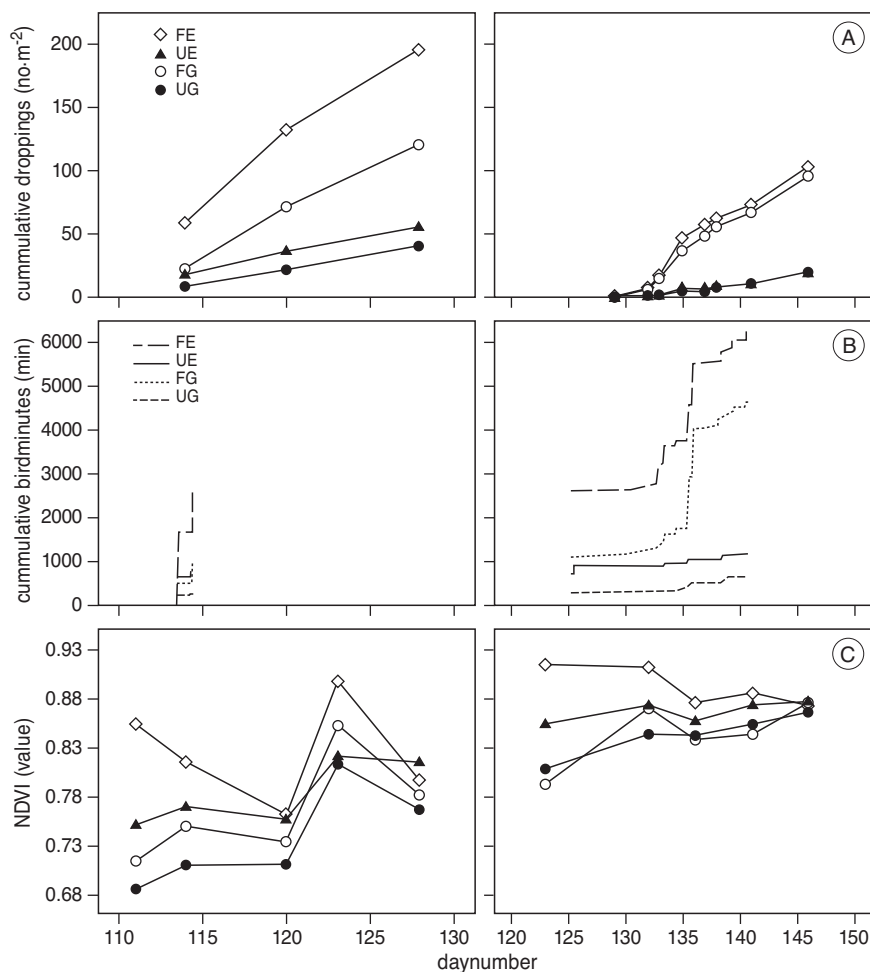
### *Behavioural parameters and grazing pressure*

Total visiting time increased gradually over time, although at different rates for each treatment (Figure 2.1A,B). Fertilised treatments had higher bird densities ( $F_{1,18} = 28.4$ ,  $P < 0.001$ , Table 2.1) and received higher grazing pressure (square root transformation,  $F_{1,18} = 93$ ,  $P < 0.001$ ). The percentage of grazed leaves of *P. maritima* and *F. rubra* corresponds closely to grazing pressure (Table 2.1). The frequency of agonistic interactions per individual goose present on the plot did not differ between treatments. The higher bird densities (Table 2.1) and the higher visiting times (Figure 2.1) were, however, reflected in greatly enhanced total number of observed interactions per plot, under fertilisation (square root transformation  $F_{1,15} = 14.5$ ,  $P < 0.01$ ). There was a good correlation between the sum of interactions and grazing pressure (Pearson correlation coefficient = 0.48,  $P < 0.05$ ,  $n=22$ ). Previous exclusion of grazing had no

Sward characteristics	n	Unfertilised				Fertilised				Test	F	G	F*G	Block
		Grazed		Ungrazed		Grazed		Ungrazed						
		UG	s.e.	UE	s.e	FG	s.e.	FE	s.e.					
Sward height (cm)	28	1.8	0.1 <sup>a</sup>	3.0	0.2 <sup>b</sup>	1.6	0.1 <sup>a</sup>	3.8	0.3 <sup>c</sup>	RB	n.s.	***	*	n.s.
Vegetation index (value)	28	0.8	0.0 <sup>a</sup>	0.8	0.0 <sup>ab</sup>	0.8	0.0 <sup>a</sup>	0.9	0.0 <sup>b</sup>	RB	**	***	**	***
Dead biomass (g dw.m <sup>-2</sup> )	28	0.2	0.1	0.2	0.1	0.2	0.1	0.1	0.0	RB	n.s.	n.s.	n.s.	n.s.
Live biomass (g dw.m <sup>-2</sup> )	28	0.7	0.1 <sup>ab</sup>	0.9	0.1 <sup>ab</sup>	0.6	0.1 <sup>a</sup>	1.2	0.2 <sup>b</sup>	RB	n.s.	**	n.s	n.s
Cover of Juncus (%)	28	18.9	4.2	27.9	8.4	16.1	3.6	17.9	4.9	RB	n.s.	n.s.	n.s.	n.s.
Cover of grasses (%)	28	55.6	3.7	52.5	8.3	5.9	4.9	60.6	5.7	RB	n.s.	n.s.	n.s.	n.s.
Nitrogen content (mg.g dw <sup>-1</sup> )	28	31.9	1.5 <sup>a</sup>	22.3	2.0 <sup>b</sup>	46.9	2.4 <sup>c</sup>	49.3	1.2 <sup>c</sup>	RB	***	n.s.	*	ns
<i>Fest./ Pucc.</i>	21	38.8	2.0 <sup>ab</sup>	30.5	4.0 <sup>a</sup>	45.8	2.0 <sup>bc</sup>	48.0	1.0 <sup>c</sup>	RB	***	n.s.	*	n.s.
Prop. of insoluble nitrogen (%)	16	83.0	0.2 <sup>a</sup>	80.0	0.7 <sup>ab</sup>	79.0	1.5 <sup>ab</sup>	78.0	1.1 <sup>b</sup>	RB	*	n.s.	n.s.	n.s
Acid Detergent Fibre (ADF) (%)	7	19.8		19.7		15.4		11.7						
<i>Juncus. gerardi</i>	8	17.3		17.3		15.3		13.5						
Water content	27	64.9	0.7 <sup>a</sup>	67.3	1.2 <sup>a</sup>	69.8	0.5 <sup>b</sup>	76.7	0.6 <sup>c</sup>	RB	***	***	***	n.s.
Non-structural carbohydrates	16	348.0	15.5 <sup>a</sup>	317.0	7.5 <sup>a</sup>	206.0	22.5 <sup>b</sup>	304.0	13.5 <sup>a</sup>	RB	**	n.s.	*	n.s.
+hemi-cellulose (mg. g dw <sup>-1</sup> )	16	1.4	0.2 <sup>a</sup>	1.8	0.2 <sup>ab</sup>	1.8	0.7 <sup>ab</sup>	2.5	0.7 <sup>b</sup>	F				
Leaf elongation (mm.day <sup>-1</sup> )														
Foraging parameters														
Peck rate (sec.peck <sup>-1</sup> )	22	0.4	0.0	0.4	0.0	0.4	0.0	0.4	0.1	RB	n.s.	n.s.	n.s.	***
Step rate (sec.step <sup>-1</sup> )	21	1.7	0.3	1.7	0.1	2.7	0.3	3.7	0.5	RB	**	n.s.	n.s.	n.s.
% of leaves grazed.day <sup>-1</sup>	16	0.8	0.2 <sup>a</sup>	1.7	0.5 <sup>a</sup>	5.7	0.3 <sup>b</sup>	7.5	0.5 <sup>b</sup>	RB	**	n.s.	n.s.	n.s.
Bird density (no.plot <sup>-1</sup> )	28	0.6	0.3 <sup>a</sup>	0.5	0.2 <sup>a</sup>	2.4	0.4 <sup>b</sup>	3.3	0.6 <sup>b</sup>	RB	***	n.s.	n.s.	n.s.
No of interactions (total over observation period)	22	2.2	0.7 <sup>a</sup>	4.3	1.9 <sup>a</sup>	24.4	4.9 <sup>ab</sup>	45.8	14.3 <sup>b</sup>	RB	***	n.s.	n.s.	n.s.
Interaction frequency (no.bird <sup>-1</sup> .10 seconds <sup>-1</sup> )	22	0.04	0.0	0.06	0.02	0.10	0.01	0.09	0.02	RB	n.s.	n.s.	n.s.	n.s.
Intake rate (g fresh.s <sup>-1</sup> )	16	0.02	0.00 <sup>a</sup>	0.04	0.01 <sup>a</sup>	0.03	0.00 <sup>a</sup>	0.07	0.00 <sup>b</sup>	RB	*	**	n.s.	n.s.
Grazing pressure (droppings.m <sup>-2</sup> .d <sup>-1</sup> )	28	0.43	0.11 <sup>a</sup>	0.55	0.20 <sup>ab</sup>	1.54	0.30 <sup>bc</sup>	2.17	0.60 <sup>c</sup>	RB	***	n.s.	n.s.	***
Hares	28	0.02	0.01 <sup>a</sup>	0.07	0.03 <sup>a</sup>	0.06	0.02 <sup>a</sup>	0.88	0.31 <sup>b</sup>	F				



**Table 2.1** Mean values of sward and foraging parameters for different treatments. Values that do not share the same superscript letter are significantly different from each other. Test results for the effect of manipulation by grazing and fertilisation are indicated by abbreviating the factors in the variance analysis as follows: F = fertilisation, G = grazing and F\*G is the interaction between fertilisation and grazing. Levels of significance are indicated using asterisks: \* = 0.05, \*\* = 0.01 and \*\*\* = 0.001. RB refers to a non-replicated randomised block ANOVA and F refers to Friedman ANOVA.



**Figure 2.1** Measures of the use of the experimental treatments over time A) Cumulative grazing pressure (droppings.m<sup>-2</sup>) by Brent Geese, B) cumulative visit time (bird minutes) on the plots expressed on an hourly basis, C) Normalised Difference Vegetation Index (NDVI), the ratio of red and infrared light reflected by the vegetation. This index is an estimator of live standing biomass. fertilised & excluded (FE); fertilised & grazed (FG); unfertilised & excluded (UE) and unfertilised & grazed (UG).



significant effect on bird density, number of interactions and grazing pressure. Hare grazing intensity was low compared to goose grazing, and concentrated on fertilised & excluded plots (FE).

Fertilisation had a significant effect upon step rate (Table 2.1) by geese. With increasing nitrogen content of the grasses, the step rate is observed to decrease (multiple linear regression:  $r^2 = 0.33$ ,  $P < 0.01$ ). Peck rate was not affected by any of the treatments. Neither peck- nor step-rate significantly changed over the course of the experiment. Instantaneous intake rate increased linearly with biomass, within the range of biomass densities encountered (multiple linear regression:  $F_{1,14} = 55.2$ ,  $P < 0.001$ , Figure 2.2). This is mainly explained by an increase in bite size, with increasing levels of biomass (data not shown). Nitrogen content was not important in explaining variation in intake rate.

In three cases during the first series of observations, we were able to follow specific family units or a particular individual goose for some time. The birds were recognisable from their behaviour and family composition and monopolised certain plots for considerable time (Figure 2.3). Plot FE2, the second replicate of the fertilised & excluded treatment, was at first occupied by a pair with an aggressive male. The male of this pair was seen to threaten other birds up to 10 m away from his female, and effectively monopolised the plot for more than three hours. It was taken over after a heroic fight, by a family of five, which had already spent 15 minutes at the fertilised & grazed plot FG1 immediately before that. This family maintained control over the plot for two hours, until all birds in the area departed due to disturbance (helicopter). Both the pair and members of the succeeding family performed short excursions to adjoining plots with different treatments. These excursions never lasted longer than 2 minutes. Another family of five occupied plot FE3 during both days for periods of more than two hours.

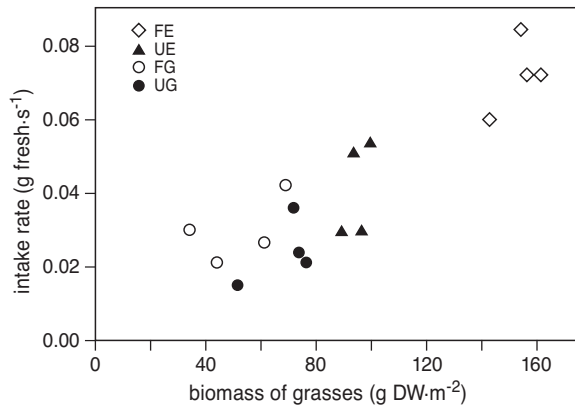
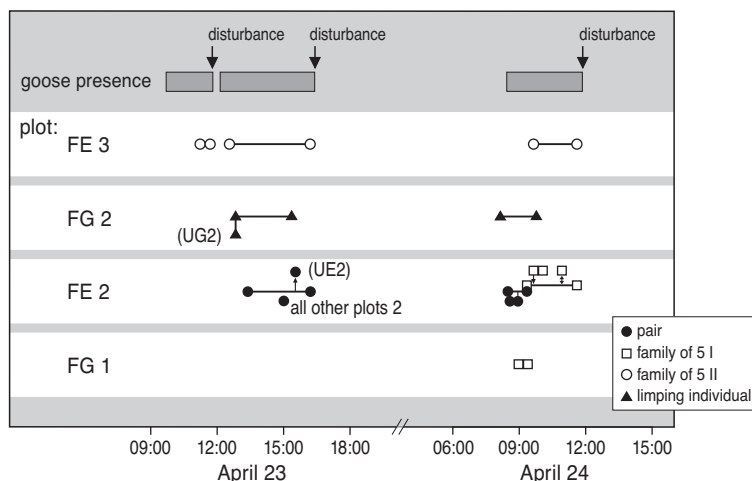


Figure 2.2 The relationship between intake rate (g fresh.s<sup>-1</sup>) and biomass on offer (g dw.m<sup>-2</sup>). Each data point represents the mean of a duplicate measurement;  $y = 0.00045x - 0.00043$ ,  $r^2 = 0.0792$ ,  $P < 0.001$ .





**Figure 2.3** Illustration of patch use at the level of the family unit. Symbols refer to particular family units whose patch choice could be observed for considerable time. Experimental plots are indicated using the treatment code and replicate number.

### *Development in plant growth and depletion over time*

Over the experimental period the differences in the green biomass-index between treatments tend to disappear (Figure 2.1C), to a large extent because of a net decline in aboveground biomass in the fertilised & excluded plots (FE) in both series. Episodes of decline in biomass are apparent in the fertilised treatments (FE,FG), coinciding with periods of grazing, but unfertilised plots (UE,UG) hardly show such decline because the intensity of use is much lower. Throughout the experiment however, differences in biomass between the grazing treatments remain present and the rank order of the treatments in terms of biomass largely remains the same. There is a parallel increase in grazing pressure (Figure 2.1A) and visiting time (Figure 2.1B) among treatments. Leaf elongation in the fertilised treatments (FE,FG) did not differ significantly from the unfertilised & excluded treatment (UE, Table 2.1).

### *Preference in relation to biomass and quality*

The three parameters of patch preference by geese that we used in this analysis (see Methods) are significantly related to nitrogen content of the main food species, when correcting for the differences between the series (Table 2.2). An interaction between sward height and nitrogen content did not contribute to explaining any of the variation in patch preference. Some of the variation in the total number of interactions could be explained by sward height (24%) in addition to nitrogen content (40%).

**Table 2.2** Summary of the multiple linear regression models relating the three parameters of patch preference to sward height and nitrogen content of the grasses. For each significant variable the estimated coefficients are given.

Parameter	Intercept	Sward height	Nitrogen content <i>Fest./ Pucc.</i>	Series	$r^2$	$P$	n
Bird density	-0.11	n.s.	0.09	-1.15	0.57	0.01	28
Sum of interactions	-47.00	9.76	1.13	n.s.	0.53	0.01	22
Grazing pressure	-2.43	n.s.	0.05	1.20	0.57	0.01	28

## Discussion

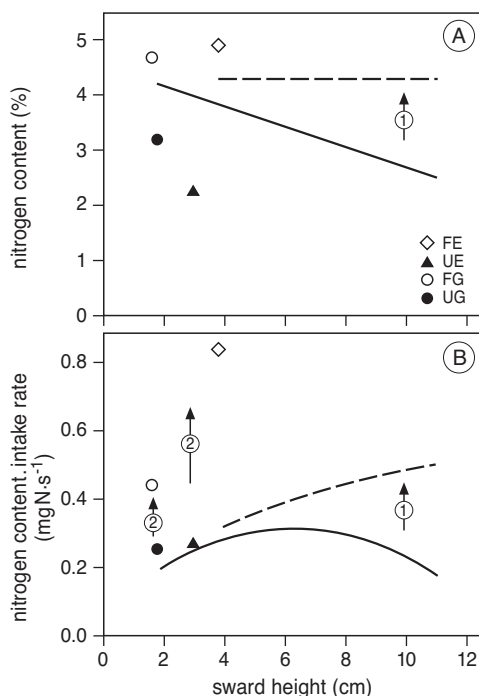
### *Patch preference*

The experimental manipulations resulted in clear differences in food quality between treatments, as measured in terms of nitrogen content, while vegetation composition was not significantly altered. Fertilised plots had higher values of nitrogen than unfertilised treatments. Levels of biomass were also affected by the treatments. Biomass was linearly related to instantaneous intake rate (Figure 2.2). In this range of sward heights Hassall *et al.* (2001) also found a linear relationship. By breaking the correlation between biomass and quality, we can now investigate their relative importance.

We evaluate three parameters of preference. Two of these, bird density and the total number of interactions are considered measures of instantaneous preference. The geese used fertilised plots in higher densities and were more active in defending those plots than unfertilised ones (Table 2.1). Grazing pressure provides a measure over a longer term, and showed the same pattern (Table 2.1). The uniformity in response at different time scales argues against an overriding effect of depletion or production. Such effects were also not detectable from a changing pattern of visits to the treatments over time (Figure 2.1A,B), or changes in peck and step rate over time. Depletion, therefore, does not appear to affect our conclusions.

Some of the fertilised plots were monopolised by a particular family unit of geese, for several successive grazing bouts (Figure 2.3). These individual observations support our other indices of preference, as dominant pairs are apparently willing to defend our manipulated plots. A similar phenomenon was observed by Stahl *et al.* (2001) and Prop & Loonen (1989), who clearly demonstrated that resources are not divided equally over flock members. Flocks consist of markedly different individuals and some of these individuals may have a profound effect on population dynamics (Teunissen *et al.* 1985) or habitat choice.

Both the factorial models (Table 2.1) and the regression models (Table 2.2) indicate a large effect of food quality, measured as nitrogen content, on patch preference by Brent Geese. This result helps us to further elaborate upon the conceptual model put forward by Riddington *et al.* (1997) and Hassall *et al.* (2001). In their experiments,



**Figure 2.4** The relationship between sward height and A) nitrogen content of forage plants (%) and B) the product of nitrogen content ( $\text{g.g}^{-1}$ ) and instantaneous intake rate ( $\text{g dry.s}^{-1}$ ) under natural and experimental conditions (nitrogen intake rate,  $\text{mg N.s}^{-1}$ ). Symbols refer to the current study (key is given in figure 2.2). Lines in A are re-constructed after Hassall *et al.* (2001) and Riddington *et al.* (1997), using raw data kindly provided by Hassall, and refer to data from November through March (dashed line, fertilised; solid line, unfertilised). Lines in B are a graphical illustration of the conceptual model put forward by Hassall *et al.* (2001), in which the intake rates were assumed to follow a functional response of type II (Holling 1959) and multiplied by a factor two in order to scale them with the measures of instantaneous intake rate that were derived in this study. Fertilisation eliminated the negative relationship between nitrogen content and sward height (arrows 1), resulting in a large effect at tall swards. The current study was performed at low levels of sward height compared to Hassall *et al.*, but fertilisation (arrow 2) had a large effect on nitrogen levels and, hence, at intake rates of nitrogen.

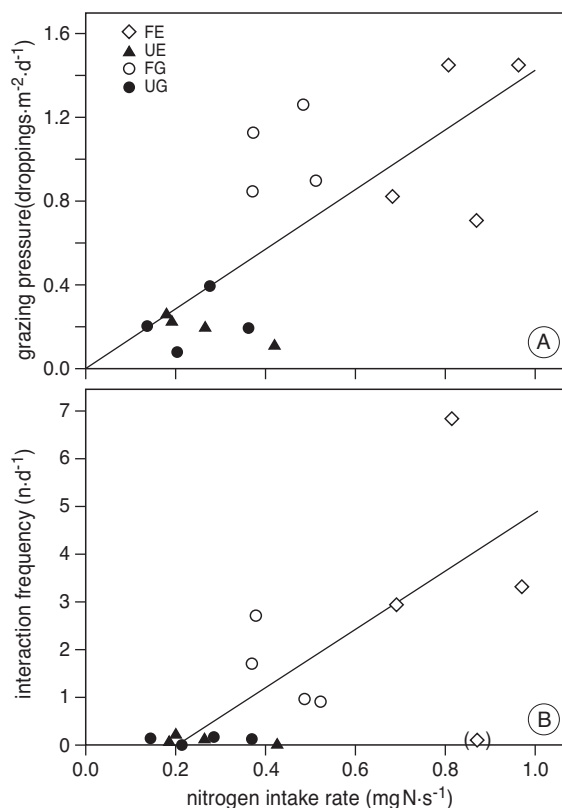
they found a preference for short sward heights under unfertilised circumstances, because of a negative correlation between sward height and nitrogen content. Elimination of this correlation by fertilisation led to a preference for tall swards. Riddington *et al.* (1997) propose that intake rate of nitrogen is the criterion for geese to select patches. This idea is graphically illustrated in Figure 2.4. According to the concept of Riddington *et al.* (1997), the product of nitrogen and intake rate (nitrogen intake rate,  $\text{mg N.s}^{-1}$ , Figure 2.4B) has an optimum at intermediate sward height as a result of a decelerating functional response (type II response of Holling 1959) and a declining N content of food

(Figure 2.4A). By fertilising the sward, this optimum disappeared in the experiment performed by Riddington and Hassall. At short sward heights (to the left of the optimum) the main constraint for the geese is imposed by intake rate, in their results. Our experiment was performed in this low range of sward heights, and we also demonstrated that intake rate increased strongly with sward height in this range. In spite of this, we find a strong effect of nitrogen content, rather than vegetation height. In our case, the levels of nitrogen differed by a factor two between fertilised and unfertilised treatments, while this difference was small in the experiment of Riddington and Hassall at low sward heights. So, as long as the differences in nitrogen content are large enough, the Brent Geese respond to it, even at low values of sward height. We thus strongly support the hypothesis by Riddington *et al.* (1997) and Hassall *et al.* (2001) that it is both food quantity and quality that determines patch choice in geese. The relationships between our parameters of preference and the product of nitrogen content and intake rate (nitrogen intake rate,  $\text{mg N}\cdot\text{s}^{-1}$ ), are highly significant (Linear regression,  $P < 0.001$ , Figure 2.5 A,B), and provide a better fit than regression models with nitrogen content alone as the independent variable. So, we have further proof that food quality plays an extremely important role, even at low sward heights. The role of food quantity will be more prominent when differences in nitrogen content are smaller relative to differences in intake rate, as was found by Hassall *et al.* (2001).

Stahl (2001) reported on two experiments on the marsh at Schiermonnikoog in which levels of biomass and quality were manipulated analogous to the present study. Her findings confirm our results that parameters of food quality affect patch choice in Brent Geese to a greater extent than do levels of biomass. In addition to that she demonstrated the existence of facilitative and competitive interactions between the different species of herbivore on the marsh. Brent Geese were shown to prefer patches that were previously grazed by Barnacle Geese with intermediate grazing pressure. Reasons for this were the higher nutrient levels in these patches, in spite of lower levels of biomass. High grazing pressures by hare, however, coincided with lower goose grazing pressure, presumably due to depletion effects.

### *Food quality and intake rate*

There is controversy, extensively discussed by van der Wal *et al.* (2000a) and Hassall *et al.* (2001), about which currency to use in studies dealing with food quality for herbivores. The set-up of our field experiment enabled us to separate effects of increased biomass availability from food quality in general. The measures of quality in our experiment are all correlated, except for the non-structural carbohydrates and hemicellulose, which were considerably lower in the fertilised & grazed (FG) treatment. In all treatments, nitrogen content was high. The lowest value observed was still above the minimum required values suggested for Brent Geese (Prop, pers. comm.) and poultry (NRC 1994). We cannot from these results comment further upon the relative importance of the different quality parameters. The quality parameters of *Juncus gerardi*, both nitrogen content and ADF, reacted to the treatments in the same way as the grasses



**Figure 2.5** The relationship between nitrogen intake rate ( $\text{mg N} \cdot \text{s}^{-1}$ ) and A) grazing pressure (linear regression  $r^2 = 0.553$ ,  $P < 0.001$ ) B) the total number of interactions observed per day of observation (linear regression  $r^2 = 0.623$ ,  $P < 0.001$ , one datapoint is excluded from calculation of this regression line with the justification that this plot was hardly visited during observations).

and reached the same levels. The geese probably do not need to distinguish between these food plant species in this period of the year.

There is, however, clear consensus about the phenomenon of a declining quality with increased standing biomass (van Soest 1994; Wright & Illius 1995; Riddington *et al.* 1997) and this has far reaching ecological consequences, in view of the fact that herbivores are sensitive to these differences (Wilmshurst *et al.* 1995; Wilmshurst & Fryxell 1995; Stahl 2001; Hassall *et al.* 2001). Fryxell (1991) provided a model illustrating that ruminants benefit from aggregating at patches of intermediate biomass, because of a declining digestibility at higher levels of forage density. Van de Koppel *et al.* (1996) showed that the density of small herbivores has an optimum over a gradient of biomass, assuming that foraging efficiency is maximal at intermediate levels of standing biomass. Such a decrease in foraging efficiency may not only stem from declining

food quality at high levels of biomass. Van der Wal *et al.* (1998) for example, demonstrated how increased handling time and search effort, caused by differences in sward structure, led to lower efficiency. Other factors may involve differences in vegetation composition or increased costs of locomotion and vigilance in taller swards. Our results exemplify the concept outlined by van de Koppel *et al.* (1996) by pointing at the importance of nutrient intake rate rather than simply food biomass intake rate. Small herbivores may choose to forage in areas of lower standing crop because of higher nutrient intake rates.

### *From patch to habitat use*

The results of this experiment contribute to our understanding of the patterns of habitat use that are observed in Brent Geese. During spring large differences exist between habitats in timing of plant growth (Bakker *et al.* 1993) and food quality of alternative foodplants (chapter 3). By their own grazing, geese affect the growth stage of plants and their quality as food (Ydenberg & Prins 1981; Stahl 2001, Table 1). In time and space, the spring staging areas are therefore not homogeneous with respect to food quality. Patch choice was demonstrated to be strongly affected by parameters of food quality (this experiment; Ydenberg & Prins 1981; Riddington *et al.* 1997; Stahl 2001). We therefore agree with Hassall *et al.* (2001) that, under these circumstances, food quality should be included in models of habitat use for geese and other small herbivores. Declining nutrient intake rates with increasing levels of standing crop may explain observed patterns of habitat use within initially homogeneous agricultural grassland. Over spring, Brent Geese were observed to aggregate at a smaller surface, with increasing primary production (chapter 5; Spaans & Postma 2001). This leads to a dichotomy in areas with an intensively grazed short sward and areas with tall sward heights that are left ungrazed. The hypothesis that this pattern emerges because of declining nutrient intake rates with increasing levels of standing crop is supported by field experiments using short term exclosures (chapter 5). Wild Brent Geese had higher grazing intensity in plots of intermediate biomass, where both intake rates and nitrogen content were higher. Alternative hypotheses, that this pattern is emerging due to spatial heterogeneity in food quality or avoidance of predation risk, need not be invoked, but may nonetheless be useful in explaining the geographical location of the patches that are being maintained.

During spring, the birds utilise pasture and marsh habitat in an order that is the reverse from that in autumn. In autumn the switch from marsh to pastoral land has been explained by Vickery *et al.* (1995) by the depletion of food plants in the preferred marsh habitat. In this depletion model, no parameter of quality needs to be invoked according to the authors, although they admit that plant quality and profitability will determine the ranking of habitats in terms of preference. When the birds move back to marsh habitat in spring they exchange productive areas with high values of standing biomass ( $99 \text{ g dry.m}^{-2} \pm 48 \text{ st. dev.}$  in April, unpublished data) for habitat with limited food availability ( $6\text{--}12 \text{ g dry.m}^{-2} \pm 6\text{--}11 \text{ st. dev.}$  in April, unpublished data). This



particular switch in spring cannot be explained using the depletion model by Vickery *et al.* (1995). Our experiment does provide an explanation, since quality differences within or among habitats may lead to higher instantaneous nutrient consumption rates in spite of lower levels of standing crop. An additional explanation for birds switching habitat in spring can be found in different levels of disturbance, as described for Barnacle Geese on our study island by Prins & Ydenberg (1985). Lower levels of disturbance on the marsh, as compared to the pasture area, allow the birds to improve their utilisation of food plants by grazing more selectively. In this view, the nutrient absorption rates on the marsh are higher due to improved digestion, in spite of lower levels of standing crop. Both explanations are not mutually exclusive, but stress the relative importance of food quality in patch choice by Brent Geese.

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## References

- Bailey JL (1967) Techniques in Protein Chemistry. Elsevier Publishing Company, The Netherlands
- Bakker C, Loonen MJJE (1998) The influence of goose grazing on the growth of *Poa arctica*: overestimation of overcompensation. *Oikos* 82: 459-466
- Bakker JP, de Leeuw J, Dijkema KS, Leendertse PC, Prins HHT, Rozema J (1993) Salt marshes along the coast of the Netherlands. *Hydrobiologia* 265: 73-95
- Boudewijn T (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl* 35: 97-105
- Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26: 105-113
- Esselink P, van Gils HAMJ (1985) Ground-based reflectance measurements for standing crop estimates. *ITC Journal* 1: 47-52
- Fales FW (1951) The assimilation and degradation of carbohydrates by yeast cells. *J. Biol. Chem.* 193: 113-124
- Fryxell JM (1991) Forage quality and aggregation by large herbivores. *Am. Nat.* 138: 478-498
- Ginnett TF, Demment MW (1995) The functional response of herbivores: Analysis and test of a simple mechanistic model. *Funct. Ecol.* 9: 376-384

- Gross JE, Shipley LA, Hobbs NT, Spalinger DE, Wunder BA (1993) Functional response of herbivores in food-concentrated patches: Tests of a mechanistic model. *Ecology* 74: 778-791
- Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* 127: 97-104
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385-398
- Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency: An experiment. *Oecologia* 95: 164-170
- Londo G (1976) The decimal scale for relevés of permanent quadrats. *Vegetatio* 33: 61-64
- Maas FM, Hoffmann I, Van Harmelen MJ, de Kok LJ (1986) Refractometric determination of sulphate and other anions in plants separated by High-Performance Liquid Chromatography. *Plant and Soil* 91: 129-131
- McKay HV, Bishop JD, Ennis DC (1994) The possible importance of nutritional requirements for dark-bellied brent geese in the seasonal shift from winter cereals to pasture. *Ardea* 82: 123-132
- NRC (1994) Nutrient requirements of poultry. National Research Council. Subcommittee on Poultry Nutrition. National Academy Press, Washington, D.C.
- Oksanen L, Fretwell SD, Arruda J, Niemelä P (1981) Exploitation ecosystems in gradients of primary productivity. *Am. Nat.* 118: 240-261
- Olf H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814
- Owen M (1980) Wild geese of the world. Batsford Ltd., London
- Percival SM, Sutherland WJ, Evans PR (1996) A spatial depletion model of the responses of grazing wildfowl to the availability of intertidal vegetation. *J. Appl. Ecol.* 33: 979-992
- Percival SM, Sutherland WJ, Evans PR (1998) Intertidal habitat loss and wildfowl numbers: applications of a spatial depletion model. *J. Appl. Ecol.* 35: 57-63
- Pettifor RA, Caldow RWG, Rowcliffe JM, Goss-Custard JD, Black JM, Hodder KH, Houston AI, Lang A, Webb J (2000) Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *J. Appl. Ecol.* 37 Suppl. 1: 103-135
- Prins HHT, Olf H (1999) Species richness of African grazer assemblages: towards a functional explanation. In: Newberry DM, Prins HHT, Brown ND (eds) *Dynamics of tropical communities*. Blackwell Science, British Ecological Society, London, pp 449-490
- Prins HHT, Ydenberg RC (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). *Oecologia* 66: 122-125
- Prop J, Deerenberg C (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28
- Prop J, Loonen M (1989) Goose flocks and food exploitation: the importance of being first. *Acta XIX Congr. Int. Orn. (Ottawa)* : 1878-1887
- Prop J, Vulink T (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Funct. Ecol.* 6: 180-189
- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153-160
- Robbins CT (1993) *Wildlife feeding and nutrition*. 2nd edition. Academic Press, San Diego
- Schaminée JHJ, Weeda EJ, Westhoff V (1998) *De Vegetatie van Nederland*. DI 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala
- Sedinger JS (1997) Adaptations to and consequences of an herbivorous diet in grouse and water fowl. *Condor* 99: 314-326
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Spalinger DE, Hobbs NT (1992) Mechanisms of foraging in mammalian herbivores: New models of functional response. *Am. Nat.* 140: 325-348
- Stahl J (2001) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD thesis University of Groningen, Groningen





- Stahl J, Tolsma PH, Loonen MJJE, Drent RH (2001) Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Anim. Behav.* 61: 257-264
- Teunissen W, Spaans B, Drent R (1985) Breeding succes in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea* 73: 109-120
- Turner MG, Wu Y, Romme WH, Wallace LL (1993) A landscape simulation model of winter foraging by large ungulates. *Ecol. Mod.* 69: 163-184
- van de Koppel J, Huisman J, van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745
- van der Meijden R (1990) Heukels' Flora van Nederland ed 21. Wolters-Noordhoff, Groningen
- van der Wal R, Madan N, van Lieshout S, Dormann C, Langvatn R, Albon SD (2000a) Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia* 123: 108-115
- van der Wal R, van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos* 82: 123-130
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000b) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van Eerden MR (1997) Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. PhD thesis University of Groningen, Groningen
- van Soest PJ (1994) Nutritional Ecology of the ruminant. Cornell University Press, Ithaca (NY)
- van Wijnen HJ, Bakker JP, de Vries Y (1997) Twenty years of salt marsh succession on a Dutch coastal barrier island. *J. Coast. Cons.* 3: 9-18
- Vickery JA, Sutherland WJ, Lane SJ (1994) The management of grass pastures for brent geese. *J. Appl. Ecol.* 31: 282-290
- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499-508
- Wilmschurst JF, Fryxell JM (1995) Patch selection by red deer in relation to energy and protein intake: A re-evaluation of Langvatn and Hanley's (1993) results. *Oecologia* 104: 297-300
- Wilmschurst JF, Fryxell JM, Hudson RJ (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behav. Ecol.* 6: 209-217
- Wright W, Illius AW (1995) A comparative study of the fracture properties of five grasses. *Funct. Ecol.* 9: 269-278
- Ydenberg RC, Prins HHT (1981) Spring grazing and the manipulation of food quality by Barnacle Geese. *J. Appl. Ecol.* 18: 443-453

Brent Geese in flight above the biological field-station "de Herdershut" on Schiermonnikoog, moving between polder and salt marsh (photo J. Stahl).





## Creating new foraging opportunities for Brent and Barnacle Geese in spring - insights from a large-scale experiment

Daan Bos & Julia Stahl

### Abstract

The implementation of a new non-disturbance policy on the Dutch Wadden-Sea island Schiermonnikoog provided an experiment to test ideas concerning the switch between habitats by spring-staging Brent and Barnacle Geese. In the experimental years (2000 and 2001) the farmers desisted from all scaring activities in the embanked pasture area (290 ha) with grasslands intensively managed for dairy farms. The adjoining salt marsh (1635 ha) already was afforded complete protection, and traditionally provided the main goose feeding area in spring. A traditional habitat switch to the marsh coincides with the spring increase of forage production in the marsh habitat, suggesting that forage availability on the marsh is limiting in early spring. Compared to three control years (1997, 98 and 99 with scaring in the pastures) both species of geese extended their usage of the agricultural habitat in the two non-scaring years, where they remained until migratory departure (April for the Barnacle Geese, late May for the Brent). Numbers of geese on the salt marsh did not change, hence non-disturbance triggered an increase of capacity for spring feeding geese at this staging site. The change was most dramatic for the Brent Goose with a doubling of numbers on the island in the years without scaring, and identification of ringed individuals showed that the birds recruiting to this new spring tradition had in previous seasons utilised other sites in the Dutch Wadden Sea.

## Introduction

During the spring staging period of Dark-bellied Brent Geese *Branta bernicla bernicla* and Barnacle Geese *Branta leucopsis* along the coasts of western Europe a spectacular switch between foraging habitats occurs as the season progresses (Vickery *et al.* 1995; Rowcliffe *et al.* 2001). Both species of geese utilise agricultural grasslands during winter and early spring, but the majority of geese change to feeding sites on salt marshes prior to departure to their Arctic breeding grounds (Ebbinge *et al.* 1999). Feeding on agricultural land is especially common in Britain and the Netherlands during the winter months up to early March. By then, almost all Barnacle Geese staging in the Netherlands have moved to salt-marsh habitats, and about 80 % of the NW European population of Brent Goose forage on salt marshes in May. These spring changes in forage and habitat preferences of massive numbers of *Branta* geese in our coastal ecosystems are intriguing and impinge on management practice (notably where geese conflict with dairy farmers). In the absence of field experiments on a sufficient scale, the causes contributing to the habitat shift are nevertheless still poorly understood. The spring staging period is of exceptional importance for migrant *Branta* geese as accumulated fat reserves are a prerequisite for successful breeding in the Arctic (de Boer & Drent 1989; Ebbinge & Spaans 1995). Understanding the factors governing habitat preference at this time of year is an essential step towards defining the capacity of coastal areas for spring goose grazing.

Previous studies examining the habitat use of geese in spring agree in implicating changes in the relative nutrient content and/or biomass on offer in the competing habitats as the underlying cause to explain the observed habitat switch. Vickery *et al.* (1995) and Rowcliffe *et al.* (2001) illustrate that depletion of forage biomass necessitates a switch of Brent Geese from intertidal flats and salt marshes to agricultural land in Britain during autumn and winter. Increasing primary production in spring allows the geese to return to these habitats. Both studies suppose that agricultural land is less attractive due to lower forage quality. Boudewijn (1984) demonstrates a gradual decline of forage quality of agricultural grassland due to ageing of the sward in the course of spring and argues that the diminishing profitability of this habitat enforces Brent Goose foraging on the salt marshes. Plant production is supposed to start later at the salt marshes. Spring staging Barnacle Geese switch from agricultural pastures to adjacent salt-marsh sites as soon as the nitrogen content of forage plants is on a par between the two habitat types (Prins & Ydenberg 1985). An additional causal factor explaining the habitat shift was put forward by Prins and Ydenberg (1985) who argued that Barnacle Geese utilise the *Festuca rubra* sward on the salt marsh more efficiently than pasture grass species due to lower levels of disturbance on the marsh habitat.

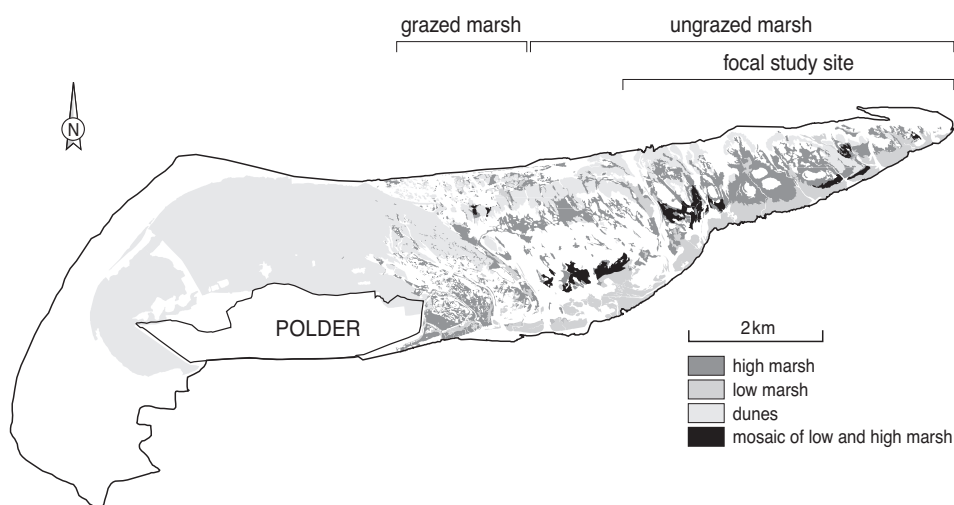
We here analyse spring habitat use of Brent and Barnacle Geese on the Dutch Wadden Sea island of Schiermonnikoog in the light of large-scale changes in goose scaring practices by farmers which provide an experiment to study the influence of disturbance on habitat switches in geese. We studied the use of pasture and salt-marsh habi-



tats by staging geese during five consecutive years (1997, 1998 and 1999 with active scaring of geese on agricultural pastures, and 2000 and 2001 totally without harassment), and collected data on the seasonal characteristics of the main forage plants.

## Study area

We conducted our study on the Dutch barrier island Schiermonnikoog (Figure 3.1; 53°30'N, 6°10'E), which features an embanked pasture area (polder, 290 ha), a cattle grazed salt marsh (185 ha) and a large area of ungrazed salt marsh (1450 ha). The pastures, used to produce grass for silage and grazed by cattle between May and November, consist of homogeneous swards of mainly *Lolium perenne* and *Poa* spp.. The pastures are heavily fertilised with approximately 400 kg N.ha<sup>-1</sup>yr<sup>-1</sup> of artificial fertiliser in addition to the application of manure. The salt marsh of Schiermonnikoog is grazed by cattle at a stocking rate of 0.5 cow.ha<sup>-1</sup> on 400 ha, from the end of May until October and remained unfertilised since the beginning of the 1990s. The long-term ungrazed salt marsh of Schiermonnikoog is characterised by a declining age of the marsh from West (ca. 100 years old) to East where the island is still extending (detailed description see Olff *et al.* 1997). The European Brown Hare *Lepus europaeus* is a resident grazer of all plant communities frequently used by geese (pers. observation). Hare numbers on the ungrazed salt marsh fluctuate between 300 and 500 animals.



**Figure 3.1** Map of the island of Schiermonnikoog, indicating the major habitats utilised by geese (agricultural pastures in the polder, low and high salt marsh) and the focal study site on the ungrazed marsh.

## Methods

### *Spatial distribution of geese*

Between 1997 and 2001, we performed regular censi to assess the total number of Brent and Barnacle Geese on the island and their distribution over the major habitat types. These counts covered the entire island following a fixed route with alternating direction between counts. Counts were independent of the tidal regime. We carried out additional counts in the pasture area at various times during daylight.

On the ungrazed salt marsh, we determined spring habitat use by geese using a range finder (Leica Vector 1000 binocular, 7 x 42), which measured the distance and compass angle between the centre of a goose flock and the observer from fixed observation points. A flock was defined as a cluster of geese of one species, either separated from other geese by at least 50 m, or foraging on a different plant community than other geese present. For groups larger than 200 individuals, multiple measurements were obtained for subgroups of c. 200 individuals. We entered the data in a Geographical Information System (GIS) and combined them with an existing vegetation map of the study site (Kers *et al.* 1998). The vegetation map (scale 1:5000) dated from 1996 and was based on a comprehensive ground survey guided by aerial photographs. The units of the map legend conform to the classification by Schaminée *et al.* (1998), and referred to plant communities at the association level. We restricted our analyses to the eastern part of the ungrazed marsh (938 ha), where the fixed observations points had an elevation of at least 5 m above MHT and to a circular area within 650 m of these observation points to prevent bias due to limited visibility. For the purpose of the analyses, we grouped plant communities with a short canopy on the low (*Salicornietum*, *Puccinellietum maritimae* and *Plantagini-Limonietum*) and the high marsh (*Armerio-Festucetum*, *Juncetum gerardii* and *Artemisietum maritimae*). The *Artemisietum maritimae* is included as the canopy of this plant community is still low and dominated by *Festuca rubra* in spring in our study area. We calculated the density of geese in these communities with a short canopy for the low and the high salt marsh. The areas of the plant communities, as well as the number of geese observed within these zones were deduced from the GIS database.

### *Vegetation parameters*

We estimated the seasonal development of standing aboveground biomass, primary production and forage quality of food plants for geese using bi-weekly sampling schemes at six sites on the low and the high livestock-ungrazed salt marsh, and five sites in the pasture area in 1998. The sites on the marsh were located on a transect from East to West, within the community dominated by *Festuca rubra* (*Armerio-Festucetum*) on the high marsh and the community characterised by *Puccinellia maritima* (*Plantagini-Limonietum*) on the low marsh. The distance between each of the sites was approximately 800 m and age of the marsh ranged along the gradient from 10 - 50 years. The sampling sites in the pastures were regularly distributed over the southern half of the pasture area at intervals of approximately 600 m. We sampled *Lolium perenne*, *Poa* spp.



in the polder and *Festuca rubra*, *Puccinellia maritima*, *Plantago maritima* and *Triglochin maritima* in the salt marsh, being important forage plants for geese (Prop & Deerenberg 1991; van der Wal *et al.* 2000). We estimated the net biomass increase of the forage plants (Net Accumulated Primary Production, g dry.m<sup>-2</sup>.d<sup>-1</sup>) from the difference of standing biomass between two sampling periods for plots excluded from grazing. For this purpose, we used mobile exclosures with a surface area of 0.5 m<sup>2</sup> (chicken wire, mesh width 5 cm). Standing live biomass of the forage plants was assessed by clipping all above ground material from 15 cm diameter turves, which we sorted, washed, dried (48 h at 70°C) and weighed to the nearest 10 mg. We determined the nitrogen content of leaf tips (upper 2 cm) of *Festuca rubra*, *Puccinellia maritima* and a mixture of the pasture grasses as a measure of forage quality. Plant samples were collected at all sampling sites during spring 1998. The samples were washed, air-dried at 70°C for 48 h and subjected to an automated CNHS-analysis (Interscience EA 1110).

We used data from the weather station of the Free University Amsterdam on Schiermonnikoog to assess precipitation on the island for the period of January through April to obtain the date at which a temperature sum of 180°C was reached in the years 1997 to 2001. The temperature sum reflects the sum of positive averages of minimum and maximum air temperature per day from 1 January onwards and is used as an indication for the starting date of grass growth.

### *Scaring regime - a large-scale experiment*

During the first three years of our study (1997-1999) an active scaring policy was effective on Schiermonnikoog to prevent geese feeding on the agricultural pastures (Bazuin & van der Wal 1991). In the attempt to drive geese from the pastures to the adjacent salt-marsh sites in order to protect the first spring harvest of grass, farmers scared geese daily using flares in addition to more traditional techniques, such as scarecrows and flags. On average, 160 flares were used each spring (pers. comm. J.B. Bazuin). Apart from normal agricultural activities there was little further disturbance except for low-intensity search for the first Lapwing *Vanellus vanellus* eggs during March and the first week of April following local tradition.

For the spring seasons of 2000 and 2001, the government implemented a new goose management scheme, which incurred increased financial compensation of goose damage to local farmers, under the stringent condition that no goose scaring of any sort was to be undertaken. From January 2000 onwards, the shooting of flares was banned and the presence of people other than the farmer himself on the pastures was restricted to the late afternoon (after 16:30, pers. comm. T. Talsma). According to our observations the local people obeyed the rules strictly. To quantify the effect of the different scaring regimes we compared data on disturbances collected in the pasture habitat during the spring seasons 1998 to 2001. Focal goose flocks foraging on agricultural pastures were selected randomly and followed during at least 1 hour. We noted all disturbances with an identifiable human related cause. We defined an event as disturbance when more than 50% of the flock flew up. The number of tourists visiting

Schiermonnikoog, another potential source of disturbance for geese, varied by less than 10 % between the five years of our study (pers. comm. Administration Wageningen Ferry Service) and we, therefore, assume that this factor did not influence the large-scale scaring experiment related to the pasture area. In the pasture area the activities of tourists were virtually restricted to passing by on bicycle, keeping to the paved paths, and generally ignored by the geese. From 15 April onwards, each year the eastern salt marsh (a breeding bird reserve) was closed to the public entirely.

### *Movements of individual birds*

To analyse switches of individual geese between staging sites and between habitat types, we used sightings of ringed Brent Geese. From the 1970s onwards, Brent Geese are marked individually with coded colour leg bands within the Brent Goose ringing scheme either on the Siberian breeding grounds or at the European wintering sites and data on re sightings are available through the ring data base maintained by Bart Ebginge and Gerard Müskens (Alterra, Wageningen, The Netherlands). On Schiermonnikoog, Brent Goose flocks in the pasture and the salt-marsh habitat were scanned regularly for the presence of ringed individuals during the entire staging period. For the purpose of this study, we analysed sightings of Brent Geese on the island from May 2000 and May 2001 (the two seasons when scaring was banned) and deduced the staging history of these individuals during previous years from the long-term data base.

### *Data analyses*

Census results were averaged for bi-weekly periods for the years 1997-1999 (active scaring) and 2000-2001 (no scaring), thereby combining data from different years according to the scaring regime. For the pastures and the salt marsh, we tested differences of goose numbers between years with and without scaring using Mann-Whitney U tests for each species and each period. To test differences of the distribution of colour-ringed Brent Geese between habitat types and between years with different scaring regimes, we applied chi square statistics.

For the salt marsh, differences in goose density between plant communities with short canopy on the low and the high salt marsh were tested per month using General Linear Modelling (GLM) with species and salt-marsh zone as well as the interaction term as fixed factors. Variation in forage quality, standing biomass and production of forage plant species was analysed using GLM, with plant species as a fixed factor and day number as well as day number-squared as co-variates. We accounted for possible interactions between the independent variables. Any non-significant factors were removed stepwise from the model and final models were defined through a post-hoc Tukey's test. When appropriate, data were square root transformed ( $y' = \sqrt{y+0.5}$  for count data) or log-transformed ( $y' = \lg_{10}(y+1)$  for vegetation parameters) to obtain homogeneity of variances before entering statistical testing, however, untransformed data are given in the graphs. Statistical analyses were carried out with SPSS 10.1 (SPSS Inc.).





## Results

### *Habitat use in years with and without scaring*

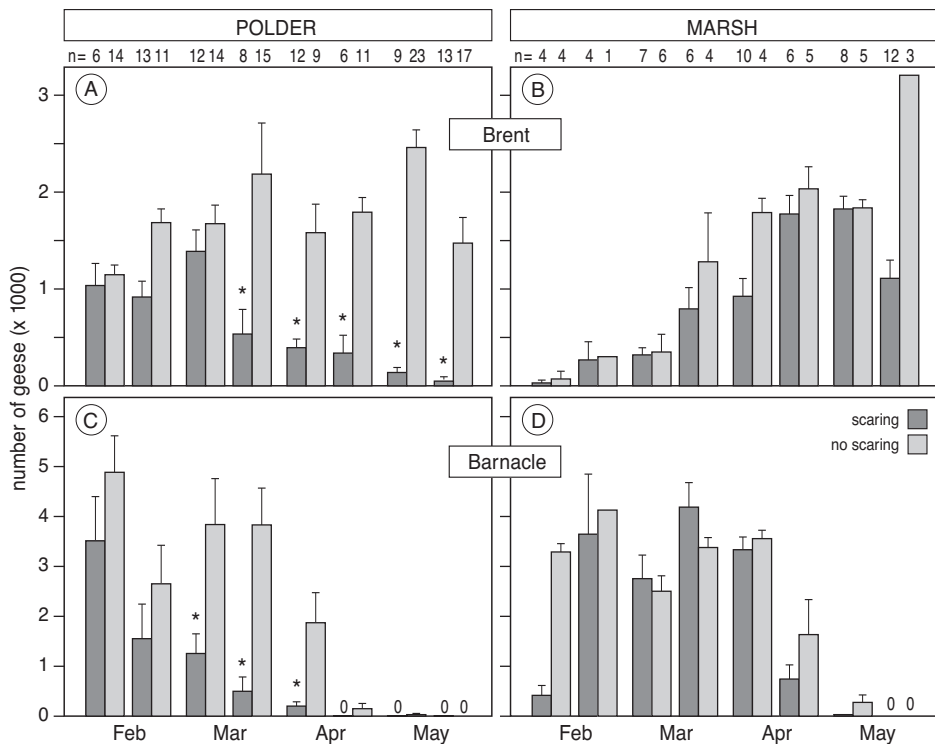
Table 3.1 reviews human related disturbances for the pasture habitat during years with differing scaring regime. We recorded hardly any human disturbances that caused flocks to fly up after the ban on active scaring from spring 2000 onwards.

The patterns of habitat use by Brent and Barnacle Geese during spring are summarised in Figure 3.2, which compares the scaring years with the non-scaring experimental years. Almost the entire local populations of both goose species foraged in pasture habitat until the second half of February. From then on, large numbers of Barnacle Geese were observed on the salt marsh (Figure 3.2D), and numbers on the agricultural pastures started to decrease (Figure 3.2C). Brent Goose numbers on the marsh increased gradually during March and April (Figure 3.2B), reaching the maximum in May just prior to departure for the breeding grounds.

The use of the agricultural habitat differed markedly between years with an active goose scaring regime (1997-1999) and years when goose scaring was banned (2000-2001). Barnacle Goose numbers in the agricultural habitat declined sharply during February in years with active disturbance, but showed a delayed decline in the absence of scaring, considerable numbers remaining until the end of April (Figure 3.2C). During March and the beginning of April, the number of Barnacle Geese in the pasture habitat differed by more than a factor three between the two scaring regimes. It will be noted that the total contingent of Barnacle Geese staging on the island was higher in the non-scaring years. Brent Goose numbers in the pasture habitat increase until the beginning of March, as new birds arrive from wintering grounds in France and Great Britain (Figure 3.2A). In years with active scaring, Brent Goose numbers decline after mid-March in the pasture habitat (Figure 3.2A), as birds switch to the salt-marsh habitat (Figure 3.2B). While in these years Brent Geese were almost absent from the agricultural habitat by the beginning of May, Brent numbers remained high (with on aver-

**Table 3.1** Frequency of human disturbances in the pasture habitat 1998-2001; observation periods were corrected for the number of geese observed and are then given as goose hours.

Year	scaring	observation effort (hrs)	observation effort in goose hrs.	human disturbances per 10.000 goose hrs.	observation period
1998	yes	24	30800	6.5	9 March till 15 April
1999	yes	40	14724	6.8	23 March till 10 May
2000	no	14	15000	0	2 May till 4 May
2001	no	39	72000	0.3	5 May till 27 May



**Figure 3.2** Spring numbers of Brent (panel A and B) and Barnacle Geese (panel C and D) on the polder (agricultural pasture) and salt marsh of Schiermonnikoog for years with (1997-99) and without (2000-01) active disturbance by farmers. Bars represent periods of two weeks and comprise several goose counts as indicated on top of the graphs. Asterisks indicate significant differences in goose numbers between the two scaring regimes ( $P < 0.05$ ).

**Table 3.2** The average number of Brent and Barnacle Geese on Schiermonnikoog during March, April and May 1997-2001 and spring temperature and precipitation as a proposition of growth conditions for forage plants; Tsum 180 indicates the date at which the sum of positive averages of minimum and maximum daily air temperature reaches 180°C (starting from 1 January) and is used as a reference for the start of grass growth.

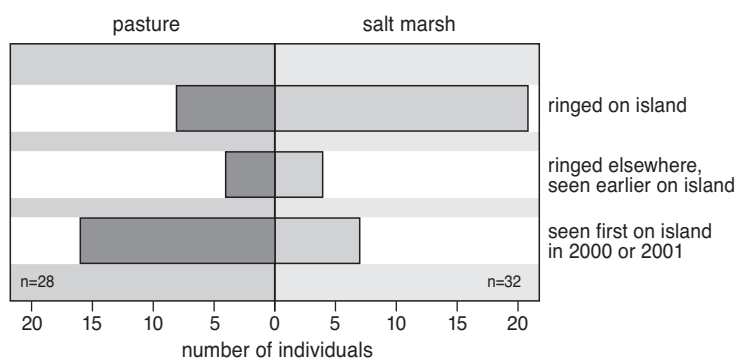
Year	Mean number of Barnacle Geese			Mean number of Brent Geese			Number of counts			Tsum 180	Precipitation until 1 May (mm)
	March	April	May	March	April	May	March	April	May		
1997	4627	1959	2	2056	1681	1755	6	10	11	1 March	117
1998	4567	3341	26	2289	2385	1615	6	7	9	11 February	239
1999	6875	3048	12	1689	2237	1624	3	4	4	no data	226
2000	7333	3513	188	2462	3918	5273	5	5	3	5 February	187
2001	13012	2946	570	3322	3302	3889	1	1	1	8 March	194



age 2,000 birds in May) after the ban of active scaring by farmers. The total population of Brent Geese on the island in May was thus doubled after scaring was banned in the pasture habitat (Table 3.2).

### *Movements of individually marked Brent Geese*

Figure 3.3 summarises the staging history of individually marked Brent Geese observed in the pasture habitat and on the salt marsh during the spring seasons of 2000 and 2001 when active scaring was banned on Schiermonnikoog. While 25 out of 32 rings recorded on the salt marsh had been regular visitors of that distinct site during previous years, only 12 out of 28 rings recorded on the agricultural pastures had been previously observed there ( $\chi^2 = 6.44$ , Yate's corrected,  $P = 0.011$ ). In the agricultural habitat, 16 individuals had not been recorded on Schiermonnikoog at all prior to the cessation of active scaring. Eight of these were sighted as staging birds along the Groningen mainland coast in other years, while three individuals had previously staged on the island of Texel, Terschelling or Ameland, respectively. For the remaining five individuals no staging records were available for previous years. Our pasture records do not allow us to judge whether the same individuals were present in both non-scaring years as there are only few records for May 2000. On the salt marsh, four out of seven newcomers stem from mainland staging sites at Groningen coast, one from Texel and two from the Friesian mainland coast. Out of the salt-marsh group, on average 74% of the ringed individuals seen in one year had been recorded at that distinct site the year before. No Brent Geese that were seen in the pasture habitat in May had a record of staging on the salt marsh of Schiermonnikoog. Similar staging histories account for the salt-marsh group: none of the Brent Geese recorded at our focal salt-marsh site was observed at the pasture site in May, during any of the study years.



**Figure 3.3** Spring history of individually marked Brent Geese recorded on the eastern salt marsh and on the agricultural pastures during May 2000 and 2001, after goose scaring was banned from the island.

# Habitat differences concerning food availability

Biomass production of plant species common in the diet of Brent and Barnacle Geese (*Festuca rubra*, *Puccinellia maritima*, pasture grasses) strongly increased during spring (Figure 3.4A). On the agricultural pastures, this increase was significantly steeper than on either high or low salt-marsh habitats (GLM: interaction between plant community

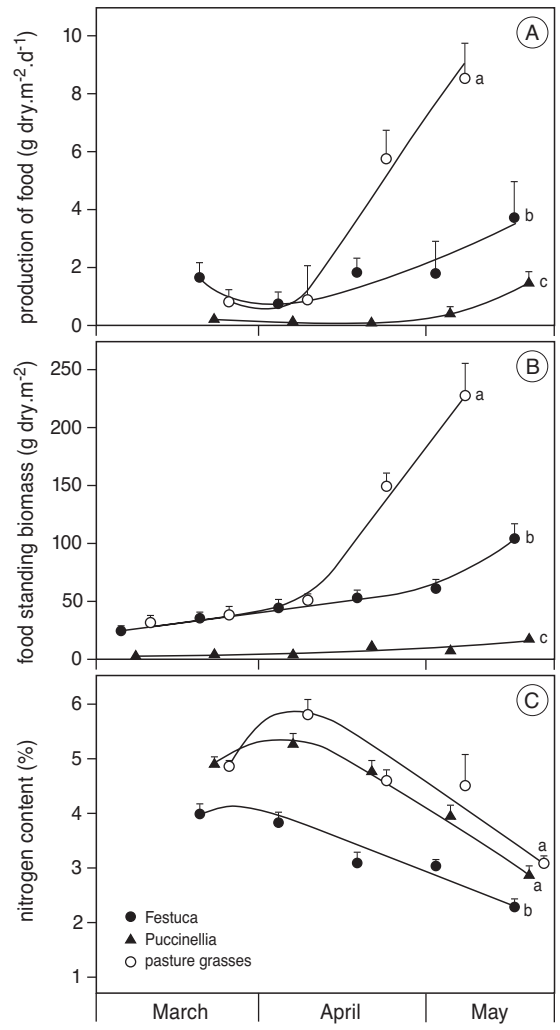


Figure 3.4 Spring phenology of forage plants during 1998. A) Increase in primary production (g dry-weight.m<sup>-2</sup>.day<sup>-1</sup>), B) Increase in above-ground living biomass of forage plant species (g dryweight.m<sup>-2</sup>) and C) Development of the nitrogen content of grasses in the polder (pasture grasses), on the high (*Festuca rubra*) and the low (*Puccinellia maritima*) salt marsh, calculated as mean + SE. Different letters indicate significant differences between regression lines. Lines drawn by eye.

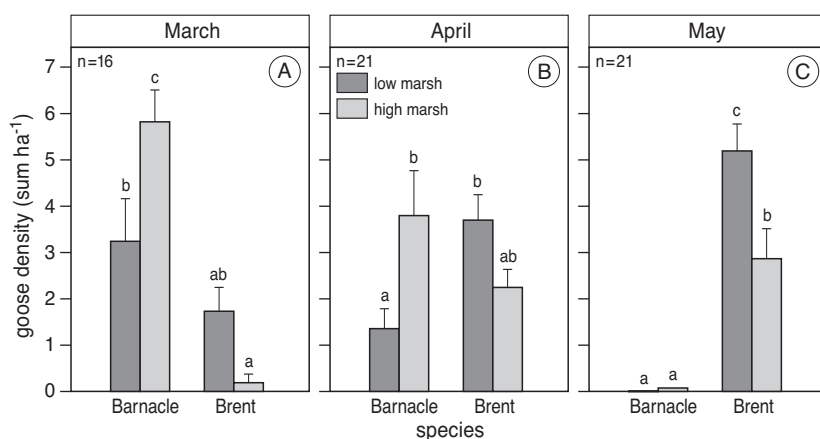


and day number  $F_{2,63} = 4.3$ ,  $P = 0.018$ ,  $R^2 = 0.62$ , simple contrasts). Biomass production on the low salt marsh started only in the second half of April and overall production was low (less than  $2 \text{ g.m}^{-2}.\text{d}^{-1}$ ). The high salt marsh was intermediate in terms of primary production when compared to the low marsh and the pasture habitat, still plant growth started early and values exceeded  $1 \text{ g.m}^{-2}.\text{d}^{-1}$  during the second half of March already. Standing biomass followed the same pattern as primary production with lowest amounts of biomass ( $0\text{-}10 \text{ g.m}^{-2}$ ) on the low marsh and highest values (over  $200 \text{ g.m}^{-2}$ ) in the pasture habitat at the end of spring (Figure 3.4B; GLM, interaction between plant community and day number  $F_{2,91} = 4.19$ ,  $P < 0.001$ ,  $R^2 = 0.82$ ).

The seasonal development of forage quality, measured as nitrogen content of leaf tissues, followed similar trajectories for all forage species sampled (Figure 3.4C). Nitrogen content first increased slightly during early April and then decreased, as the growing season proceeded. The data are best described by a regression model with day number ( $F_{1,99} = 0.029$   $P < 0.001$ ), day number-squared ( $F_{1,99} = 0.052$ ,  $P < 0.001$ ) and forage species ( $F_{2,99} = 40.8$ ,  $P < 0.001$ ) as independent variables ( $R^2 = 0.764$ ). *Festuca rubra* showed the lowest nitrogen content compared to pasture grasses and *Puccinellia maritima* during the entire spring season.

#### After the switch - goose distribution on the marsh

Densities of Barnacle Geese were significantly higher on the high marsh as compared to the low marsh for both March and April, although the species also frequently used low marsh sites in March (Figures 3.5A, B). Barnacle Geese leave for their breeding quarters by the last week of April (Figure 3.5 C). Brent Goose densities tended to be



**Figure 3.5** The average density of Brent and Barnacle Geese visiting plant communities with a short canopy on the low and the high salt marsh during March (A), April (B) and May (C). Different letters indicate significant differences between mean goose densities. The number of goose counts is indicated as n. Data comprise the years 1997-2000.

higher on the low as compared to the high marsh during all months although this difference was only significant for the month of May. During March and April, there is considerable overlap in the use of the two zones of the salt marsh by both goose species at this level of scale. For each month the interaction between goose species and salt-marsh zone explained significant variation (GLM, interaction term March:  $F_{1,80} = 15.90$ ,  $P < 0.001$ ,  $R^2 = 0.47$ , April:  $F_{1,80} = 10.01$ ,  $P < 0.005$ ,  $R^2 = 0.137$ , May:  $F_{1,80} = 9.20$ ,  $P < 0.005$ ,  $R^2 = 0.67$ ).

## Discussion

### *The nature of the habitat switch and the trigger effect of scaring*

In all five years of our study, we have observed that large numbers of Barnacle and Brent Geese gradually shift the focus of their foraging activities from the agricultural pasture habitat to the salt marsh (Figure 3.2). In years when farmers were scaring the geese to protect the first cut of grass, Barnacle Goose usage of the pasture habitat declined from mid-February onwards. Brent Goose numbers started to decline in the same area from mid-March, one month later. Without scaring activities in the years 2000 and 2001, the average number of geese in the agricultural area was significantly higher towards the end of the staging period for both species when compared to years with scaring (Figures 3.2A & C). We conclude that scaring contributed substantially to an early departure from the pasture habitat in spring. It is striking that total goose numbers utilising the salt marsh were closely similar for both species over the entire spring period, suggesting that this habitat was used to capacity. Geese foraging in the pasture in years without active scaring during late spring represent additional immigrants from other staging sites. Our information from reading coded legbands casts some light on this problem, at least for the Brent Geese, which received intensive study each spring season. In keeping with our long-term data base, individuals observed out on the eastern salt marsh tended to return each year both with and without scaring, and represent a stable staging strategy centred on the traditional habitat. By contrast, the ringed birds feeding in the pasture habitat in the past two (non-disturbed) years have a different history. In contrast to the marsh contingent, where a minority (7/32) were new sightings, a majority of the individuals in the pasture area (16/28) were new to the island. We assume that normally these Brent Geese would have passed by, but now were induced to stay for a prolonged period. Hence, the cessation of scaring has been the starting point for the Brent Geese to form a novel staging strategy utilising the pasture habitat during the entire spring period. We commenced systematic goose watching on the island in 1973, and never before observed a concentration of Brent Geese present in the enclosed pasture land right up to departure for the breeding grounds in late May. That the complete absence of harassment by flares is a necessary prerequisite to this new tradition does not mean that this is the only condition to apply. We will argue in the next section that the pasture can only be exploited effectively by Brent Geese if they are able to exert a concentrated (and unbroken)



grazing regime and thus maintain a portion of the pasture habitat in the early growth stage conducive to efficient goose usage. Freedom from disturbance sets the stage as it were.

It is intriguing to compare our data with the results of experimental implementation of refuges set-aside from hunting disturbance in Denmark (Fox & Madsen 1997; Madsen *et al.* 1998). In these experimental reserves, a large and rapid increase in the number of dabbling ducks following protection from hunting was observed. This showed that the ducks could increase their length of stay at the Danish staging sites, if habitat conditions were adequate. In contrast, Ganter *et al.* (1997) presented a case study from a Brent Goose staging site at the German Wadden Sea coast of Schleswig-Holstein, where salt-marsh habitat was lost due to embankment. Ganter *et al.* (1997) detected frequent long-distance movements of individually marked Brent Geese, displaced by the loss of their staging habitat. In their study, human activities negatively affected the conditions of the spring staging site, destroying a staging tradition and forcing geese to look for new opportunities elsewhere.

There were still sources of disturbance in the pasture area in the 'non-scaring' years, related to tourism (including traffic) and normal agricultural activities. Both increase in intensity over spring. However, the birds seemed to adapt quickly to the new situation and flew up less frequently in reaction to these ordinary sources of disturbance as compared to years with scaring (Table 3.1). Finally, we must emphasise the role of tradition and local knowledge. Although geese are obviously opportunistic and able to respond quickly to the presence of newly available habitat (van Eerden 1984; Zijlstra *et al.* 1991; this study), it has also been demonstrated that many individuals are very faithful to their staging sites. Brent Geese utilising the eastern part of the salt marsh at our study site form a very distinct group and it is interesting to note that none of these birds opted for spring staging in the pasture habitat. This gives rise to the speculation that individuals making what amount to last-minute site decisions recruited to the newly available pasture site. It would be interesting to know the previous history of these geese in more detail, in particular if they had experienced unfavourable conditions the previous year. In Pinkfooted Geese *Anser brachyrhynchus* for example, Madsen (2001) showed that individuals not attaining the abdominal profile index corresponding to breeding condition were more prone to shift spring staging site the next year.

In contrast to the situation described by Prins & Ydenberg (1985) for Barnacle Geese, the switch to the marsh was not an absolute departure from the polder habitat at a specific moment in recent years, but took place more slowly. In connection with this more gradual course of the habitat shift, it is interesting to note that Barnacle Geese tend to prolong their total staging period at Dutch staging sites during recent years and flocks can be observed at the mainland coast as late as mid-May (Koffijberg *et al.* 1997). Brent Goose numbers also build up gradually on the marsh over spring. We have discussed several processes that can explain such a gradual change, notably an increasing primary production on the marsh allowing for an increase in grazing pressure over time, a decreasing nutrient intake rate on the polder and increasing recreational pressure in the course of spring. The order in which the two habitats are

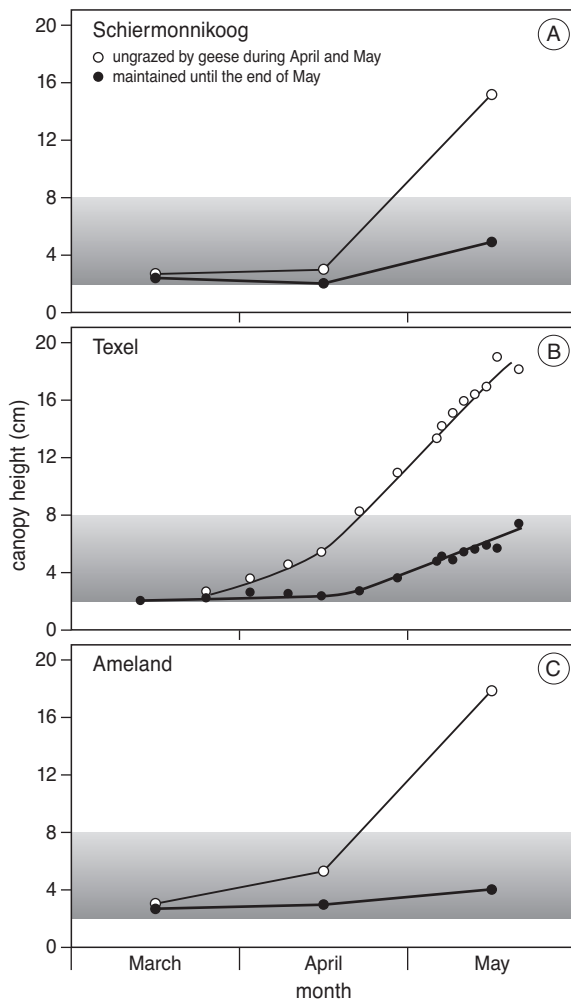
utilised coincides with the seasonal development of primary production at each site, supporting the idea that forage availability is limiting on the marsh in early spring. This shows a clear analogy with the winter situation, where the same switch is observed in the opposite direction (Vickery *et al.* 1995; Rowcliffe *et al.* 2001).

### *The goose grazing cycle in the pasture habitat*

With increasing age or standing biomass of the sward, a decline in forage quality is often observed (van Soest 1994). This effect of forage maturation occurs on the salt marsh (Stahl *et al.* 2001) as well as in the pasture habitat (Boudewijn 1984; chapter 5). Additionally, there are clear indications that small species of waterfowl, such as the Brent Goose, suffer from a declining intake rate of matter when grass swards grow tall (chapter 5). For Wigeon *Anas penelope*, this phenomenon is well established (Durant 2001). A declining rate of biomass intake, in combination with declining forage quality, leads to a preference of Brent Geese for swards with intermediate values of standing crop (Vickery & Sutherland 1992; Riddington *et al.* 1997; Hassall *et al.* 2001; chapter 5). Under undisturbed conditions the geese will cope with increasing primary production of their forage plants in spring by means of aggregation of their foraging activities in one sub-area. Through an increase of the frequency of grazing visits to one area, they are able to maintain a short, suitable sward in part of the available habitat (Spaans & Postma 2001; chapter 5). In the years without scaring on Schiermonnikoog, all grazing was concentrated on a single field by the end of May and the average number of birds on this field had increased by more than a factor two in comparison to March (chapter 5). At this site, the consumption of the major part of primary production maintained a short sward, while the vegetation grew tall in the remainder of the pastures (Figure 3.6A). An enclosure experiment at the Brent Goose reserve on Texel, demonstrated that this pattern was consistent with the hypothesis that Brent Geese have a preference for short swards. In that experiment, geese preferred patches with a short canopy over patches with a tall canopy, experimentally established using short-term enclosure in the same field (chapter 5). Without continuous grazing, the profitability of highly productive agricultural grassland as feeding habitat for Brent Geese diminishes quickly. This applied for example during the years with scaring and in the study by Boudewijn (1984).

These observations during the phase of rapid spring growth underline the importance of facilitation in maintaining the sward in a close-cropped stage, permitting efficient harvest by the geese. On the Dutch barrier island of Ameland, we observed a concentration of goose grazing towards the end of May, in pastures that were also grazed by sheep (chapter 4). Figure 3.6 illustrates the close analogy in development of the canopy for swards that are maintained by Brent Geese until May, and for ungrazed swards, at the three islands mentioned. Ungrazed pastures at each study island quickly developed a tall sward, while intensive grazing maintained a short sward. On Ameland sheep grazing assisted the Brent Geese in doing so (chapter 4). Recent grazing experiments with Brent and Barnacle Geese at salt-marsh sites on Schiermonnikoog demonstrated that Brent Geese show a strong feeding preference for swards of *Festuca rubra*,





**Figure 3.6** The seasonal development of canopy height in agricultural grass swards when continuously grazed by geese as compared to ungrazed swards. A) Schiermonnikoog spring 2000 (this study, chapter 5), B) Texel spring 2000, ungrazed plots were experimentally fenced from the beginning of March (chapter 5), C) Ameland spring 1998, ungrazed plots were left aside by the geese from April onwards; maintained plots were grazed by geese as well as sheep (chapter 4). The grey bar indicates a range of canopy heights, for which it is assumed that it can be most efficiently grazed by Brent Geese, as derived from experimental data presented in chapter 5.

previously grazed (and thereby maintained at higher forage quality) by Barnacle Geese within the same staging season (Stahl *et al.* 2001). Further exclosure experiments are called for to ascertain the presumed facilitative effect of the heavy spring grazing by Barnacle Geese on pastures preceding usage by the Brent on the same fields.

### *Habitat use on the salt marsh*

The two species of geese studied differ in their use of the salt marsh. Barnacle Geese start using the marsh earlier in the season than Brent, and are recorded in higher numbers on the high marsh. Brent Geese, on the other hand, concentrate most of their grazing on the low salt marsh (Figure 3.5). On the high marsh, Barnacle Geese mainly consume *Festuca rubra* (Prop & Deerenberg 1991), with the effect of quality enhancement of the forage through repeated grazing (Prins & Ydenberg 1985; Stahl *et al.* 2001). Nevertheless, the nitrogen content is lowest for *Festuca* in comparison to all forage species sampled (Figure 3.4C). Standing biomass and forage production, by contrast, are higher on the high marsh (Figure 3.4A & B) as compared to the low marsh. This may explain why grazing pressure by geese is higher on the high than on the low marsh in early spring.

### *Pasture and marsh as alternative foraging habitat*

It is infeasible to appoint a single parameter as main trigger for the habitat decision in staging geese. So far, we discussed the role of disturbance regimes, staging traditions and facilitative grazing by conspecifics or other herbivores and its influence on plant phenology. Differences in forage characteristics (plant availability and the nutrient mix) between the two habitat types directly interact with intake rates and can form a prime key for habitat decisions. The main forage species on the marsh (*Festuca rubra* and *Puccinellia maritima*) contained less nitrogen than the pasture grasses, and this relative difference in forage quality between habitat types even increased over time. As we measured forage quality in terms of nitrogen content only, we cannot exclude plant fibre content, amino-acid composition or contents of other nutrients in leaf tissue as parameters differentiating habitats. Our data showed that nitrogen content of salt-marsh grasses alone cannot explain the attractiveness of the marsh habitat during the years of our study. The presence of the plant species *Triglochin maritima* and *Plantago maritima* increases attractiveness of the marsh for Brent Geese. The nitrogen content of both plant species is prominent as compared to the grass species (May: *Plantago maritima* 3.6%  $\pm$  0.22 s.e., n = 7; *Triglochin maritima* 4.7%  $\pm$  0.18 s.e., n = 6) and intake rates are high for these plants (Prop & Loonen 1989; Prop 1991; Prop & Deerenberg 1991).

The overall standing biomass of food is lower on the salt marsh, and the translation of this parameter into intake rates remains to be studied in detail. Preliminary studies with captive geese did not reveal higher rates of biomass-intake for Barnacle Geese on either *Puccinellia maritima* or *Festuca rubra* swards when compared to pasture grasses,



but our first data on Brent Geese point to higher rates of intake on the marsh (Heuermann 2001). As primary production is limited on the marsh, goose numbers can only increase gradually in this habitat, following the increase in biomass production during the season. Although the pasture habitat has been largely unattractive in the past due to scaring by farmers, an early habitat switch of the majority of geese was restricted by limited forage production on the marsh. The cessation of scaring allowed an increased utilisation of agricultural grassland through the aggregation of geese in space and time, as a response to the high primary production here.

In conclusion of our analyses, we want to emphasise that the best choice between alternative staging habitats remains above all an individual choice for birds differing in their needs and prospects (e.g. concerning subsequent breeding) as well as their ability to cope with habitat characteristics (e.g. disturbance). The case study of Schiermonnikoog demonstrated that the creation of new spring foraging opportunities for geese in an agricultural habitat mainly attracted birds from other staging sites, obviously eager to explore new sites, while birds with an island pedigree kept with their traditional habitat switch to the salt marsh. The study of the repercussions of these individual decisions in terms of reproductive benefits remains duty of continued investigation during the coming years.

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## References

- Bazuin JBL, van der Wal CA (1991) Wildbeheerplan van het wildbeheer- en jachtgezelschap Schiermonnikoog. WBE, Schiermonnikoog pp. 1-24
- Boudewijn T (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl* 35: 97-105
- de Boer WF, Drent RH (1989) A matter of eating or being eaten? The breeding performance of Arctic geese and its implications for waders. *WSG Bull.* 55: 11-17
- Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anatidae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle
- Ebbinge BS, Berrevoets C, Clausen P, Ganter B, Guenther K, Koffijberg K, Mahéo M, Rowcliffe JM, St.Joseph A, Südbek P, Syroechkovski EE, Jr. (1999) Dark-bellied Brent Goose *Branta bernicla bernicla*. In: Madsen J, Cracknell G, Fox AD (eds) Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International, Wageningen. National Environmental Research Institute, Rønde, pp 284-297
- Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26: 105-113
- Fox AD, Madsen J (1997) Behavioural and distributional effects of hunting disturbance on water birds in Europe: Implications for refuge design. *J. Appl. Ecol.* 34: 1-13
- Ganter B, Prokosch P, Ebbinge BS (1997) Effects of saltmarsh loss on the dispersal and fitness parameters of Dark-bellied Brent Geese. *Aquat. Cons.* 7: 141-151
- Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* 127: 97-104
- Heuermann N (2001) Experimentally testing foraging preferences with captive brent and barnacle geese. Msc. thesis Universität Osnabrück, University of Groningen
- Kers AS, van der Brug SR, Schoen L, Bos D, Bakker JP (1998) Vegetatie kartering Oost Schiermonnikoog, 1993-1996. Report Laboratory of Plant Ecology, University of Groningen
- Koffijberg K, Voslamber B, van Winden E (1997) Ganzen en zwanen in Nederland: overzicht van pleisterplaatsen in de periode 1985-94. SOVON Vogelonderzoek, Beek-Ubbergen
- Madsen J (2001) Spring migration strategies in Pink-footed Geese *Anser brachyrhynchus* and consequences for spring fattening and fecundity. *Ardea* 89: 43-55
- Madsen J, Pihl S, Clausen P (1998) Establishing a reserve network for waterfowl in Denmark: A biological evaluation of needs and consequences. *Biol. Conserv.* 85: 241-255
- Olf H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814
- Prins HHT, Ydenberg RC (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). *Oecologia* 66: 122-125
- Prop J (1991) Food exploitation patterns by Brent Geese *Branta bernicla* during spring staging. *Ardea* 79: 331-342
- Prop J, Deerenberg C (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28
- Prop J, Loonen M (1989) Goose flocks and food exploitation: the importance of being first. *Acta XIX Congr.Int.Orn.(Ottawa)* : 1878-1887
- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153-160
- Rowcliffe JM, Watkinson AR, Sutherland WJ (2001) The depletion of algal beds by geese: a predictive model and test. *Oecologia* 127: 361-371
- Schaminée JHJ, Weeda EJ, Westhoff V (1998) De Vegetatie van Nederland. DI 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala



- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Stahl J, Rothkegel C, Drent RH (2001) Staging barnacle and brent geese versus resident brown hare: crossing the boundary between facilitation and resource competition. In: Stahl J (ed) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. University of Groningen, Groningen
- van der Meijden R (1990) Heukels' Flora van Nederland ed. 21. Wolters-Noordhoff, Groningen
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van Eerden MR (1984) Waterfowl movements in relation to food supply. In: Evans PR, Goss Custard JD, Hale WG (eds) Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge, London, pp 84-100
- van Soest PJ (1994) Nutritional Ecology of the ruminant. Cornell University Press, Ithaca (NY)
- Vickery JA, Sutherland WJ (1992) Brent geese: a conflict between conservation and agriculture. *British Crop Protection Council* 50: 187-193
- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499-508
- Zijlstra M, Loonen MJJE, van Eerden MR, Dubbeldam W (1991) The Oostvaardersplassen as a key moulting site for Greylag Geese *Anser anser* in western Europe. *Wildfowl* 42: 45-52

Young sheep on the "Nieuwlandsreid", the livestock-grazed salt marsh on Ameland  
(photo A.J. van der Graaf).





## Short and long-term facilitation of goose grazing by livestock

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### Abstract

The impact of livestock grazing on the distribution of dark-bellied Brent Geese *Branta bernicla bernicla* in the Dutch Wadden Sea during spring was studied. It is hypothesised that livestock facilitate grazing for geese on the short term (within season) as well as on the long term (over years). We measured grazing pressure by geese in areas of salt marsh and polder that were either grazed (spring grazed) or ungrazed during spring (summer grazed). Additionally, we carried out a choice experiment with captive geese to test the preference between spring-grazed and summer grazed polder swards. We furthermore compared patterns of use by geese between long-term ungrazed and grazed salt marshes. In May, there is a difference in grazing pressure by geese between polder pastures that are either grazed or ungrazed during spring. In this month, the ungrazed polder pastures are abandoned and the geese shift either to grazed polder pastures or to the salt marsh. Vegetation in the polder that had been spring-grazed had a lower canopy height and a higher tiller density than summer-grazed vegetation. Captive geese showed a clear preference for vegetation that had been grazed by sheep during spring over ungrazed vegetation.

Goose grazing pressure was negatively correlated to canopy height both on the polder and on the salt marsh. Marshes that were intensively grazed by livestock generally had higher grazing pressure by geese than long-term ungrazed or extensively grazed salt marshes, within the plant communities dominated by *Festuca rubra* and *Puccinellia maritima*.

## Introduction

Salt marshes and agricultural pastures in embanked (polder) areas in the Dutch Wadden Sea are important spring-staging areas for Brent *Branta bernicla bernicla* and Barnacle Geese *Branta leucopsis* (Koffijberg *et al.* 1997; Madsen *et al.* 1999). The birds traditionally shift between these two main habitats as the season progresses (Prins & Ydenberg 1985; Vickery *et al.* 1995; chapter 3). The feeding conditions during spring are of crucial importance for reproduction at the Arctic breeding sites, as breeding success depends upon the rate of fattening during spring (Ebbinge & Spaans 1995). Management of the coastal areas by grazing with livestock during summer affects the feeding conditions for Brent Geese in winter (Sutherland & Allport 1994; Vickery *et al.* 1994), and on salt marshes long-term effects of grazing with livestock on habitat choice were observed for Barnacle Geese (Aerts *et al.* 1996). In this study, we will examine to what extent livestock grazing affects the habitat use by geese within a single spring season, as well as on the long term. Our focus is on the Brent Goose, but Brent and Barnacle Geese co-occur in some of our study areas in early spring and we are not always able to distinguish between the two species.

### *Within-season grazing facilitation*

On the island of Schiermonnikoog, Brent Geese shift between agricultural pasture and the salt marsh in mid-April. Traditionally, the shift is explained by a relative change in quality of the vegetation on both the polder and the salt marsh. The onset of spring growth of the vegetation is later on the salt marsh compared to the polder. Therefore, in mid-April the quality and biomass of the salt-marsh grasses rises, whereas the polder grasses decrease in quality (Boudewijn 1984; Prins & Ydenberg 1985; McKay *et al.* 1994) and the swards get so tall that the geese may even get problems handling it (chapter 5). There appears to be a limit to the number of geese on the salt marsh of Schiermonnikoog, as the spring-staging population on this island has remained stable (at about 2-3,000 animals) for over 25 years, despite a rapid increase in total Brent Goose numbers in the Netherlands since 1980 (van der Wal *et al.* 2000). On the neighbouring island of Ameland, however, the spring-staging population of Brent Geese has continued to increase the last 25 years from about 4,000 to about 20,000 birds, most of which remain foraging in the polder the entire spring period (Koffijberg *et al.* 1997; Kersten *et al.* 1997). The question rises why it is possible for the geese to remain on the polder throughout April and May on Ameland, whereas the polder is abandoned during these months on Schiermonnikoog. We hypothesise that an important difference between the islands lies in the grazing management. On Schiermonnikoog cattle graze the polder from May. These cattle-grazed pastures thus remain ungrazed throughout most of the spring-staging period of the geese. In contrast, on Ameland part of the polder is grazed by sheep all year round. We suppose that the grazing by sheep maintains the grass sward at a height and quality that is preferred by the geese (Hassall *et al.* 2001, compare Sutherland & Allport 1994). This process of one herbivore creating





attractive swards for other herbivores, is known as grazing facilitation. The most well-known example of grazing facilitation is the enhancement of plant production caused by the grazing of wildebeest in the Serengeti (McNaughton 1976; McNaughton 1979; McNaughton 1984; McNaughton 1985). In general grazing causes rapid turnover of plant material as plants produce fresh new leaves or tillers of a higher quality compared to the old leaves and reduces the standing dead and litter biomass (Prins *et al.* 1980; Grant *et al.* 1981; Jones *et al.* 1982; Ruess *et al.* 1983; Cargill & Jefferies 1984; Parsons & Penning 1988; Madsen 1989; Summers 1990; Coughenour 1991; Gauthier *et al.* 1995; Rowcliffe *et al.* 1995; Post & Klein 1996; Fox *et al.* 1998; Mayhew & Houston 1999).

### *Grazing facilitation over multiple years*

The process of facilitation is relevant at short time-scales (within growing seasons), but is important at longer time-scales as well. Livestock grazing by cattle, for example, strongly affects the vegetation composition on salt marshes in Europe, with serious consequences for geese. Under ungrazed conditions, salt-marsh vegetation changes due to natural succession (Roozen & Westhoff 1985; Jensen 1985; Bazely & Jefferies 1986; Adam 1990; Westhoff & van Oosten 1991; Bakker *et al.* 1993; Kiehl *et al.* 2000) and tall plant species that are unpalatable to geese ultimately dominate the marsh (Jensen 1985; Olff *et al.* 1997; van Wijnen & Bakker 1997). Livestock grazing favours short palatable grasses such as *Puccinellia maritima* on the lower parts of the salt marsh and *Festuca rubra* on the high marsh (Dijkema 1983a; Kiehl *et al.* 1996; Bakker *et al.* 2002). Results from several studies suggest that Brent and Barnacle Geese prefer these intensively grazed areas over ungrazed areas (Ebbinge & Boudewijn 1984; Aerts *et al.* 1996; Stock & Hofeditz 2000).

### *Hypotheses*

To test our hypothesis that livestock grazing facilitates goose grazing within one spring season, we compared goose grazing pressure and vegetation parameters for spring- and summer-grazed sites on both the polder and salt marsh of Ameland and Schiermonnikoog. Secondly, we compared grazing pressure by geese and vegetation parameters between marshes at four different locations, that were intensively grazed by livestock in summer, extensively grazed or long-term ungrazed, to test the hypothesis that livestock grazing facilitates goose grazing in the long term. Finally, a complementary approach was taken by setting up a small-scale preference experiment on Schiermonnikoog, in which captive geese were offered a choice between patches either ungrazed or previously grazed by sheep.

## Methods

### Study Area

This study was performed at four study sites in the Dutch Waddensea (Fig. 1); the islands of Ameland (53°27'N, 5°50'E) and Schiermonnikoog (53°30'N, 6°10'E), and two sites at the mainland coast referred to as Noord Friesland (53°23'N, 5°50'E) and Groninger Coast (53°25'N, 6°25'E).

Both islands have a polder and a salt marsh, part of which is grazed. The embanked polder areas contain intensively grazed and fertilised (up to 400 kg N.ha<sup>-1</sup>.yr<sup>-1</sup>) pasture, protected by a seawall. The vegetation consists mainly of agricultural grass species such as *Lolium perenne* and *Poa* spp. The polder of Ameland (2000 ha) is much larger than the polder of Schiermonnikoog (265 ha). Only the eastern part of the polder of Ameland (240 ha) was used for this study. The polder of Schiermonnikoog is grazed by cattle between May and November, on the polder of Ameland there is additional sheep grazing year-round. In both polder areas, farmers do an effort to scare geese from their land. The grazed salt marsh of Ameland consists of a part (300 ha) that is spring-grazed by sheep from mid-April onwards and from the end of May onwards also by cattle, and a second part (50 ha) that is only summer-grazed by cattle. Both areas are grazed at a stocking rate of 0.5 Livestock Unit per hectare (LU.ha<sup>-1</sup>). One Livestock Unit refers to one adult cow or 10 sheep. The spring-grazed part is lightly fertilised (100 kg N.ha<sup>-1</sup>.yr<sup>-1</sup>). The vegetation on both sites is a mixture of *Puccinellia maritima* and *Festuca rubra*, the sites are only separated by a gully. The long-term ungrazed salt marsh of Ameland (100 ha) is less than 70 years old (Westhoff & van Oosten 1991). The grazed salt marsh of Schiermonnikoog (185 ha) is only summer-grazed by cattle at 0.5 LU.ha<sup>-1</sup>, from the end of May onwards and is unfertilised. The long-term ungrazed salt marsh of Schiermonnikoog (1450 ha) is characterised by an age gradient from West (ca. 100 years old) to East (still growing). In addition to 2,000 Brent Geese, about 6,000 Barnacle Geese utilise the marsh on Schiermonnikoog. On Ameland about 20,000 Brent Geese stage in spring, whereas the number of Barnacle Geese is negligible. Brent Geese leave the spring feeding grounds in late May (Ebbinge *et al.* 1999), while the majority of Barnacle Geese departs during April (Ganter *et al.* 1999).

To compare marshes with different livestock grazing regimes, we additionally collected data from two salt-marsh sites at the Dutch mainland coast, Noord Friesland and Groninger Coast (Figure 4.1). The marshes we compare within these study sites, differ from each other in stocking rate and will be referred to as either extensively or intensively grazed. Noord Friesland is used by about 24,000 Brent Geese and 36,000 Barnacle Geese in spring. The majority of the marsh (1400 ha) is intensively grazed with cattle and sheep during summer at 1-2 LU.ha<sup>-1</sup>. About 300 hectares of the marsh at Noord Friesland are extensively grazed at 0.4 LU.ha<sup>-1</sup>. Adjacent to the marsh there are also large areas (1000 ha) of agricultural grass lands that are occasionally flooded during winter (summer polders), which are heavily utilised by Barnacle, but hardly by Brent Geese (Engelmoer 1998). The Groninger Coast is used by about 3,800 Brent and

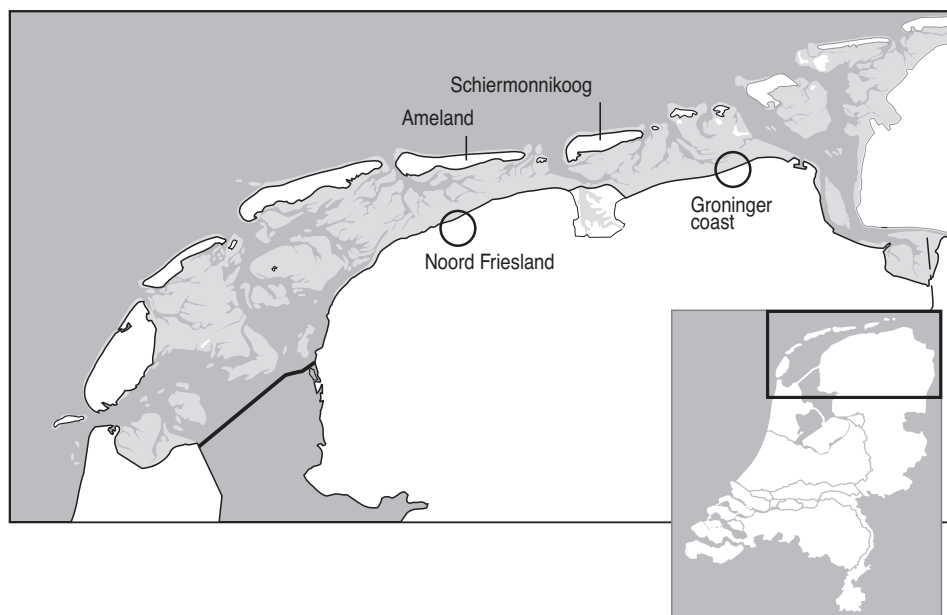


Figure 4.1 Location of the study sites

4,500 Barnacle Geese in spring. The marsh (1600 ha) is grazed with cattle, sheep or horses and along the entire coast intensively (about  $1 \text{ LU} \cdot \text{ha}^{-1}$ ), extensively (about  $0.5 \text{ LU} \cdot \text{ha}^{-1}$ ) and ungrazed marshes alternate each other.

### Site selection

In order to compare effects of livestock grazing on the distribution of geese, we selected sites with different grazing management in which dropping counts and vegetation measurements were performed along fixed transects. On the polder areas, pastures were classified as spring-grazed if any (sheep) grazing had been going on during the spring-staging period, and summer-grazed when they had not been grazed during this period (March-May). In the polder of Ameland six spring- and six summer-grazed pastures were selected. In the polder of Schiermonnikoog only five summer-grazed pastures were selected, as no livestock grazing occurred here before the end of the spring-staging period. On the salt marsh of Ameland we sampled in both parts of the grazed salt marsh, the part that is only grazed by cattle and thus remains ungrazed during the spring-staging season of the geese, and the part that is also grazed by sheep and thus grazed during the spring-staging season. We will refer to these parts as summer-grazed and spring-grazed, respectively. Finally we established transects in the *Festuca rubra* community of the long term ungrazed salt marsh of Ameland ( $n = 6$ ), the *Puccinellia maritima* and *Festuca rubra* communities of the summer-grazed ( $n = 2 \times 6$ ) and

the long-term ungrazed (age 10-50 years,  $n = 2 \times 6$ ) salt marshes of Schiermonnikoog, the *Puccinellia maritima* and *Festuca rubra* communities of the intensively grazed ( $n = 2 \times 6$ ) and the extensively grazed ( $n = 2 \times 6$ ) salt marshes of the Groningen Coast and the *Puccinellia* community of the intensively grazed ( $n = 9$ ) and the extensively grazed ( $n = 5$ ) salt marshes of Noord Friesland.

### *Dropping counts*

At each selected site we established one transect. Each transect consisted of five plots (4 m<sup>2</sup>), with a distance between plots of about 10 meters. From the beginning of March until the end of May 1998, goose droppings were counted and removed from all plots weekly. The number of droppings was used to calculate the goose grazing pressure as the total number of droppings m<sup>-2</sup>.day<sup>-1</sup>.

### *Vegetation parameters*

In May 1998 vegetation composition was assessed, applying visual cover estimates of dead material, bare ground and plant species in every plot. Tiller density was measured in April 1998 on the salt marsh and polder of Ameland. Tiller density was measured by counting the number of tillers in a 5 cm by 5 cm area, repeated 10 times at random within each transect. Canopy height was measured monthly, by dropping a polystyrene disk (24 g, Ø20 cm) along a calibrated sward stick. This was randomly repeated six times in every plot. At the end of April, samples of leaf tips of forage grasses were taken from every transect on Ameland, to measure forage quality. The samples were washed, air-dried at 70°C and nitrogen content was measured using an automated CNHS-analyser (Interscience EA 1110). Nomenclature of species follows van der Meijden (1990).

Information on overall vegetation composition of salt marshes, in terms of the cover of plant communities for the different grazing regimes, was derived from GIS vegetation maps. These maps refer to the same marshes in which our transects are located. For comparison we additionally included a 110 ha large stretch of marsh at Noord Friesland, which has been ungrazed for more than 20 years. The maps, kindly provided by Rijkswaterstaat (Monitoring programme, Ministry of Transport and Public Affairs), were all derived from interpretation of aerial photographs in combination with a field survey. The scale of mapping is 1:10,000 and the date of mapping varies between 1988 and 1995. The legend units for each map were aggregated to plant communities at the level of the association following Schaminée *et al.* (1998).

### *Choice experiment*

In spring 1999 a choice experiment with a pair of captive Brent Geese was carried out, to test the preference for vegetation that was previously grazed by sheep or left ungrazed. The experiment was carried out on the polder of Schiermonnikoog, where the



pastures usually are only grazed in summer by cattle. An enclosed area (about 1 ha) of polder pasture was grazed by 9 sheep and 5 lambs from 15 March onwards, while the surrounding sward remained ungrazed during spring. The stocking rate of sheep was gradually increased over the season by reducing the area of the enclosure to maintain sward height at 3-5 cm. During the period from April 15<sup>th</sup> until May 21<sup>st</sup>, 11 feeding trials (each lasting 3 hrs) were performed with a pair of captive Brent Geese that was offered the choice between feeding in grazed or ungrazed swards. For this purpose, a cage of nylon netting (4 by 4 m) was placed on the vegetation, so that half of the cage included previously ungrazed swards and the other half the swards recently grazed by sheep. Prior to each feeding trial canopy height and nitrogen content of leaf tips was measured as described above. The geese were observed from a hide for a minimum of 9 bouts of 10 minutes and time spent foraging in each part of the cage was recorded for both geese. At the end of the trial all droppings were counted for each treatment. The birds were moved to a new cage for each new trial. Preference was calculated as the percentage of time the two geese were foraging in each treatment as related to the total time spent foraging. As it is likely that the geese were not acting independently of one another, the results were pooled in the analysis. Observation bouts of 10 with no feeding at all were discarded and during each trial the geese forage at least 10% of the time. The geese had ad libitum access to fresh water, which was placed in a tray in the middle of the cage. When not used in the feeding trials the geese were maintained at polder swards on site and supplementary fed with waterfowl pellets (Anseres II). The experiments with geese were approved by the Dutch commission for use of experimental animals (DEC), licence nr. BG07697/2382.

### *Statistics*

All parameters met the statistical assumption of normality (Kolmogorov-Smirnov test:  $P > 0.05$ ). For all comparisons, except canopy height and goose grazing pressure, an ANOVA followed by a Scheffé's post-hoc test was used. Canopy height on each transect was calculated as the mean of the 30 measurements per transect. Canopy height and grazing pressure, data that were collected each month and each week, respectively, were analysed using Repeated Measurements ANOVA. To improve the equality of variances a square-root transformation,  $X' = \sqrt{(X + 0.5)}$ , was conducted for grazing pressure and canopy height (Zar 1996). An arcsine-square-root transformation was conducted for percentage values (Zar 1996). Correlations were determined using Pearson correlation. All tests were carried out using SPSS 10.1 for Windows. Standard errors are given unless noted otherwise.

# Results

## Polder

The difference between the summer- and spring-grazed areas is most pronounced in May; the summer grazed polders of Schiermonnikoog and Ameland, which are ungrazed during spring, are abandoned whereas goose grazing pressure rises on the spring-grazed areas on Ameland (Figure 4.2). Only in this month there is a significant difference in goose grazing pressure between the spring-grazed and the summer-grazed polder of Ameland (Table 4.1, Repeated Measurements Anova with three repetitions, week 19-21,  $F_{1,10} = 13.8$ ,  $P = 0.04$ ). In fact, within the pastures that we sampled, all goose grazing in the polder was concentrated on 4 spring-grazed pastures, while 2 spring-grazed pastures and 6 summer-grazed pastures were not visited by the geese in May. This proportion is significantly different from a random choice of 4 pastures out of 12 (contingency test  $\chi^2_c = 5.06$ ,  $P < 0.05$ ).

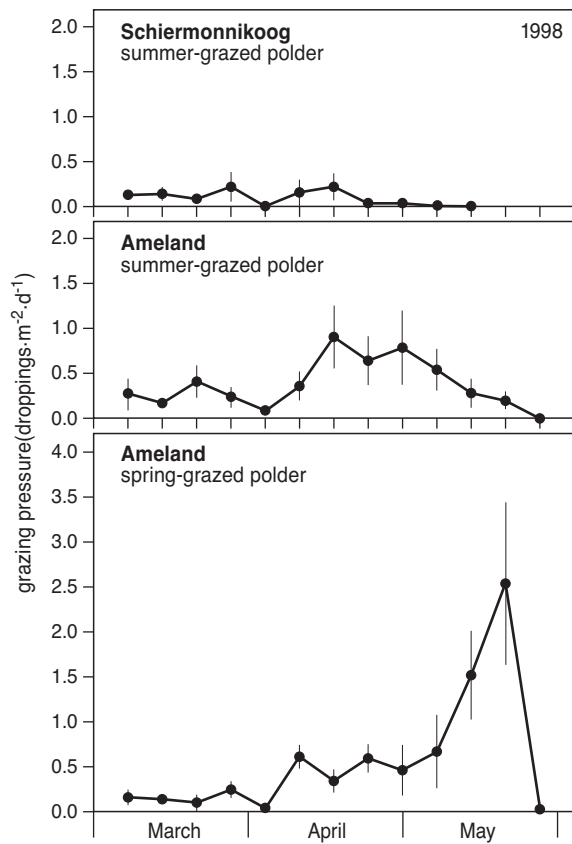


Figure 4.2 Goose grazing pressure for different grazing regimes in the polder of Schiermonnikoog and Ameland over the spring season of 1998 (mean  $\pm$  SE).



**Table 4.1** Vegetation and grazing parameters (mean  $\pm$  SE) for the polders of Ameland. Values for Schiermonnikoog are given for comparison, but differences are not tested. Significant differences ( $P < 0.05$ ) between values for spring- and summer-grazed areas in the polder of Ameland are indicated with different letters. Spring averages are for the months of March until May.

		Grazing Management Polder					
		Ameland summer-grazed		Ameland spring-grazed		Schiermonnikoog summer-grazed	
		mean	se	mean	se	mean	se
Spring goose grazing pressure (no. droppings.m <sup>-2</sup> .day <sup>-1</sup> )							
	Spring average	0.40	0.11 a	0.62	0.17 a	0.10	0.05
	May	0.34	0.14 a	1.58	0.51 b	0.008	0.05
Canopy height (cm)							
	Spring average	6.66	1.02 a	4.09	0.66 a*	6.10	0.32
	May	12.64	2.80 a	6.53	1.91 a	9.9	1.6
						(n=3)	
Tiller density (10 <sup>3</sup> tillers.m <sup>-2</sup> )		14.88	1.67 a	17.85	0.81 a		
Live material (%)		99.5	0.28 a	98.9	0.45 a		
Nitrogen content (% , end of April)		4.67	0.24 a	3.97	0.14 b	4.50	0.59

\*  $P = 0.055$

On average over the entire spring staging season of 1998 there were no significant differences in canopy height and tiller density between the spring- and summer-grazed polder of Ameland (Table 4.1). For nitrogen content we found a higher value in summer-grazed than in spring-grazed swards. We found a significant negative correlation between average canopy height and average goose grazing pressure on the polder of Ameland over the whole season as well as in May (Pearson  $r = -0.69$ ,  $P = 0.013$ ,  $n = 12$  and Pearson  $r = -0.68$ ,  $P = 0.014$ ,  $n = 12$ ).

### Choice experiment

Our grazing treatment with sheep had a significant influence on canopy height and biomass in the choice experiment. Canopy height and biomass were highly correlated (Pearson  $r = 0.95$ ,  $n = 22$ ,  $P < 0.001$ ). Canopy height increased significantly over time from 3.4 to 23 cm in the ungrazed treatment (ANCOVA, interaction day x treatment,  $F_{1,18} = 67.5$ ,  $P < 0.001$ ) and remained constant at  $4 \pm 0.1$  cm in the grazed vegetation. The nitrogen content of the sward declined over time (linear regression,  $F_{1,18} = 19.1$ ,  $P < 0.001$ ), irrespective of the treatment (linear regression,  $F_{1,18} = 0.079$ , n.s.). The geese had a clear preference for grazed over ungrazed vegetation, as measured with the observational data (T-test,  $t = 5.4$ ,  $P < 0.001$ ) or the dropping-counts (T-test,  $t = 4.5$ ,  $P = 0.001$ ). The geese foraged approximately 80% of the time on the grazed vegetation and only 20% of the time on the ungrazed vegetation, there was no significant effect of the time of testing through the season. Percentage foraging time



did not differ between the two geese (mean = 32.7%, paired T-test,  $t = -1.0$ , n.s.) and the geese also did not differ in preference for any of the treatments (contingency test,  $\chi^2 = 1.04$ , n.s.).

### Salt marsh

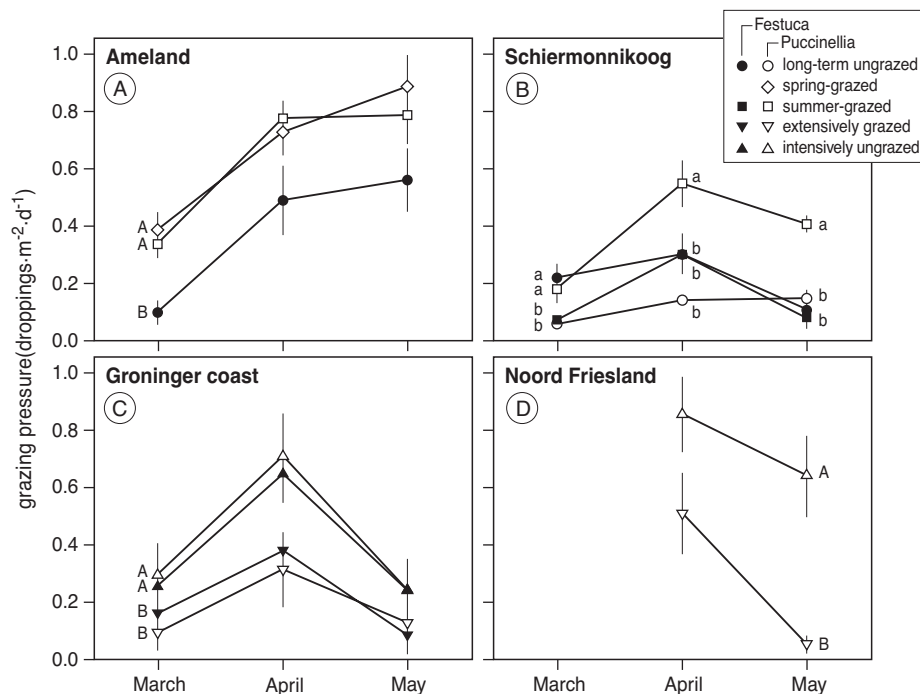
On Ameland canopy height was significantly lower and tiller density significantly higher on the spring-grazed part of the salt marsh than on the summer-grazed part, whereas no differences were found in vegetation composition (Table 4.2) between those two parts of the grazed marsh. Grazing pressure increased continually during spring (Figure 4.3), with no difference between the spring-grazed and the summer-grazed part.

Goose grazing pressure on the salt marshes we sampled increased for each grazing regime at each location during the months of March and April (Figure 4.3). In contrast, in May grazing pressure continues to rise on the marshes of Ameland, whereas it decreases at all other locations after the Barnacle Geese left for their Arctic breeding grounds. At each site, there are significant differences between livestock grazing regimes in terms of goose grazing pressure and vegetation parameters (Tables 4.2 - 4.5): Extensively grazed marshes at the Groninger Coast have a lower goose grazing pressure than intensively grazed marshes (Figure 4.3, Repeated measurements ANOVA grazing regime:  $F_{1,23} = 5.6$ ,  $P = 0.026$ ) and data from Noord Friesland give the same result (Figure 4.3, Repeated Measurements ANOVA grazing regime,  $F_{1,25} = 10.6$ ,  $P = 0.003$ ). The long-term ungrazed marsh on Ameland has a lower goose grazing pressure than both parts of the grazed marsh, although this comparison is confounded by differences in fertilisation and plant community. At Schiermonnikoog, the effect of grazing regime was significant (Repeated measures ANOVA grazing regime,  $F_{1,20} = 5.8$ ,  $P=0.025$ ), and

**Table 4.2** Vegetation and grazing parameters (mean  $\pm$  SE) for the grazed and long-term ungrazed salt marsh of Ameland. Significant differences ( $P < 0.05$ ) are indicated with different letters. The category edible grasses includes *Puccinellia maritima*, *Festuca rubra*, *Juncus gerardi* and *Poa* spp. Tall plant species include *Elymus atherica*, *Artemisia maritima* and *Atriplex portulacoides*.

	Ameland summer-grazed		Ameland spring-grazed		Ameland long-term ungrazed	
	mean	se	mean	se	mean	se
Spring goose grazing pressure (no. droppings $m^{-2}.day^{-1}$ )	0.63	0.06 <sup>a</sup>	0.65	0.06 <sup>a</sup>	0.37	0.07 <sup>b</sup>
Canopy height (cm)	3.54	0.20 <sup>a</sup>	1.59	0.34 <sup>b</sup>	5.61	0.86 <sup>c</sup>
Tiller density ( $10^3$ tillers. $m^{-2}$ )	23.17	1.40 <sup>a</sup>	32.51	3.28 <sup>b</sup>	8.08	0.86 <sup>c</sup>
Cover of live material (%)	80.5	1.89 <sup>a</sup>	84.1	1.07 <sup>a</sup>	60.2	2.59 <sup>b</sup>
Cover of edible grasses (%)	64.9	5.40 <sup>a</sup>	49.67	10.58 <sup>a</sup>	45.0	4.13 <sup>a</sup>
Cover of tall plant species (%)	0.07	0.04 <sup>a</sup>	0.01	0.01 <sup>a</sup>	0.06	0.03 <sup>a</sup>





**Figure 4.3** Comparison of goose grazing pressure on *Puccinellia* and *Festuca* community at different salt-marsh sites along the Dutch coast for different livestock-grazing management regimes; A) Ameland, B) Schiermonnikoog, C) Groninger Coast, D) Noord Friesland. Significant effects of grazing treatment within each study area (Repeated measurements ANOVA) are indicated using different capital letters. On Schiermonnikoog a significant interaction was found, and significant differences are therefore indicated per month with lower case letters.

the long-term ungrazed marsh had significant lower grazing pressure than the summer-grazed marsh for the *Puccinellia* community for each month (Figure 4.3). However, there was also a significant interaction between plant community and grazing regime (Repeated measures ANOVA plant community x grazing regime,  $F_{1,20} = 33.4$ ,  $P < 0.001$ ), caused by the fact that the grazing pressure in March on the *Festuca* community was higher in long-term ungrazed marsh than in the grazed salt marsh. Canopy height and goose grazing pressure are negatively correlated at the transect-level on the salt marsh of Ameland (Pearson  $r = -0.71$ ,  $P = 0.001$ ,  $n = 18$ ), Noord Friesland (Pearson  $r = -0.53$ ,  $P = 0.04$ ,  $n = 14$ ) and the Groningen Coast (Pearson  $r = -0.66$ ,  $P < 0.001$ ,  $n = 26$ ), while on Schiermonnikoog this overall correlation was not significant (Pearson  $r = -0.29$ , n.s.,  $n = 24$ ). With reduced stocking rates of livestock, or without livestock grazing, the vegetation develops a taller canopy in both plant communities in each of the study areas, and in many of the comparisons the effect is also noticeable in a lower cover of plant species that are palatable for geese (Tables 4.2 - 4.5).

The differences in vegetation composition between marshes with different grazing regime are also found at the level of plant communities. From the vegetation maps it appeared that on Ameland and Noord Friesland, a smaller part of the long-term ungrazed marsh consists of plant communities with short vegetation (*Festucetum*, *Puccinellietum* and *Juncetum*, together 60% short vegetation) than on the grazed marsh (> 95% short vegetation; Table 4.6). At the older long-term ungrazed salt marsh of Schiermonnikoog less than 30% of the area consists of plant communities suitable for geese, compared to 50% for the grazed marsh and 76% for the young long-term ungrazed marsh.

**Table 4.3** Vegetation parameters (mean  $\pm$  SE) per livestock grazing regime for the salt marsh of Schiermonnikoog. Significant differences ( $P < 0.05$ ) are indicated with different letters. The category edible grasses includes *Puccinellia maritima*, *Festuca rubra*, *Juncus gerardi* and *Poa* spp. Tall plant species include *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides*.

	<i>Puccinellia</i>				<i>Festuca</i>			
	Grazed		Long-term ungrazed		Grazed		Long-term ungrazed	
	mean	se	mean	se	mean	se	mean	se
Spring goose grazing pressure (no. droppings m <sup>-2</sup> .day <sup>-1</sup> )	0.38	0.03 <sup>a</sup>	0.11	0.01 <sup>b</sup>	0.15	0.04 <sup>b</sup>	0.21	0.02 <sup>b</sup>
Canopy height (cm)	2.8	0.1 <sup>a</sup>	5.7	0.2 <sup>b</sup>	3.7	0.1 <sup>a</sup>	7.3	0.3 <sup>b</sup>
Tiller density (no. 25 cm <sup>-2</sup> )	47.9	6.2 <sup>a</sup>	17.1	2.7 <sup>b</sup>	69.7	6.4 <sup>a</sup>	40.9	3.2 <sup>b</sup>
Cover edible grasses (%)	47.0	4.6 <sup>a</sup>	5.7	1.0 <sup>b</sup>	80.3	1.7 <sup>a</sup>	57.0	4.8 <sup>b</sup>
Cover of tall plant species (%)	1.6	0.5 <sup>a</sup>	2.8	1.0 <sup>a</sup>	2.9	0.7 <sup>a</sup>	24.2	6.2 <sup>b</sup>
Nitrogen content	3.5	0.2 <sup>a</sup>	3.4	0.0 <sup>a</sup>	2.5	0.2 <sup>a</sup>	2.4	0.1 <sup>a</sup>

**Table 4.4** Vegetation and grazing parameters (mean  $\pm$  SE) per livestock grazing regime for the *Puccinellia*-dominated salt marsh of Noord Friesland. Significant differences ( $P < 0.05$ ) are indicated with different letters. The category edible grasses includes *Puccinellia maritima*, *Festuca rubra*, *Juncus gerardi* and *Poa* spp. Edible plants include all edible grasses and *Plantago maritima* and *Triglochin maritima*. Tall plant species include *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides*.

	Intensively grazed		Extensively grazed	
	mean	se	mean	se
Spring goose grazing pressure (no. droppings m <sup>-2</sup> .day <sup>-1</sup> )	0.8	0.1 <sup>a</sup>	0.3	0.1 <sup>b</sup>
Canopy height (cm)	4.2	0.4 <sup>a</sup>	17.1	4.8 <sup>b</sup>
Cover edible grasses (%)	57.5	6.8 <sup>a</sup>	49.8	4.9 <sup>a</sup>
Cover edible plants (%)	80.8	4.2 <sup>a</sup>	49.8	4.9 <sup>b</sup>
Cover of tall plant species (%)	2.7	0.6 <sup>a</sup>	12.2	10.3 <sup>a</sup>



**Table 4.5** Vegetation and grazing parameters (mean  $\pm$  SE) per livestock grazing regime for the salt marsh of Groningen Coast. Significant differences ( $P < 0.05$ ) are indicated with different letters. The category edible grasses includes *Puccinellia maritima*, *Festuca rubra*, *Juncus gerardi* and *Poa* spp. Tall plant species include *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides*..

	<i>Puccinellia</i>				<i>Festuca</i>			
	Intensively Grazed		Extensively Grazed		Intensively Grazed		Extensively Grazed	
	mean	se	mean	se	mean	se	mean	se
Spring goose grazing pressure (no. droppings m <sup>-2</sup> .day <sup>-1</sup> )	0.4	0.1 <sup>a</sup>	0.2	0.1 <sup>b</sup>	0.4	0.1 <sup>a</sup>	0.2	0.1 <sup>b</sup>
Canopy height (cm)	4.3	0.6 <sup>a</sup>	9.8	1.1 <sup>b</sup>	4.5	0.6 <sup>a</sup>	6.6	0.6 <sup>b</sup>
Cover edible grasses (%)	48.3	2.1 <sup>a</sup>	45.3	3.3 <sup>a</sup>	52.8	3.2 <sup>a</sup>	57.2	1.9 <sup>a</sup>
Cover of tall plant species (%)	6.1	0.9 <sup>a</sup>	19.8	3.7 <sup>b</sup>	8.6	2.2 <sup>a</sup>	15.4	2.2 <sup>b</sup>

**Table 4.6** Cover of plant communities for different livestock grazing regimes above the pioneer zone on the salt marshes of Ameland, Schiermonnikoog and Noord Friesland (in percentages). Communities that are especially relevant for geese are indicated with an asterix. Tall vegetation refers to the sum of the cover of plant communities with a tall canopy. Short vegetation is defined by the combined cover of Festucetum, Puccinellietum and Juncetum. Data are derived from vegetation maps.

Location	Grazing regime	Age	Puccinellietum*	Festucetum *	Juncetum	Atriplex Elytrichietum	Artemisietum	Halimionetum	Tall vegetation	Short vegetation
Ameland	Grazed	Old	7	92	0	2	0	0	2	98
	Ungrazed	Young	17	43	0	38	2	0	40	60
Schiermonnikoog	Grazed	Old	5	22	22	26	21	3	50	50
	Ungrazed	Old	9	8	13	37	19	14	71	29
	Ungrazed	Inter	10	19	20	18	19	13	51	49
	Ungrazed	Young	52	20	4	9	4	10	24	76
Noord Friesland	Grazed		87	3	6	2	3	0	5	95
	Extensively grazed		67	14	14	4	0	2	6	94
	Ungrazed		60	0	0	28	0	12	40	60

## Discussion

### *Within season facilitative effects of livestock*

Our data from the polder of Ameland and from the choice experiment suggest that, towards the end of spring, geese prefer vegetation that has previously been grazed. In May, spring-grazed swards in the polder of Ameland were lower in canopy height and higher in tiller density than swards that had been ungrazed during spring, however, these differences were not significant (Table 4.1). For nitrogen content we even found the opposite of our hypothesis: nitrogen content was higher in the summer-grazed areas. However, in this comparison we used the six pastures that had been spring grazed, but two of these pastures were not visited by the geese in May. When the two spring-grazed areas that were not visited by geese in May are excluded from the analysis, there is a significant difference in canopy height in May (summer-grazed mean  $\pm$  SE =  $12.64 \pm 2.80$ , spring-grazed =  $3.86 \pm 0.15$ ,  $t_8 = 2.927$ ,  $P = 0.019$ ) and no difference in nitrogen content (summer-grazed mean  $\pm$  SE =  $4.67 \pm 0.24$ , spring-grazed =  $4.05 \pm 0.18$ ,  $t_8 = 1.842$ ,  $P = 0.103$ ). We also observed no effect of previous grazing on nitrogen content in the choice experiment on the polder of Schiermonnikoog in 1999. The observed patch choice of the captive geese in the grazing experiment is consistent, however, with data from previous studies showing that geese discard tall, ungrazed swards (Summers & Critchley 1990; Vickery & Sutherland 1992; Riddington *et al.* 1997), as such swards in general are characterised by higher fibre content (Boudewijn 1984; Demment & van Soest 1985), lower nitrogen concentration (Hassall *et al.* 2001) and a lower tiller density (Grant *et al.* 1981; Jones *et al.* 1982; McNaughton 1984; Belsky 1986; Parsons & Penning 1988; Vickery *et al.* 1994). Besides effects of forage maturation on food quality, goose intake rates of biomass can become depressed at higher levels of canopy height due to problems with handling the long leaves (for Brent Geese see chapter 5; for Wigeon *Anas penelope* see Durant 2001). In addition, increased levels of dead biomass could depress the intake rate of biomass at higher levels of standing crop (van der Wal *et al.* 1998), but this effect is negligible in intensively managed agricultural swards where the amount of dead biomass is small. Furthermore, taller swards may increase the costs of locomotion or decrease predator detection. Over spring, primary production is increasing rapidly and towards the end of the spring-staging period of the geese the differences between spring-grazed and summer-grazed swards will become exceedingly pronounced. We propose this as reason for a high goose grazing pressure in sheep-grazed polder swards in May on Ameland, whereas it was negligible in swards that had been ungrazed during spring on Ameland, Schiermonnikoog or Noord Friesland (Figure 4.2) in 1998. Taking the preference experiment on Schiermonnikoog as an additional line of evidence, we can conclude that, within a growing season, livestock facilitates goose grazing.



### *Within season facilitative effects of goose grazing*

Even in the absence of livestock, grazing facilitation by geese and other herbivorous wildfowl can be observed. In the Hudson Bay Area (Canada) Lesser Snow Geese *Chen caerulescens caerulescens* enhance production and quality of salt-marsh vegetation through increased nitrogen cycling mediated by faeces deposition (Cargill & Jefferies 1984; Bazely & Jefferies 1985; Hik & Jefferies 1990). Fox *et al.* (1998) showed that spring-grazing Greenland White-fronted Geese *Anser albifrons flavirostris* improved nitrogen content of *Phleum pratense* and the amount of tissue available for geese, excluding an effect of faeces. Also Wigeon were found to increase protein content and quality (Mayhew & Houston 1999). Different studies suggest that herbivorous birds adopt a rotational grazing strategy, returning to a previously grazed spot when the yield in terms of biomass or protein content is highest (Prins *et al.* 1980; Prop 1991; Rowcliffe *et al.* 1995; Drent & van der Wal 1999; Mayhew & Houston 1999). However, Hutchings & Gordon (2001) question whether the observed grazing pattern is a strategy or merely a consequence of short-term individual decisions. Also in polder areas in the Netherlands, geese were shown to be able to maintain a suitable sward by repeated grazing. The Brent Goose reserve of Zeeburg (100 ha, Texel, 53°05'N, 4°50'E) consists of intensively managed agricultural pastures and supports about 10,000 geese during winter and spring until the second half of May. In Zeeburg grazing pressure by Brent Geese depends on primary production and the geese concentrate their grazing in a restricted area, abandoning more and more fields as the spring season progresses (Spaans & Postma 2001). This concentration of grazing on a restricted area when levels of primary production increase is of crucial importance for maintaining a short and suitable sward. Experiments with exclosures in pastures that were intensively utilised by geese in this reserve confirmed that temporarily ungrazed patches (> 4 - 8 weeks) get abandoned (chapter 5). At the time of our study, on both Ameland and Schiermonnikoog the geese were actively chased away by farmers when foraging on their land, thus keeping the geese from concentrating in one area and maintaining the sward in a short condition.

Between the spring- and summer-grazed parts of the salt marsh on Ameland we found differences in canopy height and tiller density, but no difference in vegetation composition or goose grazing pressure. This might be related to a difference between salt marsh and polder in the level of primary production, which is lower on the salt marsh compared to agricultural pastures, due to differences in fertilisation, water availability and salt stress. In combination with lower levels of disturbance on the salt marsh, the geese may be able to cope with the primary production themselves, and to maintain a suitable sward by intensifying their grazing pressure over the course of the season (Figure 4.3).

### *Long-term effects of livestock grazing on salt marshes*

In the absence of livestock grazing, natural succession leads to changes in vegetation composition (Table 4.3 - 4.6; Adam 1990; Olff *et al.* 1997) and grazing pressure by geese (Figure 4.3; Aerts *et al.* 1996). In our comparison of grazing regimes we have sampled plant communities that are known to be utilised by geese, the *Puccinellietum* and the *Festucetum*. Even within these communities differences in species composition can be pronounced. Long-term ungrazed marsh develops a taller sward and often has higher cover of plant species that are unpalatable for geese, whereas livestock grazing favours short and palatable grass species (Table 4.2 - 4.5). This was also found by Stock & Hofeditz (2000) in a comparison between sheep-grazed salt marsh and marsh that had been ungrazed for 9 years on the Hamburger Hallig, Germany. Grazing pressure by geese is significantly higher in the more intensively grazed situation for most of the comparisons we made, except for the *Festuca* community on Schiermonnikoog (Figure 4.3). Above that we found that, without livestock grazing, the total surface cover of plant communities that are suitable for geese decreases (see Table 4.6; Andresen *et al.* 1990; Gettner *et al.* 2000; Bakker *et al.* 2002). Productive long-term ungrazed marshes quickly become unsuitable as a habitat for small herbivores over the years, due to natural succession (Aerts *et al.* 1996; Bergmann & Borbach-Jaene 2001; chapter 7). On the barrier marshes this process takes several decades (van de Koppel *et al.* 1996; Olff *et al.* 1997), and this explains why the old ungrazed marsh on Schiermonnikoog has much larger cover of communities with tall canopy than the young ungrazed marsh (Table 4.6). The declining suitability of ungrazed marsh for small herbivores is a compound effect of the increase in canopy height, dead biomass and cover of tall unpalatable plant species coinciding with decreased tiller density, cover and biomass of forage species. Together these changes are likely to result in reduced intake rates of biomass for the small herbivores, and reduced average forage quality.

### *Implications for management*

By the end of spring, primary production has reached high levels on polder areas along the Wadden Sea, such that virtually unlimited numbers of birds could be sustained if only biomass were important. However, forage maturation effects and increasing leaf lengths diminish the suitability of swards for geese, where standing biomass accumulates. These effects can be counteracted by continuous grazing of the sward during spring, either by livestock or by geese themselves. Especially the latter scenario requires undisturbed conditions, as human disturbance was shown to severely constrain the use of inland feeding areas (chapter 3). Thus, appropriate management can strongly enhance the capacity of highly productive inland feeding areas by maintaining a short sward and keeping low levels of disturbance, as for example shown by Spaans & Postma (2001). Note, however, that maintaining a short sward is not a panacea, as forage availability might be limiting under conditions of low primary productivity



(Hassall *et al.* 2001). For inland feeding areas on the winter grounds, managed to accommodate as many geese as possible, it is more effective to provide swards of intermediate canopy height in order to strike a balance between forage availability and forage quality (Vickery *et al.* 1994; Riddington *et al.* 1997). Finally, as pointed out by Prop & Black (1997), there is reason to assume that agricultural grassland may not satisfy all nutritional requirements of *Branta* Geese in spring, potentially affecting subsequent reproduction. The use of inland feeding areas as a management tool to support the population of Brent Geese should, therefore, be treated with caution. It is more appropriate to try and maintain or even enhance the capacity of natural habitat to support the geese in spring.

Livestock grazing on salt marshes improves the feeding conditions for geese, with the highest goose grazing pressure in areas where stocking rates are highest. Brent and Barnacle Geese rely upon young or grazed salt marshes during spring, as undisturbed natural succession leads to a declining suitability of the habitat for these small herbivores (van de Koppel *et al.* 1996). Because young marsh is relatively rare, there is an argument to maintain considerable areas of marsh under grazing in the Wadden Sea, in order to support current numbers of geese in the Wadden Sea in spring (Esselink 2000; chapter 8). However, livestock grazing also affects other taxa that are characteristic of salt marshes, such as breeding birds (Norris *et al.* 1998; Eskildsen *et al.* 2000), entomofauna (Andresen *et al.* 1990; Meyer *et al.* 1995) and of course plants (Dijkema 1983b; Bakker *et al.* 2002), and management should not entirely be guided by the needs of single species. A lengthy discussion on this issue is given elsewhere (Stock & Kiehl 2000; Bakker *et al.* 2002), but the central tenet for us is that the management should be guided by clearly defined ecological objectives and a continuous monitoring of developments.

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## References

- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of Greylag geese *Anser anser* and Barnacle geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. *Z. Ökol. Natursch.* 5: 65-75
- Andresen H, Bakker JP, Brongers M, Heydemann B, Irmeler U (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137-148
- Bakker JP, Bos D, de Vries Y (2002) To graze or not to graze, that is the question. In: Proceedings of the 10th International Scientific WaddenSea Symposium (eds. K Essink, M van Leeuwe, A Kellerman & WJ Wolff): Ministry of Agriculture, Nature Management and Fisheries, Groningen (in press)
- Bakker JP, de Leeuw J, Dijkema KS, Leendertse PC, Prins HHT, Rozema J (1993) Salt marshes along the coast of the Netherlands. *Hydrobiologia* 265: 73-95
- Bazely DR, Jefferies RL (1985) Goose Faeces: a source of nitrogen for plant growth in a grazed salt marsh. *J. Appl. Ecol.* 22: 693-703
- Bazely DR, Jefferies RL (1986) Changes in the composition and standing crop of salt marsh communities in response to the removal of a grazer. *J. Ecol.* 74: 693-706
- Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. *Am. Nat.* 127: 870-892
- Bergmann HH, Borbach-Jaene J (2001) Abschlussbericht des Forschungsprojektes Auswirkungen von Bewirtschaftungsänderungen auf die Habitatwahl, Raumnutzung und das Verhalten von Nonnengans und Ringelgans am Beispiel der Leybucht im Nationalpark Niedersächsisches Wattenmeer. Universität Osnabrück, Osnabrück
- Boudewijn T (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. *Wildfowl* 35: 97-105
- Cargill SM, Jefferies RL (1984) The effects of grazing by Lesser Snow Geese *Anser caerulescens caerulescens* on the vegetation of a sub-arctic salt marsh. *J. Appl. Ecol.* 21: 669-686
- Coughenour MB (1991) Biomass and nitrogen responses to grazing of upland steppe on Yellowstone's northern winter range. *J. Appl. Ecol.* 28: 71-82
- Demment MW, van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125: 641-672
- Dijkema KS (1983a) The saltmarsh vegetation of the mainland coast, estuaries and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 185-269
- Dijkema KS (1983b) Use and management of mainland salt marshes and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 303-312
- Drent RH, van der Wal R (1999) Cyclic grazing in vertebrates and the manipulation of the food resource. In: Olff H, Brown VK, Drent RH (eds) Herbivores Between Plants and Predators, Blackwell Science, Oxford, pp 271-299
- Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anatidae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle
- Ebbinge BS, Berrevoets C, Clausen P, Ganter B, Guenther K, Koffijberg K, Mahéo M, Rowcliffe JM, St. Joseph A, Südbeck P, Syroechkovski EE, Jr. (1999) Dark-bellied Brent Goose *Branta bernicla bernicla*. In: Madsen J, Cracknell G, Fox AD (eds) Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International, Wageningen. National Environmental Research Institute, Rønde, pp 284-297
- Ebbinge BS, Boudewijn T (1984) Richtlijnen voor het beheer van rotganzen in het nederlandse wadden-gebied. RIN rapport 84/4, Rijksinstituut voor Natuurbeheer, Leersum
- Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26: 105-113





- Engelmoer M (1998) Pleisterende ganzen en zwanen langs de Friese Waddenkust - seizoen 1997/98. Altenburg & Wymenga Ecologisch onderzoek, Veenwouden
- Eskildsen K, Fiedler U, Hälterlein B (2000) Die Entwicklung der Brutvogelbestände auf der Hamburger Hallig. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 61-65
- Esselink P (2000) Nature management of coastal marshes. Interactions between anthropogenic influences and natural dynamics. PhD thesis University of Groningen, Groningen
- Fox AD, Kristiansen JN, Stroud DA, Boyd H (1998) The effects of simulated spring goose grazing on the growth rate and protein content of *Phleum pratense* leaves. *Oecologia* 116: 154-159
- Ganter B, Larsson K, Syroechkovskiy EV, Litvin KE, Leito A, Madsen J (1999) Barnacle Goose *Branta leucopsis*. In: Madsen J, Cracknell G, Fox AD (eds) Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International, Wageningen. National Environmental Research Institute, Rønde, pp 271-283
- Gauthier G, Hughes RJ, Reed A, Beaulieu J, Rochefort L (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *J. Ecol.* 83: 653-664
- Gettner S, Heinzel K, Kohlus J (2000) Die Entwicklung der aktuellen Vegetation auf der Hamburger Hallig nach Änderung der Nutzung. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 24-33
- Grant SA, Barthram GT, Torvell L (1981) Components of regrowth in grazed and cut *Lolium perenne* swards. *Grass Forage Sci.* 36: 155-168
- Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* 127: 97-104
- Hik DS, Jefferies RL (1990) Increases in the net above-ground primary production of a salt marsh forage grass; a test of the predictions of the herbivore-optimization model. *J. Ecol.* 78: 180-195
- Hutchings NJ, Gordon IJ (2001) A dynamic model of herbivore-plant interactions on grasslands. *Ecol. Mod.* 136: 209-222
- Jensen A (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. *Vegetatio* 60: 37-48
- Jones MB, Collet B, Brown S (1982) Sward growth under cutting and continuous stocking managements: sward structure, tiller density and leaf turnover. *Grass Forage Sci.* 37: 67-73
- Kersten M, Rappoldt K, van Scharenburg K (1997) Wadvogels op Ameland. In: Versluys M, Engelmoer R, Blok D, van der Wal R (eds) Vogels van Ameland. Friese Pers Boekerij bv, Leeuwarden
- Kiehl K, Eischeid I, Gettner S, Walter J (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. *J. Veg. Sci.* 7: 99-106
- Kiehl K, Schröder H, Bredemeier B, Wiggershaus A (2000) Der Einfluss von Extensivierung und Beweidungsaufgabe auf Artenzusammensetzung und Struktur der Vegetation. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 34-42
- Koffijberg K, Voslammer B, Van Winden E (1997) Ganzen en zwanen in Nederland: overzicht van pleisterplaatsen in de periode 1985-94. SOVON Vogelonderzoek, Beek-Ubbergen
- Madsen J (1989) Spring feeding ecology of Brent Geese *Branta bernicla*: Annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. *Dan. Rev. Game Biol.* 13: 4-16
- Madsen J, Cracknell G, Fox AD (1999) Goose populations of the Western Palearctic. A review of the status and distribution. Wetlands International Publ. No. 48 Wetlands International, Wageningen. National Environmental Research Institute, Rønde
- Mayhew P, Houston D (1999) Effects of winter and early spring grazing by Wigeon *Anas penelope* on their food supply. *Ibis* 141: 80-84
- McKay HV, Bishop JD, Ennis DC (1994) The possible importance of nutritional requirements for dark-bellied brent geese in the seasonal shift from winter cereals to pasture. *Ardea* 82: 123-132
- McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191: 92-94
- McNaughton SJ (1979) Grazing as an optimization process: grass-ungulate relationships in the Serengeti. *Am. Nat.* 113: 691-703

- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form and coevolution. *Am. Nat.* 124: 863-886
- McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol. Monogr.* 55: 259-294
- Meyer H, Fock H, Haase A, Reinke HD, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep grazing. *Helgoländer Meeresuntersuchungen* 49: 563-589
- Norris K, Brindley E, Cook T, Babbs S, Forster Brown C, Yaxley R (1998) Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? *J. Appl. Ecol.* 35: 621-634
- Olf H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814
- Parsons AJ, Penning PD (1988) the effect of the duration of regrowth on photosynthesis, leaf death and the average rate of growth in a rotationally grazed sward. *Grass Forage Sci.* 43: 15-27
- Post ES, Klein DR (1996) Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. *Oecologia* 107: 364-372
- Prins HHT, Ydenberg RC (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). *Oecologia* 66: 122-125
- Prins HHT, Ydenberg RC, Drent RH (1980) The interaction of Brent Geese *Branta bernicla* and Sea plantain *Plantago maritima* during spring staging: field observations and experiments. *Acta Bot. Neerl.* 29: 585-596
- Prop J (1991) Food exploitation patterns by Brent Geese *Branta bernicla* during spring staging. *Ardea* 79: 331-342
- Prop J, Black JM (1997). Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. In: Mehlum F, Black JM, Madsen J (eds) Proceedings of the Svalbard Goose symposium. Norsk-Polarinstitutt, Oslo, Norway, pp 175 193
- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153 160
- Roozen AJM, Westhoff V (1985) A study on long-term salt marsh succession using permanent plots. *Vegetatio* 61: 23-32
- Rowcliffe JM, Watkinson AR, Sutherland WJ, Vickery JA (1995) Cyclic winter grazing patterns in Brent Geese and the regrowth of salt-marsh grass. *Funct. Ecol.* 9: 931-941
- Ruess RW, McNaughton SJ, Coughenour MB (1983) The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an east african sedge. *Oecologia* 59: 253-261
- Schaminée JHJ, Weeda EJ, Westhoff V (1998) De Vegetatie van Nederland. D1 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitates durch Nonnen- und Ringelgänse. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 43-55
- Stock M, Kiehl K (2000) Empfehlungen zum Salzwiesenmanagement im Nationalpark Schleswig-Holsteinisches Wattenmeer. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 74-77
- Summers RW (1990) The effect on winter wheat of grazing by Brent Geese *Branta bernicla*. *J. Appl. Ecol.* 27: 821-833
- Summers RW, Critchley CNR (1990) Use of grassland and field selection by Brent Geese *Branta bernicla*. *J. Appl. Ecol.* 27: 834-846
- Sutherland WJ, Allport GA (1994) A spatial depletion model of the interaction between bean geese and wigeon with the consequences for the habitat management. *J. Anim. Ecol.* 63: 51 59
- van de Koppel J, Huisman J, van der Wal R, Olf H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745



- van der Meijden R (1990) Heukels' Flora van Nederland ed 21. Wolters-Noordhoff, Groningen
- van der Wal R, van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos* 82: 123-130
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van Wijnen H, Bakker JP (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. *J. Coast. Cons.* 3: 19-26
- Vickery JA, Sutherland WJ (1992) Brent geese: a conflict between conservation and agriculture. *British Crop Protection Council* 50: 187-193
- Vickery JA, Sutherland WJ, Lane SJ (1994) The management of grass pastures for brent geese. *J. Appl. Ecol.* 31: 282-290
- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499-508
- Westhoff V, van Oosten MF (1991) De Plantengroei van de Wadden eilanden. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Zar JH (1996) *Biostatistical Analysis*. Prentice-Hall, Inc., N.J.,

Flock of Brent Geese in the polder of Schiermonnikoog (photo J. Stahl).





# CHAPTER 5

## Brent Geese aggregate to cope with increased levels of primary production

Daan Bos, Johan van de Koppel and Franz J. Weissing

### Abstract

We report on an aggregative response of Brent Geese to increased productivity of the vegetation during the growing season on agricultural fields on the island of Schiermonnikoog, the Netherlands. Plant standing crop was found to be maintained at low levels in the fields where geese activity focussed, whereas the remainder of the fields escaped herbivore control and developed a high standing crop. This pattern can be explained by the fact that the functional response of the geese is not monotonically increasing, but dome-shaped. As a consequence, continuously grazed swards are more suitable for feeding than temporarily ungrazed swards. We present an optimal foraging model showing that, beyond a threshold level, increased primary productivity leads to spatial heterogeneity in standing crop, under this assumption. Further increases in productivity lead to a progressive release of vegetation from herbivore control, which will develop a high standing crop. Interestingly, our model suggests that aggregative behaviour in herbivores only maintains the intake near the potential maximum if the environment is stable and predictable. Processes that disrupt an exact match between local primary production and consumption, like a misjudgement of patch quality by the herbivore, may lead to a less than optimal intake, as suitable vegetation becomes depleted.

## Introduction

Prediction of the spatial distribution and the population numerical response of animal populations requires thorough understanding of the relationship between resource density and intake rate. For many species, vertebrates and invertebrates alike, this relation is a continuously increasing function and is then referred to as a functional response of Holling type II (Holling 1959; Spalinger & Hobbs 1992; Gross *et al.* 1993). There is wide recognition though, for the fact that the functional response may have an alternative shape (Abrams 1982; Hobbs & Swift 1988; Fryxell 1991), with profound consequences for the system under study. Herbivores, for example, may be confronted with a dome-shaped functional response for several reasons. With increasing resource density, the vegetation composition, structure and tissue quality change. Reduced energy absorption due to a declining digestibility (Fryxell 1991; Illius & Gordon 1991) is one of the better studied examples leading to a lower performance of ruminants at high resource densities, but more mechanisms have been identified, e.g. increased costs of locomotion or vigilance (van de Koppel *et al.* 1996), increased handling time (van der Wal *et al.* 1998) or reduced concentrations of nitrogen (Riddington *et al.* 1997; Hassall *et al.* 2001).

When higher rates of intake or absorption can be achieved at intermediate levels of resource density, herbivores are predicted to benefit from aggregation (McNaughton 1984; Fryxell 1991; Hutchings & Gordon 2001). Fryxell (1991) presented a model illustrating this phenomenon for a system without spatial heterogeneity. In this system, individual herbivores suffer from forage maturation due to excess forage production in relation to their consumption. Animals at higher densities keep the sward in a nutritious stage by repeated defoliation and thus facilitate each other. We studied an analogous case of herbivores in a productive environment, but included spatial heterogeneity. The motivation for constructing the model originated from field observations of spring-staging Brent Geese *Branta bernicla bernicla*, foraging on productive agricultural grassland along the coast of the Dutch Wadden Sea.

Geese rely heavily on forage of high quality (Owen 1980) and are, therefore, often observed on shortly grazed swards or newly emerging vegetation (Boudewijn & Ebbinge 1994). Several studies support the hypothesis that Brent Geese select swards in order to maximise intake of nitrogen (Ydenberg & Prins 1981; Hassall *et al.* 2001; Chapter 2) and that intake rate of nitrogen may actually decline at high levels of standing crop (van de Koppel *et al.* 1996; Riddington *et al.* 1997; van der Wal *et al.* 1998; Hassall *et al.* 2001). It is hypothesised that these processes may form the mechanism behind observed patterns of habitat use by geese during spring staging. In spring, the geese are confronted with increasing levels of primary production. As described by Spaans and Postma (2001), Brent Geese increase their grazing intensity as primary production increases. For this, they revisit an increasingly smaller share of the original area they utilised, with increasing frequency. When the geese depart for the breeding grounds at the end of May, a bi-modal pattern in sward structure has emerged with shortly grazed areas and large areas that are left ungrazed.



The objective of this paper is 1) to provide support for the hypothesised mechanisms with empirical data, 2) to simulate this pattern of use qualitatively in a model based on a dome-shaped functional response and 3) to explore the consequences of this concept using the model. The paper is organised in two sections, a field study and a modelling study. We will start with the field study, because the model is motivated by its results.

## Field study

### Methods

#### STUDY SITES

Field data on habitat use by Brent Geese in spring were collected on two barrier islands in the Dutch Wadden Sea, Texel (53°05'N, 4°50'E) and Schiermonnikoog (53°30'N, 6°10'E). Both islands have large tracts of embanked agricultural grassland (polder) and a different area of salt marsh. Schiermonnikoog is frequented by about 3,000 Brent (van der Wal *et al.* 2000) and up to 8,000 Barnacle Geese *Branta leucopsis* (Stahl 2001) during spring. The geese forage on polder grassland (270 ha) during early spring, but move to the marsh (1500 ha) in February/March (Barnacle Geese) and April (Brent Geese). The polder areas are used for grass production and cattle grazing by farmers and consist of homogeneous swards, containing mainly *Lolium perenne* and *Poa trivialis*. Fields are heavily fertilised with approximately 400 kg N.ha<sup>-1</sup> of artificial fertiliser in addition to the application of manure. On Schiermonnikoog the farmers have actively disturbed the geese in the polder during the months of April and May until 1999, but from the year 2000 onwards they have agreed to actually host the birds in the southern half of the polder. Approximately 10,000 Brent Geese stage on Texel during spring, mainly foraging in the Brent Goose reserve “Zeeburg” in the north-eastern part of the island. Adjacent to the reserve is a small (45 ha) ungrazed salt marsh that is only used to a very limited extent by the geese, as it is dominated by tall unpalatable plant species. The pastures in the reserve (110 ha) consist of homogeneous swards of *Lolium perenne* and *Poa trivialis*, that are managed by fertilisation (110 kg N.ha<sup>-1</sup>) and aftermath grazing with livestock in order to accommodate the geese as good as possible. Disturbance to the geese is very limited because access for any traffic, including pedestrians is restricted.

#### FIELD PATTERNS

We counted Barnacle and Brent Geese in the polder areas of the Wadden Sea island Schiermonnikoog on a regular basis during the spring of 2000 and 2001, and attributed the birds to specific clearly delineated fields. The censuses were performed between 8.00 A.M. and 20.00 P.M. at different times for each count, and each count the whole polder area (290 ha) was scanned. In March, April and May 2000, we established transects through all pastures in the polder of Schiermonnikoog. At intervals of 10 m along these transects two measurements of canopy height were taken and accumulated



dropping density was estimated in a circular plot of 4 m<sup>2</sup>. Dropping density is a reliable measure for the comparison of grazing intensity, since geese defecate at regular intervals (Owen 1971). Canopy height was measured with a 24 g, 20 cm diameter polystyrene disc that was dropped on the vegetation, sliding along a calibrated stick. The average canopy height was calculated for plots with and without fresh goose droppings.

#### PATCH CHOICE EXPERIMENT

At the Brent Goose reserve “Zeeburg” in the polder of the Wadden Sea island of Texel, we experimentally tested our hypothesis that swards of intermediate biomass are preferred over swards with higher values of biomass. For this, we excluded wild geese from small plots at 2 pastures that were known to be grazed intensively by geese, for 5 different periods of time. The plots were 16 m<sup>2</sup> in size and fenced using chicken wire of 50 cm high and 5 cm mesh size. The fences for the different treatments were erected 8, 5, 3, and 1 week(s) prior to May 7th 2000 and the control treatment was not excluded. The fields were managed according to standard practice by fertilising them with an artificial fertiliser (110 kg N.ha<sup>-1</sup>). Each treatment was replicated four times at field I and three times of field II according to a randomised block design. At the 7th of May, all fencing was removed.

After removal of the fences, droppings were counted and removed daily in a 4 m<sup>2</sup> circular sub-plot, that was placed within each experimental plot and marked with an inconspicuous stick in the centre. Canopy height was measured every other day with five replicates per plot, using the method described above. Four sets of sods (10 cm x 10 cm) were taken from each plot and used to estimate the instantaneous rate of biomass intake (see below). Forage quality was measured as the nitrogen content of leaf tips (top 2 cm) from a mixture of the polder grasses. Forage quality samples were washed, air-dried at 70°C and nitrogen content was determined using an automated CNHS-analyser (Interscience EA 1110).

#### INTAKE RATE

Instantaneous intake rate of biomass was estimated, using three captive Brent Geese, brought individually into an experimental outdoor enclosure (4 m x 4 m) for the measurements. The geese were allowed to eat from sods of 10 cm x 10 cm, taken from the field plots, that were weighed before and after the trial to the nearest 10 mg (Sartorius pro 32/34F). Removed biomass ( $W_r$ , g fresh weight) was measured as the weight loss of the sod during the trial, corrected for evaporation. Evaporation rate (g.s<sup>-1</sup>) was estimated from the weight loss of a similar sod under the same circumstances. Time spent pecking per sod was carefully estimated by visual observation, supported by software that was specifically designed for the purpose, and summed to obtain an estimate of total pecking time ( $T_p$ ). The intake rate (g fresh.s<sup>-1</sup>) was calculated by dividing removed biomass ( $W_r$ ) by total pecking time ( $T_p$ ). Each trial, one goose was offered one sod of each treatment at the same time, positioned in a regular grid but in random order. Each goose was used to test each of the sods at least once. The trials took place during the second week of May 2000. During the experimental trials and the 8 weeks before,





the geese were housed on grass in a 100 m<sup>2</sup> enclosure connected to the test area, and additionally fed with dried food pellets and grass presented as sods. Water was always available *ad libitum*. The geese had been captured from the wild in 1996 and had been housed in a large open aviary until 8 weeks before the experimental trials. All catching, handling and non-invasive experimentation with captive geese in this study was conducted under a permit from the Dutch Ministry of Agriculture, Nature Management and Fisheries and from the Commission for the use of Animals in Experimental trials of the University of Groningen (DEC, permit no. BG07696/2382).

#### DATA ANALYSES

The average number of Brent and Barnacle Geese per field and per month in the polder of Schiermonnikoog was divided by the area of the fields they were observed upon during that month in order to estimate bird density. For the enclosure experiment in the polder of Texel, the accumulated number of droppings for the first week and the second week after the start of the experiment was used to estimate preference for the plots. Data on canopy height were averaged per plot to avoid pseudo-replication. These data were analysed using a Randomised Block ANOVA (Zar 1996). In this analysis 'grazing treatment' was entered as a fixed factor and 'block' was entered as a random factor. Instantaneous intake rate measurements were assumed to be independent measures and directly related to canopy height and the canopy height squared in a linear regression analysis. Count data were square-root transformed ( $y' = \sqrt{y+0.5}$ ), to obtain homogeneity of variances. Statistical analyses were carried out with SPSS 10.1 (SPSS Inc.).

## Results

### *Field patterns*

In March of the years 2000 and 2001, almost all fields in the polder of Schiermonnikoog were frequented by geese, but towards May an aggregation was observed (Figure 5.1). In these months, a dichotomy arose between short-grazed areas and fields that were abandoned. In March the proportion of Barnacle Geese among all geese was still high (70% of total), but thereafter the majority of birds were Brent Geese. The canopy height of pasture fields that were maintained by the geese remained low (Figure 5.2) and was  $4.9 \pm 0.55$  cm in May, while the canopy height in ungrazed fields increased sharply to  $15.2 \pm 0.36$  cm (T-test,  $t = 5.7$ ,  $P = 0.001$ ). The average density of geese increased in both years (Figure 5.3A,B). This is especially clear if we focus on the field that was grazed until the end of May, as the average number of geese here increased by a factor 4 in 2000 and by more than a factor 2 in 2001, in spite of a decline in the total number of geese. The increased average density of birds was mainly caused by an increased presence in time, as the proportion of counts when birds were present on the field increased from 30% to over 80% of the counts. When birds were present, the average density of birds was constant at  $128 \pm 11$  geese.ha<sup>-1</sup> (linear regression, effect of time:  $F_{2,48} = 0.64$ , n.s.).

Pattern of use in the Bancks polder, 2000

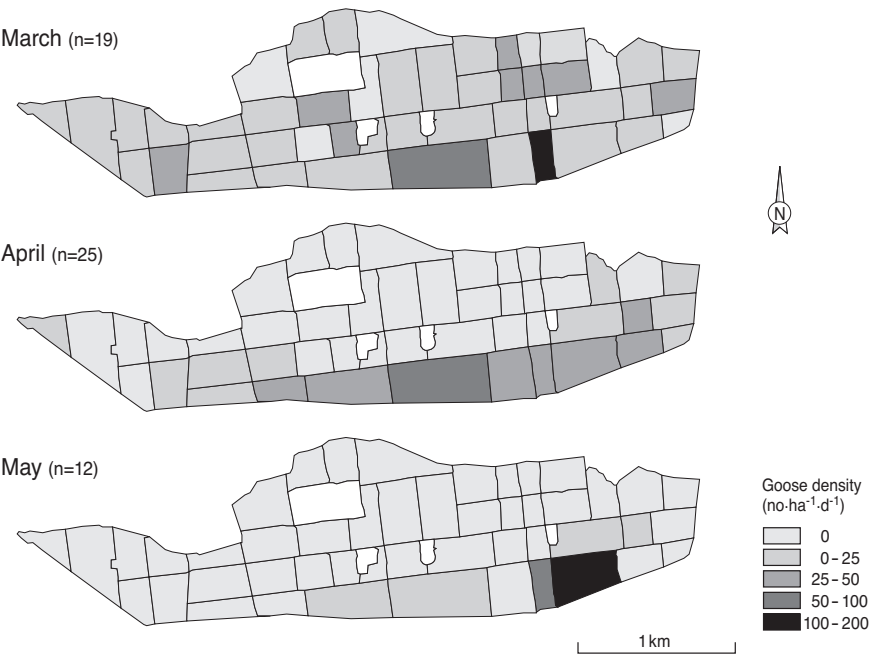


Figure 5.1 Maps of the average density of Brent and Barnacle Geese in polder fields on the island of Schiermonnikoog, illustrating the aggregation of geese over spring of the year 2000. The number of counts that were performed each month is indicated between brackets.

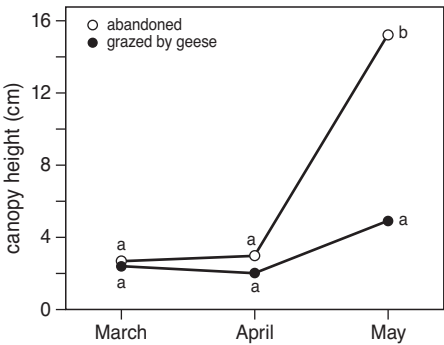


Figure 5.2 Development of canopy height (cm) in spring in the polder of Schiermonnikoog for the year 2000 on polder grassland that is either grazed (as observed from the presence of fresh droppings) or not grazed by geese. Significant differences are indicated using different letters ( $P < 0.05$ ).

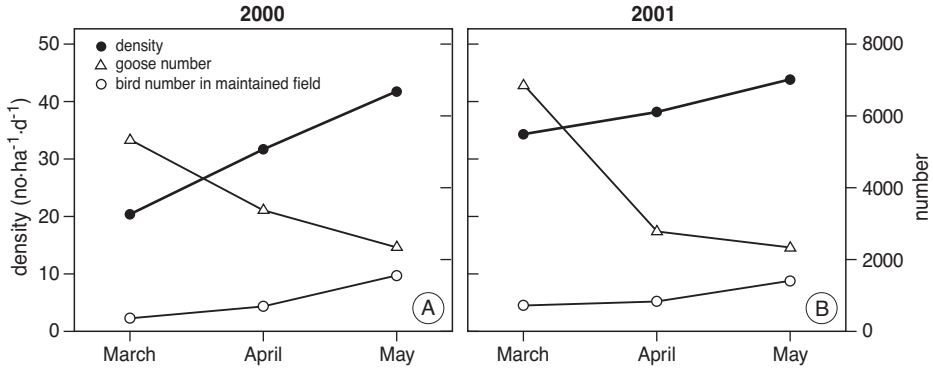


Figure 5.3 Development in herbivore numbers and herbivore density (no.ha<sup>-1</sup>.d<sup>-1</sup>) in spring in the polder of Schiermonnikoog for the years A) 2000 and B) 2001, based on regular counts.

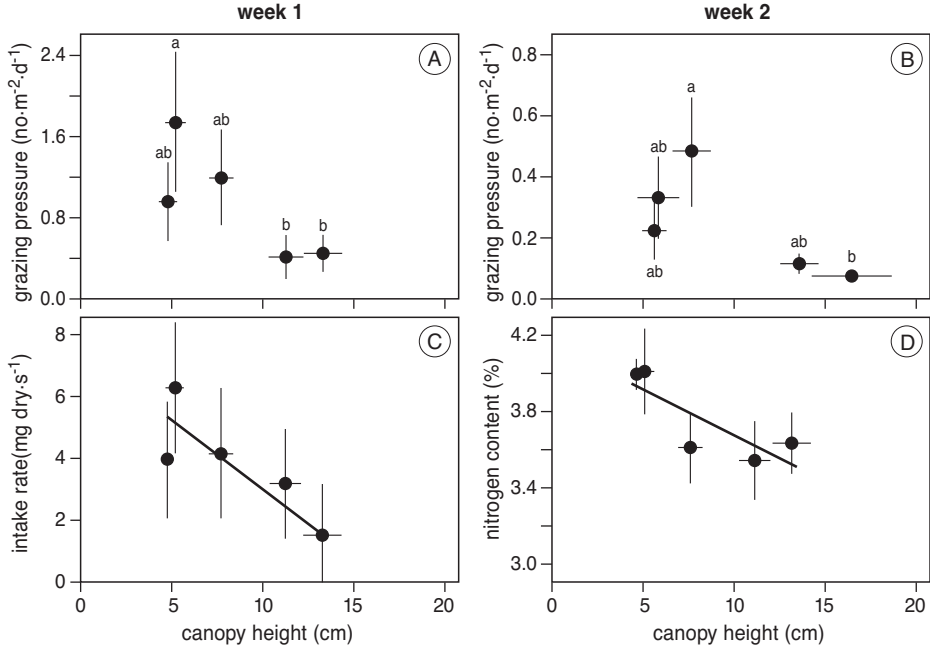
### Intake rate and patch choice experiment

Canopy height on the experimental plots in the Brent Goose reserve on Texel, was positively related to green biomass (Pearson  $r = 0.784$ ,  $P < 0.001$ ,  $n = 56$ ), and the plots that were excluded longest had significantly taller canopy height ( $F_{4,30} = 3.39$ ,  $P < 0.001$ ). The experiment took place at a moment when the geese had already started to leave the island and lasted two weeks (7 - 21st May 2000). Total grazing pressure was much lower during the second week and, therefore, the data were analysed separately for the two weeks. Preference, measured as accumulated grazing pressure, was highest for plots that had been excluded for a short period in the first (Figure 5.4A;  $F_{4,24} = 3.39$ ,  $P = 0.025$ ) as well as in the second week (Figure 5.4B;  $F_{4,24} = 3.0$ ,  $P = 0.037$ ) after opening of the exclosures. Instantaneous intake rate of matter, as measured using the captive Brent Geese, declined with canopy height (Figure 5.4C; linear regression,  $F_{1,113} = 4.06$ ,  $P = 0.046$ ,  $R^2 = 0.034$ ), and so did nitrogen content (Figure 5.4D; linear regression,  $F_{2,32} = 10.7$ ,  $P = 0.02$ ,  $R^2 = 0.402$ ).

## Modelling study

### The model

In order to better understand the spatial patterns described above on the basis of individual foraging decisions, we constructed a spatially implicit, discrete simulation model. The model consists of a large number of small patches. At the start of a time step, the 'model geese' redistribute over the patches according to expected intake rate. The biomass (B) in each patch changes due to time-dependent production and the total consumption by the geese present on this patch. A detailed description of the model assumptions is given below. An overview of the relevant model parameters and their reference values is given in Table 5.1.



**Figure 5.4** The effects of temporary enclosure on goose grazing pressure (droppings.m<sup>-2</sup>.day<sup>-1</sup>) during the A) first and B) second week after opening of the enclosures (note that grass continued to grow and vegetation height is thus higher for each treatment in the second week), C) intake rate of biomass (mg dry.s<sup>-1</sup>) and D) forage quality, measured as nitrogen content (%). Treatments that do not differ significantly share the same letter in panel A and B.

#### VEGETATION GROWTH

Each time step of length  $\Delta t$ , the plant biomass (g.m<sup>-2</sup>) in a patch changes due to production and consumption (formula 1).

$$\Delta B = [G(B,t) - N.F(B).t_{\text{tot}}].\Delta t \quad (1)$$

Here,  $G(B,t)$  describe daily primary productivity (g.m<sup>-2</sup>.day<sup>-1</sup>) in relation to standing biomass and time of season ( $t$ , days).  $N$  is the number of geese present,  $F(B)$  is the intake rate per goose as a function of plant biomass (the functional response, g.s<sup>-1</sup>, see below) and  $t_{\text{tot}}$  = daylength. We are interested in a system where primary production increases systematically in the course of the season. In a first attempt, this relation was modelled as follows:

$$G(B,t) \cong G(t) = \gamma.(G_0 + G_1.t) \quad (2a)$$



**Table 5.1** Parameters used in the simulation model with units, reference value and the range over which parameters are varied.

Parameter	Range		Reference value	Unit	Explanation
	Min	Max			
a	0.002	0.01	4.00E-03	m <sup>2</sup> .s <sup>-1</sup>	search rate
B <sub>(t=t0)</sub>	5	25	10	g.m <sup>-2</sup>	(initial) biomass density
B <sub>0</sub>			20	g.m <sup>-2</sup>	crown or root-reserves that cannot be grazed
Δt	1	16	2	hours	time step size
ε <sub>max</sub>	0	0.5	0.2	-	potential variation around perceived intake rate in a patch
F <sub>min</sub>			10	g Nitrogen.d <sup>-1</sup>	minimum required nitrogen consumption per goose
γ	1	5	3	-	index of productivity
G <sub>0</sub>			2.40E-02	g.m <sup>-2</sup>	constant
G <sub>1</sub>			4.00E-04	g.m <sup>-2</sup>	constant
h <sub>0</sub>			100	s.g <sup>-1</sup>	constant in regression biomass-handling time
h <sub>1</sub>	0.2	1	0.5	s.g <sup>-2</sup> .m <sup>2</sup>	coefficient in regression biomass-handling time
K			200	g.m <sup>-2</sup>	vegetative carrying capacity
t <sub>tot</sub>			57600	s	daylength
N	1	15	1	no	(starting) number of geese
P	500	7500	500	m <sup>2</sup>	total area
p	5	25	15	m <sup>2</sup>	size of patch
q			6	%	nitrogen content of the vegetation
ρ	1	5	3	-	index of productivity
r <sub>0</sub>			4.20E-03	g.m <sup>-2</sup>	constant
r <sub>1</sub>			2.00E-05	g.m <sup>-2</sup>	constant
t	0	90		day	time

In words, primary productivity is independent of biomass, but increases linearly with time of season. The parameters (see Table 5.1) were chosen such that the productivity increases by a factor 2.5 from the start (t=0) to the end (t=90). The factor γ (gamma) was changed systematically in order to investigate the dependence of the simulation results on system productivity. In a second and more realistic attempt we used a modified logistic growth function to model primary production:

$$G(B,t) = r(t) \cdot (B+B_0) \left( 1 - \frac{B+B_0}{K+B_0} \right) \quad (2b)$$

where

$$r(t) = \rho \cdot (r_0 + r_1 \cdot t) \quad (2c)$$

Eqn. (2b) corresponds to the logistic growth equation for total biomass  $B + B_0$ , where  $B = B(t)$  refers to the vegetative biomass accessible to the herbivores while  $B_0$  represents the crown or root-reserves of plants that cannot be grazed (Fryxell 1991).  $K$  is the vegetative carrying capacity. The optimum level of growth is found at  $B = 0,5.(K - B_0)$ . The intrinsic growth rate  $r(t)$  is assumed to increase linearly with time of season, and the parameters were chosen such that productivity increases by a factor 2.5 from the start ( $t=0$ ) to the end ( $t=90$ ), for a given level of biomass. The factor  $\rho(\rho)$  was changed systematically in order to investigate the dependence of the simulation results on system productivity.

#### INTAKE RATE

Our description of the functional response ( $F(B)$ ) of the herbivores was based on a Holling type II curve. However, we achieved a dome-shaped function by assuming a negative linear relationship between handling time  $h$  and biomass.

$$F(B) = a.B.(1+a.h(B).B)^{-1} \quad (3a)$$

with

$$h(B) = h_0 + h_1.B \quad (3b)$$

As will be discussed below, there are several mechanisms that can lead to a dome-shaped response, and we have chosen for this alternative mainly for convenience. The maximum of the curve  $F(B)$  is located at  $B = \sqrt{(a.h_1)^{-1}}$ .

#### PATCH SELECTION

The geese are assumed to make no travel costs and the criterion for patch selection is the perceived intake rate of biomass, under the condition that the expected intake and availability in the patch exceed a minimum level specified ( $F_{\min}$ ). Perceived intake rate differs from  $F(B)$  by  $\epsilon$  (formula 3c), an error term randomly taken from a uniform distribution ( $\epsilon \in [-\epsilon_{\max}, \epsilon_{\max}]$ ).

$$\text{preference} = F(B).(1+\epsilon) \quad (3c)$$

Most results presented are based on simulations with only one herbivore. We will later discuss the additional assumptions that were taken when models with multiple geese were studied.

#### SPATIAL AND TEMPORAL SCALE

We assume that geese are not constantly moving between patches, but rather utilise them for some time before moving on. Long step sizes, however, would constrain the herbivores in their ability to choose between patches. Hence, we assumed time step size to range between 1 hour and a complete daylight period of 16 hours. The choice of



the spatial scale of patches is very much intertwined with the decision on temporal scale, as small patch sizes would lead to artefacts caused by depletion, when time step sizes are large. In contrast, large patches lead to strong discretisation effects, as will be shown in the next paragraph. In the standard models presented here, patch size ( $p$ ) varies between 5 and 25 m<sup>2</sup>, while total area ( $P$ ) is fixed at 500 m<sup>2</sup> for model runs with a single goose.

### Simulation results

#### A SINGLE GOOSE

The general pattern emerging from our model is a dichotomy between continuously grazed model patches and patches that are abandoned, sooner or later (Figure 5.5). From the start of a model run, the biomass in the patches continues to increase up to a level that yields the maximum intake rate. From that moment onwards, some patches are abandoned, not to be visited anymore during that model run and herbivore grazing intensity increases over time in the patches that are still grazed. The total number of patches that is grazed by the herbivore during the last phase of a simulation is lower when the system is more productive (Figure 5.6). Under these assumptions, the biomass density in the grazed patches is maintained at a value that is close to the optimum of the intake rate curve, as was illustrated in Figure 5.5. However, the model results depend to some extent on parameter values for patch size, productivity and error ( $\epsilon_{\max}$ ) in interaction with each other. The sensitivity of the model for these parameter is explored in Figure 5.7. Under low productivity ( $\gamma = 1$ ), the herbivore is able to maintain low plant density in the entire area, and the consumption is constrained by primary production until the end of the simulation. Biomass is thus not over-abun-

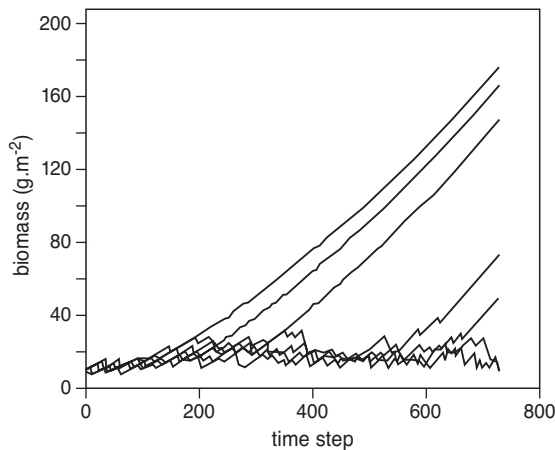
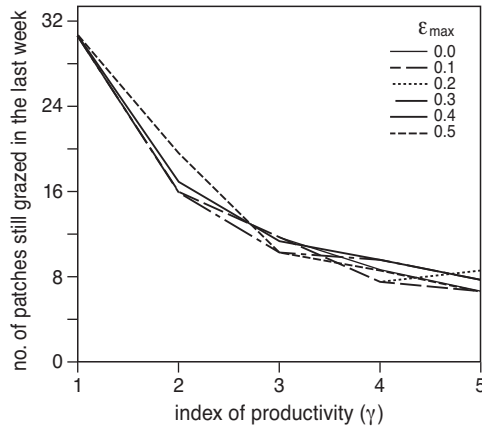


Figure 5.5 Biomass development over time in a few representative patches for a model run with default parameter settings and one goose.

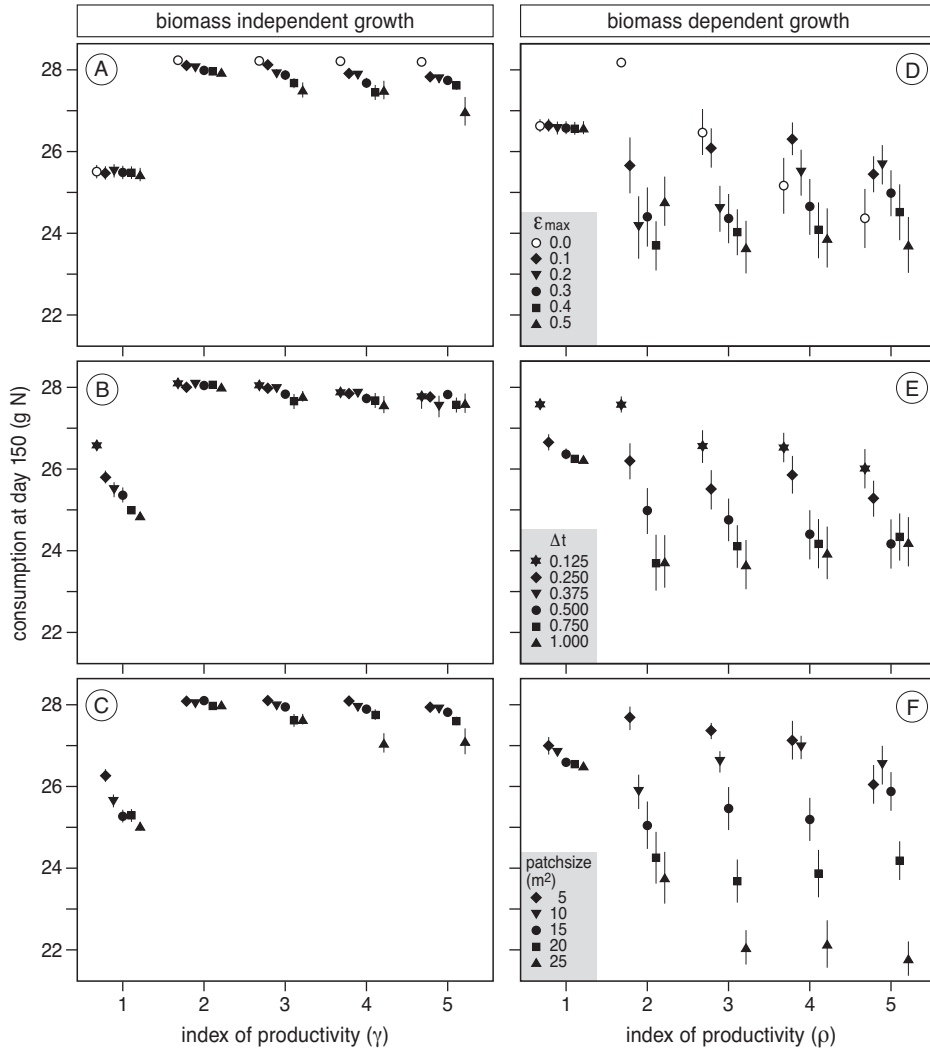


**Figure 5.6** The effect of varying system productivity and error in perceived intake rate on the number of patches used during the last 2 weeks of a model run, for model runs with default parameter settings and one goose.

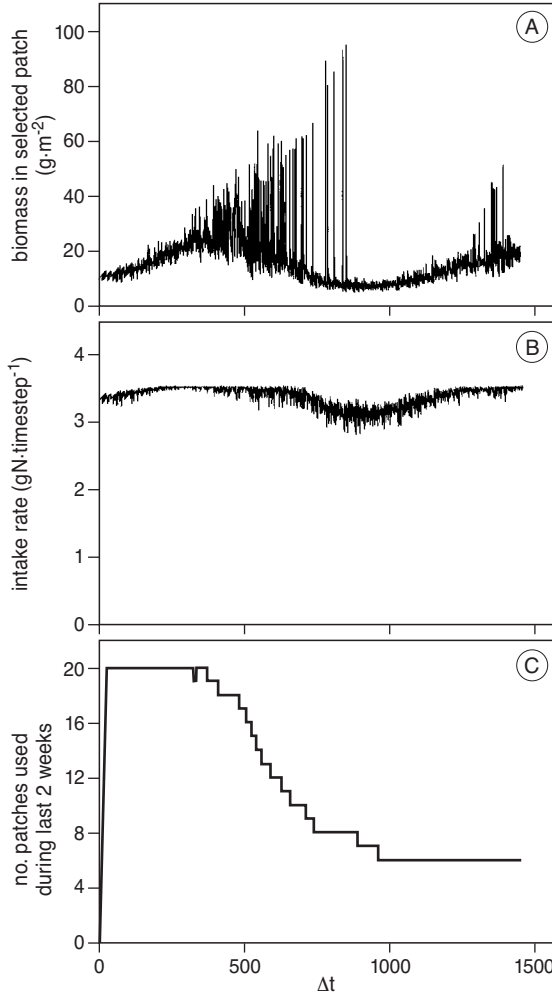
dant, the maximum intake rate is not reached and no aggregation takes place. For that reason, variation in  $\epsilon_{\max}$  or patch size hardly has an effect when  $\gamma = 1$  (Figures 5.7A,B,C). Variation in time step size (Figure 5.7B) has little effect on the model outcome, under biomass-independent growth. Without error ( $\epsilon_{\max} = 0$ ), the model is not sensitive to patch size or productivity (Figure 5.7A,C), but when the herbivore is not able to precisely distinguish between patches of different intake rate ( $\epsilon_{\max} > 0$ ), this leads to focussing on a set of patches with combined area that yields insufficient primary production. The habitat is then slowly depleted and temporarily exploited at a level of biomass below that of maximum instantaneous intake rate. When patches are relatively large and production is high, these effects may be considerable (Figure 5.7C). The dynamics of this phenomenon are illustrated in Figure 5.8. When too many patches have escaped from herbivore control, the standing crop becomes depleted in the patches that are continuously grazed and the herbivore every once in a while visits a patch with high plant standing crop (Figure 5.8A). The situation of temporary depletion is sooner or later restored by the increase in primary production with time (Figure 5.8A). However, the intake rate is somewhat lower during this phase (Figure 5.8B), until the standing crop has recovered, while the number of patches used during the last two weeks (Figure 5.8C, note the time lag of two weeks) stops declining until that moment.

With primary production depending upon biomass, the sensitivity of the model to parameter values for patch size, time step size, productivity and error increases sharply (Figures 5.7D,E,F). Under most combinations of parameter values, the intake at the last day of a model run is considerably lower than the potential maximum, caused by depletion in the continuously grazed patches. Again, this is caused by the herbivores aggregating in a set of patches with combined area that yields insufficient primary pro-





**Figure 5.7** Sensitivity of model results to parameter variation in relation to system productivity: maximal error in perceived intake rate (A, D), step size (B, E) and patch size (C, F) under biomass independent (one set of results presented in A - C) and biomass dependent primary production (one set of results presented in D - F). Simulations where the bird did not survive are excluded (time step size  $\Delta t = 8$  hrs and patch size = 5 m<sup>2</sup>).



**Figure 5.8** Illustration of model behaviour under productive conditions ( $\gamma = 4$ ) and relatively large patch size ( $p = 25 \text{ m}^2$ ) leading to temporary depletion of the habitat, for a model run with one goose and  $\varepsilon_{\max} = 0.2$ . A temporary depletion is observed under high levels of production and large patch size, when the herbivores cannot exactly estimate the potential intake rate in a patch. A) The level of biomass in the patch that is selected by the herbivore, B) the realised nitrogen intake rate of the herbivore and C) the number of patches that are used during the previous two weeks for each time step.



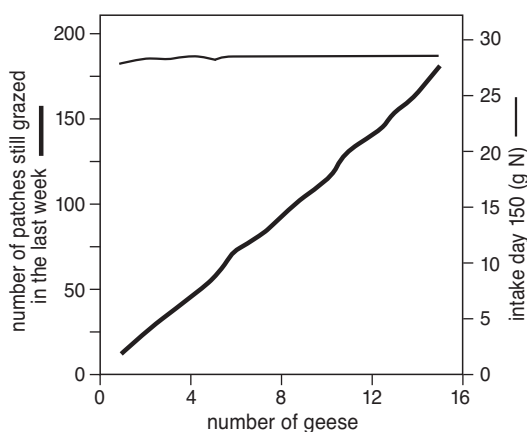
duction. However, under biomass dependent primary production a positive feedback is triggered, leading to stronger depletion, given the assumption that the optimum level of biomass for primary production is higher than that for instantaneous intake rate.

#### SENSITIVITY FOR OTHER PARAMETERS

The sensitivity of the model for initial biomass and total area is low as long as they are above the minimum required for survival. A fivefold increase in these parameters, leads to deviations in the output parameters studied that are smaller than 3%. Changing the parameters of the functional response ( $h_0$  and  $h_1$ ) has an immediate effect on total consumption over spring and consumption at day 150, but the qualitative behaviour of the model remains unaffected.

#### MULTIPLE GEESSE

Up to now, we only studied situations with a single herbivore. The situation may be different when multiple herbivores are in the system, and in order to check this possibility we also ran the model with the numbers of individuals ranging between one and fifteen. For model simulations with multiple geese, we increased the total area  $P$  to 0.75 ha. When studying model systems with multiple herbivores, the order in which they are distributed may be very important, especially when direct interference is studied. We did not include interference in our model, and assumed a linear dominance hierarchy, as a result of which the geese were (re-)distributed over the model patches at each time step in the same order. For the present analysis the fate of individual geese and the consequences of this choice of hierarchy are not pursued any further.



**Figure 5.9** The consumption per animal ( $\text{g N} \cdot \text{day}^{-1}$ ) in relation to herbivore numbers and the area of habitat that is maintained at the end of a simulation. Variation in the number of herbivores does not affect the intake per individual, but it does affect the total number of patches that are used in the last 2 weeks of a model run. Models are run with biomass independent growth, default parameter settings and a total area of 7,500  $\text{m}^2$ .

Model runs with multiple geese showed the same qualitative behaviour as those with a single goose. Figure 5.9 illustrates the effect of increasing the number of herbivores in the system for conditions of biomass-independent primary production. Per-capita consumption is not affected, as the increase in numbers is compensated for by an increased total area that is utilised. The same qualitative pattern is found under biomass dependent primary production.

## Discussion

### *Use of productive habitat in spring*

During spring, the geese in our simulation model as well as in the field, limit their use to a restricted area of the productive grassland and increase the intensity of grazing. Two processes could lead to such an increase in grazing intensity, namely an aggregation of herbivores into a more dense flock that spends the same amount of time, or a reduction in the revisitation interval (aggregation in space or time). The latter situation is most important in our field example from Schiermonnikoog (Figure 5.3). Aggregations of herbivores have been observed for many species of herbivore, such as Wildebeest *Connochaetus taurinus* (McNaughton 1976) or Red deer *Cervus elaphus* (Clutton-Brock *et al.* 1982). Possible mechanisms that lead to an aggregation of herbivores at swards of intermediate biomass are 1) spatial heterogeneity in forage quality, 2) the reduction of predation risk through enhanced predator detection or dilution and 3) a preference for continuously grazed swards (Fryxell 1991). Our experiment provides support for the interpretation that the observed aggregation by Brent Geese is caused by a preference for continuously grazed swards, due to declining rates of nutrient intake at higher levels of biomass (> 10 cm canopy height). Very similar experimental results were obtained by Wilmshurst *et al.* (1995) and Langvatn and Hanley (1993) for captive Red deer, by Gibb *et al.* (1997) for cattle, as well as by Bos *et al.* (chapter 2), Stahl *et al.* (2001) and Riddington *et al.* (1997) for wild geese. The consequence of this behaviour is an 'escape' of vegetation in areas that are left ungrazed.

### *Declining nutrient intake rates*

Several reasons can result in a declining performance of the herbivores, when levels of biomass increase. In our experimental study, a decline in instantaneous intake rate of mass was observed (Figure 5.4C), presumably due to increased handling time. Such a decline in instantaneous intake rate has previously only been demonstrated for Wigeon *Anas penelope* (Durant 2001) and Barnacle Geese (van der Wal *et al.* 1998), but most of the functional response models published for herbivores (Spalinger & Hobbs 1992; Gross *et al.* 1993; Illius & Gordon 1999; Schwinning & Parsons 1999), follow the type II response as defined by Holling (1959). Above that, in our experiment, we also observed a small decrease in forage quality, measured as nitrogen content (Figure 5.4D), with increasing levels of biomass. The protein content and digestibility are



often related negatively to standing biomass (Riddington *et al.* 1997) and maturation stage (Demment & van Soest 1985; van Soest 1994). Hence, the intake rate of nitrogen or energy declines with biomass at the short (Hassall *et al.* 2001; Chapter 2) or the longer term (Arnold 1964; Fryxell 1991). Note that the formulation of the functional response used in the present model study yields equivalent results to the multiplication of a Holling II functional response with a function describing a declining forage quality with increasing biomass. Finally, there may be other factors leading to a lower performance of herbivores in taller swards, such as differences in vegetation composition or increased costs of locomotion and vigilance.

### *Model predictions*

The inclusion of spatial heterogeneity in our model, in combination with a dome-shaped functional response leads to fundamentally different predictions than many of the existing alternative models. Under the assumption of a continuously increasing functional response (Ungar & Noy-Meir 1988; Vickery *et al.* 1995; Percival *et al.* 1996; Lang *et al.* 1997; Illius & Gordon 1999; Pettifor *et al.* 2000), the herbivores would be predicted to always select the patches with highest vegetation density. In the absence of strong interference, this leads to a homogenisation of biomass levels across patches (Sutherland 1996). In contrast, our model and that by Hutchings & Gordon (2001) predict the emergence of shortly grazed patches among otherwise ungrazed vegetation. In the field, such patterns have been described for cattle (Andresen *et al.* 1990; Gibb *et al.* 1997), geese (Spaans & Postma 2001) and sheep (Arnold 1964) at the scale of hundreds of meters, as well as for sheep at small (cm, Berg *et al.* 1997) to intermediate scales (m, Kiehl 1997).

Herbivores can increase their grazing intensity locally in response to increasing productivity, by the behavioural response of aggregation in space or time. This phenomenon was implied by Fryxell (1991), and specifically mentioned or modelled by McNaughton (1984), Arnold (1964) and Hutchings & Gordon (2001). In contrast to Hutchings & Gordon (2001) and Fryxell (1991) our model predicts that the intake per individual is independent of overall herbivore density, in highly productive habitat (Figure 5.7). The crucial difference is found in our assumption that the herbivores are able to relocate and re-graze previously visited patches. This is a reasonable assumption for geese in homogeneous polder grassland, given the fact that birds walking in flocks graze contiguous areas and that the birds are highly mobile. In the model by Hutchings & Gordon (2001), and the field data by Arnold (1964), sheep have lower performance at low stocking rate as the probability of encountering previously grazed patches is lower under these circumstances.

Effectively, when patches are abandoned, the consumption by the herbivores as a group is matched to the primary production in the continuously grazed area. In theory, the habitat could now be utilised at the level of biomass that would yield the maximum rate of intake. However, our simulation study shows that this situation only arises under the specific model assumptions of biomass independent primary productivity,

absence of travel costs and an error-free determination of patch profitability. A biologically realistic assumption of limited information, defined as an error in the perceived rate of intake of the model patches, leads to a certain degree of over-exploitation in the continuously grazed patches and a reduced intake. This effect is stronger at high levels of primary production and affected by the patch size used in the model. Due to limited information, the herbivores initially do not immediately respond to the fact that vegetation has grown beyond the optimum level of biomass. Then, after feeding for a while on an area larger than what would be ideal, they concentrate on an area that is smaller than the optimum size, given the current level of production and depletion occurs. Under biomass-dependent growth the effects of depletion can be very strong due to a positive feedback between biomass and primary production. The same phenomenon was observed by WallisDeVries (1996), and is partly related to the discrete character of the model (See box 5.1, page 107). However, it points at a more general finding that vegetation 'escapes' more easily than it is 'recaptured'. Vegetation that has grown beyond the point of maximum intake requires relatively high grazing pressure before it can turn back to a state of low biomass. However, most of the grazing pressure is focussed on remaining patches in a low biomass state, and thus the net difference between growth and consumption is mostly positive. Any factor that disrupts an exact match between consumption and production either leads to a situation where the herbivores deplete the continuously grazed patches and feed with lower intake rate or where they are forced to eat with low intake rate at patches with high biomass levels. Examples of these factors are fluctuations in primary production, travel costs (WallisDeVries 1996), search time (Hutchings & Gordon 2001) and social interactions. In practice several processes can buffer these effects. Apart from increasing production over time, there can be a decreasing consumption due to emigration. In the case of the Brent Geese there is a continual movement towards the marsh habitat and staging sites that are further along the route to the breeding sites.

An implication of our concept is that small groups, or even individual herbivores, are predicted to be able to regulate vegetation density in highly productive systems. This is in contrast to predictions by van de Koppel *et al.* (1996) which state that the density of small herbivores will be low under conditions of high primary productivity. The apparent discrepancy with the model by van de Koppel *et al.* (1996) is found in the time scale that is considered. Van de Koppel *et al.* (1996) only allow for a population numerical response of the herbivores rather than an aggregative numerical response, and they implicitly assume that systems characterised by high primary productivity are also characterised by different successional stages of vegetation. We illustrate that, within a season, herbivores may be able to regulate vegetation density in a restricted area by an aggregative response. However, the limited grazing intensity in the remainder of the area can result in a vegetational change, rendering the habitat unsuitable in the long run. Temporary absence of herbivores for other reasons, e.g. breeding in the case of the Brent Geese can also allow vegetation succession to proceed (Adam 1990). Under these circumstances, the grazing system will remain stable only when the original composition of the sward is maintained by larger herbivores or farming activities.



The experiments by Stock & Hofeditz (2000) illustrate this process. After the removal of sheep at the salt marsh on the Hamburger Hallig (Germany), vegetation composition of the productive sward, once dominated by *Puccinellia maritima*, started to change and slowly lost its value for Barnacle Geese in autumn and spring.

### *Model variations and limitations*

Productive habitats in which these processes occur are not isolated, but are often used in conjunction to other habitats. In our example of the Brent Goose, the productive polder grasslands are used in spring prior to moving to salt marsh habitat. Based on the theory of Ideal Free distribution (Fretwell & Lucas 1970), it is to be expected that the timing of a switch to alternative habitat is dependent upon the relative fitness, often approximated by the relative rates of intake, that can be achieved in either habitat. For conservation purposes it is desirable to be able to predict the timing of switches between habitat and the rates of intake achieved. However, the current model does not allow such a prediction as the effects of hysteresis lead to non-robust model behaviour. Especially under logistic growth, the results are dependent upon settings of the model that are not biologically relevant, such as model patch size and model step size. This problem is not encountered in models that use a continuously increasing functional response, or that analyse system behaviour under equilibrium conditions. We suggest to explore next whether different foraging rules and different model structures would alter our conclusions and predict intake rate of herbivores in a robust and reliable manner. An example of such a model could be one in which patch-choice decisions are taken at multiple levels of scale, a suggestion that was also raised by Spalinger & Hobbs (1992), with small-scale displacements (e.g. by walking) between time steps and larger scale movements (e.g. flying) after longer time intervals. Such a model variation would obey the experimental result by WallisDeVries *et al.* (1999) that foraging selectivity is scale-dependent.

In contrast to the patch depletion models presented by Sutherland (1996), the effects of interference cannot be studied as easily in our patch model, under the assumption of a dome-shaped functional response and high primary productivity. The reason for this lies in the fact that the size of patches needs to be small and the number of patches high, in order to prevent artefacts of scale. As grazing in the patches with biomass densities lower than the optimum value for intake rate results in an homogenisation of patches with regard to biomass, there are many patches with only very little difference in potential (interference free) intake rate. Direct interference will lead to a dilution of birds over multiple patches, without affecting their intake, unless additional assumptions are made regarding interactions across patch boundaries. In spite of this, the grazing intensity per patch will remain the same, as individual birds will exert the same grazing pressure in a patch in multiple time steps as multiple birds would have exerted in a single time step.

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## References

- Abrams PE (1982) Functional responses of optimal foragers. *Am. Nat.* 120: 382-390
- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Andresen H, Bakker JP, Brongers M, Heydemann B, Irmiler U (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137-148
- Arnold GW (1964) Factors within plant associations affecting the behaviour and performance of grazing animals. In: Crisp DJ (ed) *Grazing in terrestrial and marine environments*. Blackwell Scientific, Oxford, pp 133-154
- Berg G, Esselink P, Groeneweg M, Kiehl K (1997) Micropatterns in *Festuca rubra*-dominated saltmarsh vegetation induced by sheep grazing. *Plant Ecology* 132: 1-14
- Boudewijn TJ, Ebginge BS (1994). General review. Dark bellied Brent Geese in the Wadden Sea area. In: van Nugteren J (ed) *Brent Geese in the Wadden Sea. The Dutch society for the preservation of the Wadden Sea*, Harlingen, pp 39-49
- Clutton-Brock TH, Guinness FE, Albon SD (1982) *Red deer*. University of Chicago Press, Chicago
- Demment MW, van Soest PJ (1985) A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125: 641-672
- Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anatidae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle
- Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 17-36
- Fryxell JM (1991) Forage quality and aggregation by large herbivores. *Am. Nat.* 138: 478-498
- Gibb MJ, Huckle CA, Nuthall R, Rook AJ (1997) Effect of sward surface height on intake and grazing behaviour by lactating Holstein Friesian cows. *Grass Forage Sci.* 52: 309-321
- Gross JE, Shipley LA, Hobbs NT, Spalinger DE, Wunder BA (1993) Functional response of herbivores in food-concentrated patches: Tests of a mechanistic model. *Ecology* 74: 778-791
- Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. *Oecologia* 127: 97-104
- Hobbs NT, Swift DM (1988) Grazing in herds: when are nutritional benefits realized? *Am. Nat.* 131: 760-764
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91: 385-398
- Hutchings NJ, Gordon IJ (2001) A dynamic model of herbivore-plant interactions on grasslands. *Ecol. Mod.* 136: 209-222
- Illius AW, Gordon IJ (1991) Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. *J. Agr. Sci.* 116: 145-158





- Illius AW, Gordon IJ (1999) Scaling up from functional response to numerical response in vertebrate herbivores. In: Olff H, Brown VK, Drent R (eds) *Herbivores: between plants and predators*. Blackwell Sciences, Oxford, pp 397-425
- Kiehl K (1997) Vegetationsmuster in Vorlandsalzwiesen in Abhängigkeit von Beweidung und abiotischen Standortfaktoren. Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg e.V., Kiel
- Lang A, Houston A, I, Black JM, Pettifor RA, Prop J (1997). From individual feeding performance to predicting population dynamics in barnacle geese: The spring staging model. In: Mehlum F, Black JM, Madsen J (eds) *Proceedings of the Svalbard Goose symposium*. Norsk-Polarinstitut, Oslo, pp 203-211
- Langvatn R, Hanley TA (1993) Feeding-patch choice by red deer in relation to foraging efficiency: An experiment. *Oecologia* 95: 164-170
- McNaughton SJ (1976) Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science* 191: 92-94
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form and coevolution. *Am. Nat.* 124: 863-886
- Owen M (1971) The selection of feeding site by white fronted geese at the new grounds, Slimbridge. *J. Appl. Ecol.* 9: 385-398
- Owen M (1980) *Wild geese of the world*. Batsford Ltd., London
- Percival SM, Sutherland WJ, Evans PR (1996) A spatial depletion model of the responses of grazing wildfowl to the availability of intertidal vegetation. *J. Appl. Ecol.* 33: 979-992
- Pettifor RA, Caldow RWG, Rowcliffe JM, Goss-Custard JD, Black JM, Hodder KH, Houston AI, Lang A, Webb J (2000) Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *J. Appl. Ecol.* 37 Suppl. 1: 103-135
- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153-160
- Schwinning S, Parsons AJ (1999) The stability of grazing systems revisited: spatial models and the role of heterogeneity. *Funct. Ecol.* 13: 737-747
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Spalinger DE, Hobbs NT (1992) Mechanisms of foraging in mammalian herbivores: New models of functional response. *Am. Nat.* 140: 325-348
- Stahl J (2001) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD thesis University of Groningen, Groningen
- Stahl J, Rothkegel C, Drent RH (2001) Staging barnacle and brent geese versus resident brown hare: crossing the boundary between facilitation and resource competition. In: Stahl J (ed) *Limits to the co-occurrence of avian herbivores. How geese share scarce resources*. University of Groningen, Groningen
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitates durch Nonnen- und Ringelgänse. In: Stock M, Kiehl K (eds) *Die Salzwiesen der Hamburger Hallig*. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 43-55
- Sutherland WJ (1996) *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford
- Ungar ED, Noy-Meir I (1988) Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. *J. Appl. Ecol.* 25: 1045-1062
- van de Koppel J, Huisman J, van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745
- van de Koppel J, Rietkerk M, van Langevelde F, Kumar L, Klausmeier CA, Fryxell JM, Hearne J, van Andel J, de Ridder N, Skidmore A, Stroosnijder L, Prins HHT (2002) Spatial Heterogeneity and Irreversible Vegetation Change in Semiarid Grazing Systems. *Am. Nat.* 159: 209-218
- van der Wal R, van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos* 82: 123-130
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69

- van Soest PJ (1994) Nutritional Ecology of the ruminant. Cornell University Press, Ithaca (NY)
- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark-bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499-508
- WallisDeVries MF (1996) Effects of resource distribution patterns on ungulate foraging behaviour: a modelling approach. *Forest Ecology and Management* 88: 167-177
- WallisDeVries MF, Laca EA, Demment MW (1999) The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia* 121: 355-363
- Wilmschurst JF, Fryxell JM, Hudson RJ (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behav. Ecol.* 6: 209-217
- Ydenberg RC, Prins HHT (1981) Spring grazing and the manipulation of food quality by Barnacle Geese. *J. Appl. Ecol.* 18: 443-453
- Zar JH (1996) Biostatistical Analysis. Prentice-Hall, Inc., N.J.



## Box 5.1 Vegetation 'escapes' more easily than it is 'recaptured'

Daan Bos & Johan van de Koppel

Ecological theory predicts that herbivores can benefit from aggregation in productive habitat (McNaughton 1984; Fryxell 1991; Hutchings & Gordon 2001), when foraging efficiency decreases at high plant standing crop. By focusing on a limited part of the grazing area, a short sward is maintained, and intake is kept at a high level. Results of experimental field studies are in line with this hypothesis (Wilmshurst *et al.* 1995; Wilmshurst & Fryxell 1995), and aggregation is observed in the field (Spaans & Postma 2001). A spatially implicit simulation study, described in this chapter, indeed indicates that short-term foraging decisions, where herbivores consistently opt for swards with intermediate levels of biomass, may lead to patterns of aggregation in productive habitat. However, the simulation also revealed that, in spite of an over-abundance of food in the entire area, local depletion of standing biomass may take place in swards that are continued to be grazed by the herbivores. This phenomenon occurs when the area on which the herbivores have concentrated their grazing effort is too small to yield sufficient primary production to compensate for grazing losses, for instance due to a decrease in primary productivity, due to sub-optimal foraging decisions of the herbivore (Arnold 1964; WallisDeVries 1996), or due to an increase in herbivore numbers. The simulation results were sensitive to the values of patch size and time step size chosen, and insight in the robustness of these results is thus hampered by discretisation effects (this chapter). We thus seek analytical confirmation of the suggestion put forward in this chapter, that vegetation, once escaped to a state of high plant standing crop, may not easily be grazed back again to a state of low plant standing crop.

Following the framework of van de Koppel *et al.* (2002), we developed a spatially-implicit model of plant growth and herbivore grazing within a bounded area  $D$ . The net rate of change of plant biomass at a particular location  $x,y$  within  $D$  is described as:

$$\frac{dB}{dt} = G(B) - F(B)N \quad (1.)$$

where  $G$  describes plant growth as a function of local plant standing crop ( $B$ ), and  $F$  describes consumption of herbivores as a function of local plant and herbivore density ( $N$ ). We specified the model further by assuming that plant growth is maximal at low plant standing crop, and decreases linearly with increasing plant standing crop (Figure box5.1):

$$G(B) = r \left( 1 - \frac{B}{K} \right) \quad (2.)$$

Here,  $r$  is a growth coefficient of the vegetation and  $K$  is the carrying capacity. We assume that herbivore consumption rate first increases with plant standing crop, but later decreases due to constraints on intake (this chapter):

$$F(B) = a \frac{B}{1 + a(h_0 + h_1 B)} \quad (3.)$$

where  $a$  is the search rate, and  $h_0$  and  $h_1$  are constants defining the handling time. More general, this phenomenon of a declining foraging efficiency could alternatively be caused by

constraints on digestion (Fryxell 1991) or a negative correlation between nutrient content and plant standing crop (Hassall *et al.* 2001). The consumption rate in vegetation with intermediate values of plant standing crop is thus higher than that in vegetation with high plant standing crop. Here, we assume that local herbivore density is proportional to the per capita herbivore consumption in the spot under consideration:

$$N = \alpha \cdot F(B) \quad (4.)$$

This situation may arise, for example, when emigration from, or immigration to a patch are affected by the intake in that patch. The total amount of herbivores in the area can be expressed as the integral over the entire area  $D$ , for both sides of the equation:  $\int \int N \, dx dy = \int \int \alpha F(B) \, dx dy$ . By taking  $\alpha$  out of the integral and by dividing both sides by the size of domain,  $A$ , we can express  $\alpha$  as  $N_{avg} / F_{avg}$ , where  $N_{avg} = \int \int N \, dx dy / A$  and  $F_{avg} = \int \int F(B) \, dx dy / A$ . Substitution in equation 4 now produces:

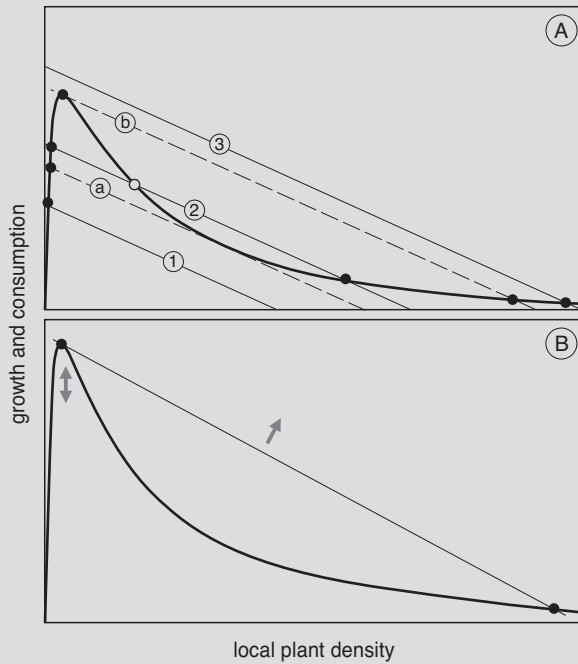
$$N = \frac{N_{avg}}{F_{avg}} \cdot F(B) \quad (5.)$$

where  $N_{avg}$  refers to the average herbivore density over the area under consideration and  $F_{avg}$  equals the average intake in the entire area. This allows us to simplify the plant differential equation (1) to:

$$\frac{dB}{dt} = G(B) - F(B)^2 \frac{N_{avg}}{F_{avg}} = G(B) - C(B) \quad (6.)$$

The function  $C(B)$  is the “consumption curve” (Figure box5.1) describing the local amounts of forage removed by herbivores as a function of its local availability and the average consumption rate in the entire area. The shape of this function resembles  $F(B)$ , having the maximum at the same value of  $B$ .

Because we are interested in a system where primary production generally increases in the course of the season, we now investigate the effects of increased primary productivity on the balance between local plant growth and herbivore grazing (Figure box5.1A). We assume that an increase in primary productivity is reflected in a proportional increase in both  $r$  and  $K$ . If productivity is low (Figure box5.1A, solid line labelled ‘1’), only one equilibrium at low plant standing crop exists. At low productivity, herbivores are homogeneously distributed, and utilise the entire area. At intermediate levels of productivity there are two equilibria, one at high and one at low plant density (Figure box5.1A). At high levels of primary productivity, a situation may arise in which all vegetation is in a state of high plant density, indicated in Figure box5.1A by the one intersection of line ‘3’ with the consumption curve. In this situation the herbivores also use the entire area, but at low consumption rate per unit biomass. However, local intensification of herbivore grazing (aggregation) enables the herbivores to cope with these high levels of primary productivity up to a certain extent. The stippled line ‘b’ in Figure box5.1A refers to the upper level of primary productivity above which herbivores are not able to maintain a low plant density, and associated high consumption rates, in the entire area. After primary productivity has increased from low levels to this critical boundary level, a further increase in productivity leads to a spatial bifurcation in plant standing crop. According to our model, focusing of herbivore grazing allows a part of the vegetation to escape to high standing crop. We made one extra assumption, that patches of vegetation ‘escape’ from grazing one by one, and turn to a



**Figure box5-1** Plant growth and herbivore consumption for a small-scale location within the area of consideration. The straight lines represent plant growth ( $G(B)$ , lines 1,-2,3, a and b), for different levels of productivity ( $r$  and  $K$ ), and the curves represent herbivore consumption ( $C(B)$ ). A) Given a level of average consumption, the system may have one or two stable states, depending on the level of primary productivity. Stable states are indicated with black solid dots, an unstable state is given by an open circle. Lines 1, 2 and 3 refer to low, intermediate and high levels of primary productivity respectively. Stippled lines a and b refer to the boundary conditions of plant growth below and above which local plant density in part of the area switches to a different state. B) Aggregation by herbivores under increasing primary productivity is expressed in a steeper herbivore consumption curve, as indicated by the grey arrows.

state of high plant density, rather than all turning to the state of high plant density at once. So the herbivores aggregate on patches with low plant density, where consumption rates are highest, allowing them to maintain a short sward in that part of the area. The aggregation of herbivores, in response to the higher levels of primary production, leads to a change in the consumption curve, which is illustrated in Figure box 5.1B. The consumption curve becomes steeper. This means that more biomass is removed per unit area in the patches that are continued to be grazed. Mathematically, this is caused by a net decrease in average consumption,  $F_{avg}$ , because the herbivores spend part of the time foraging in patches with high plant density and associated low intake rate. With every subsequent increase in primary productivity, more patches escape from grazing and aggregation becomes more pronounced.

The point that we would like to stress here is that there is a large 'barrier' for the herbivores to regain patches of vegetation that have turned to a state of high plant density. The primary productivity has to diminish below the level of consumption in the high biomass state, before vegetation in a patch will return to a low biomass state. This mathematical condition is indicated by the stippled line 'a' in Figure box5.1A. The critical level to which productivity has to decrease to allow the herbivores to 'recapture' vegetation in ungrazed swards (line 'a' in Figure box5.1A) is much lower than the critical level at which vegetation starts to 'escape' (line 'b' in Figure box5.1A). As a result, when part of the vegetation has escaped from grazing control following an increase in productivity, the vegetation is not recaptured when productivity returns to the former levels. Rather than that, a decrease occurs in plant density in the patches that are still under intensive herbivore grazing and, depending on the degree of the decline in productivity, this may lead to a decline in intake rate of the herbivores. This indicates that, in productive systems, a herbivore population is vulnerable to fluctuations in primary productivity, as loss of control over grazed swards cannot be easily regained.

In summary, the model analysis confirms that a hump-shaped functional response in herbivores leads to spatial bifurcation in plant standing crop at high levels of productivity. Beyond a threshold production level, increased primary production leads to a progressive release of vegetation from herbivore control. This vegetation will develop a high standing crop, unsuitable for herbivore grazing, whereas focusing of herbivore activity maintains a short sward in the remaining part of the vegetation. This way, herbivore foraging efficiency remains high, despite a distinct decrease in the overall suitability of the vegetation. However, the analysis indicates that temporary fluctuation in productivity, commonplace in natural environments, may lead to a less than optimal intake, as suitable vegetation becomes depleted. These findings support the results from the simulation study mentioned above (this chapter).

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# 6

CHAPTER

## Long-term vegetation changes in experimentally grazed and ungrazed back barrier marshes in the Wadden Sea

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### Abstract

Vegetation succession in three back-barrier salt marshes in the Wadden Sea was studied using a data set comprising 25 years of vegetation development recorded at permanent quadrats. The effect of livestock grazing on succession was assessed by comparing quadrats where grazing was experimentally prevented or imposed. We studied changes at the species level as well as at the level of the plant community. Special attention is given to effects on plant species richness and community characteristics that are relevant for lagomorphs (hares and rabbits) and geese. Inundation frequency and grazing were most important in explaining the variation in species abundance data. The three marshes studied overlap in the occurrence of different plant communities and the observed patterns were consistent between them. Clear differences in frequency and abundance of plant species were observed related to grazing. Most plant species had a greater incidence in grazed treatments. Species richness increased with elevation, and was 1.5 to 2 times higher in the grazed salt marsh. Grazing negatively influenced *Atriplex portulacoides* and *Elymus athericus*, whereas *Puccinellia maritima* and *Festuca rubra* showed a positive response. The communities dominated by *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* were restricted to the ungrazed marsh. Communities dominated by *Puccinellia maritima*, *Juncus gerardi* and *Festuca rubra* predominantly occurred at grazed sites. As small vertebrate herbivores prefer these plants and communities for foraging, livestock grazing thus facilitates for them.

## Introduction

Vegetation succession in salt marshes has been described by various authors for many different marsh types (Ranwell 1968; Westhoff 1987; Adam 1990). Salt marshes are suitable systems for studying vegetation succession because they are relatively simple and species-poor. Understanding the patterns of development and the processes behind them helps to gain insight into the functioning of ecosystems in general and is relevant for the sustainable management of salt marshes.

### *Elevation and sedimentation*

Elevation of the marsh plays an important role in structuring salt-marsh ecosystems, as it is directly related to inundation frequency and hence to sediment deposition, evaporation, aeration, nutrient status, temperature and salinity (Adam 1990). The distributions of salt-marsh plants are strongly related to the gradients in elevation (Sanchez *et al.* 1996; Olff *et al.* 1997). Sediment type also affects vegetation composition to a large extent and is influenced by the position of the marsh in the tidal basin. Back-barrier salt marshes, or barrier-connected marshes according to de Jong *et al.* (1999), have developed on top of a sandy substrate, show less sediment accretion and have soils with a thinner layer of clay than more sheltered mainland salt marshes (Dijkema 1983a). Olff *et al.* (1997) showed that the pool of nitrogen is positively related to the thickness of the clay layer. They studied a chronosequence on one of these back-barrier marshes and they concluded that succession there is caused mainly by the continual increase in nutrient availability. In back barrier salt marshes, most elevational variation is caused by elevational differences in the sandy subsoil (van Wijnen & Bakker 1997), and each elevational position was shown to have its own characteristic successional sequence. The final stages on high and low marsh are characterised by tall-growing species (Olff *et al.* 1997), suggesting that light competition becomes more important with increasing nutrient availability. Similar conclusions were drawn from studies in which permanent quadrats have been studied for several years (Bakker 1985; Jensen 1985; Roozen & Westhoff 1985), though the study period is often short, relative to the speed of vegetation change.

### *Grazing with livestock*

Grazing with livestock affects biotic and abiotic components of the marsh (Jensen 1985; van Wijnen *et al.* 1999). Empirical studies show that short-growing plants characteristic of early succession are favoured by grazing (Aerts *et al.* 1996; Kiehl *et al.* 1996). Ungrazed high marshes tend to become dominated by tall *Elymus athericus* (Andresen *et al.* 1990; Olff *et al.* 1997), and tall *Atriplex portulacoides* becomes dominant on the low marsh (Bakker 1985; Jensen 1985; van der Wal *et al.* 2000b). Brackish marshes become covered with tall *Phragmites australis* when grazing is absent. This happens, for example, in estuarine marshes such as the Dollard (Esselink *et al.* 2000)





or close to large dune systems where fresh water is seeping through (Hobohus 1986; Neckermann 1987). The plant species richness is higher in grazed than in ungrazed high marsh (Bakker 1989) at the scale of 4m<sup>2</sup>.

### *Importance of marshes and their management by grazing*

Salt marshes in the Wadden Sea are important spring staging habitat for waterfowl such as Brent *Branta bernicla bernicla* and Barnacle Geese *Branta leucopsis* and a year round habitat for lagomorphs, such as hares *Lepus europaeus*. These small vertebrate herbivores forage on low plant species such as *Puccinellia maritima*, *Festuca rubra*, *Triglochin maritima* and *Plantago maritima* (Prop & Deerenberg 1991; van der Wal *et al.* 2000a). Natural succession of salt marshes has been shown to affect the occurrence of these plants, leading to a decline in the importance of the marsh as a habitat for these small herbivores (van de Koppel *et al.* 1996; van der Wal *et al.* 2000b).

From 600 BC onwards, salt marshes in the Wadden Sea have been grazed with livestock in summer (Behre 1985) and currently about half of the marsh area in the Wadden Sea is grazed (de Jong *et al.* 1999). Large areas of marsh have been taken out of grazing over the past twenty years due to lack of interest from farmers (Dijkema 1983b) or for nature conservation purposes (Stock & Kiehl 2000). Grazing is still one of the most important and common management tools on salt marshes and, therefore, proper insight is required into effects of grazing on salt-marsh ecosystems. In this paper we describe vegetation development in different plant communities, where grazing with livestock was experimentally ceased or imposed. The goal of the analysis presented here was 1) generalisation of effects of grazing management at back-barrier marshes in the Wadden Sea, 2) comparison of short term and long-term experiments and 3) evaluation of effects of livestock grazing on plant species that are important for other herbivores such as geese and hare. The patterns of development between high and low marsh were compared using data from three back barrier salt marshes over a period of more than 25 years.

## **Methods**

### *Study sites and permanent quadrats*

The study was performed at six study sites on the two Dutch Wadden Sea islands of Terschelling (53°26'N, 5°28'E), Schiermonnikoog (53°30'N, 6°10'E) and the Danish peninsula of Skallingen (55°30'N, 8°20'E), (Appendix 1). All these marshes are characterised by a sandy substrate and classified as back-barrier salt marshes (de Jong *et al.* 1999). Extensive parts of these marshes are grazed with livestock. On Skallingen c. 1100 ha are grazed with 0.5 cow ha<sup>-1</sup> and 0.5 sheep ha<sup>-1</sup> (Jensen 1985). The western part of the Terschelling marsh (200 ha) is grazed with cattle at a stocking density of 0.5 cow ha<sup>-1</sup> (State Forestry Commission, pers. comm.). On Schiermonnikoog stocking rates decreased from 1.5 cow ha<sup>-1</sup> in the 1970s to 0.5 cow ha<sup>-1</sup> at 400 ha, from 1995

onwards. None of the marshes in our study are artificially drained. Tidal amplitude ranges from 1.5 m at Skallingen to 2.3 m at Schiermonnikoog (van Wijnen & Bakker 1997).

In the early 1970s, exclosures were erected and areas were fenced off at the six study sites (see Appendix 1). Two exclosures were constructed on the grazed marsh at Terschelling in 1972 (site 1 and site 2) with a size of 30 x 30 m, and observations started in 1976. At Schiermonnikoog (site 4 and site 5) seven exclosures measuring 50 m x 12.5 m were built in 1974 and 1972 respectively, while observations had started one year before that. Six exclosures of 40 m x 60 m, constructed in 1972 (Jensen 1985), were studied at Skallingen (site 6) from 1976 onwards. In addition, hitherto ungrazed areas were grazed anew in 1972 on Terschelling (site 3) and on Schiermonnikoog (site 5). All this resulted in four experimental treatments. Those quadrats on which grazing by livestock was stopped or imposed are referred to as 'experimentally ungrazed' and 'experimentally grazed', respectively. The other quadrats are classified as 'control grazed' and 'control ungrazed' because no experimental change in management took place.

Paired 2 m x 2 m quadrats were established inside and outside the grazing treatments. Vegetation relevés were made annually at Schiermonnikoog and every three years at Skallingen and Terschelling. The relevés were made in late summer, initially according to the scale of Braun-Blanquet (Westhoff & van der Maarel 1973), from 1976 onwards following the decimal scale (Londo 1976). The Braun-Blanquet data were transformed to percentage values as described by Bakker (1989). Nomenclature of taxa following van der Meijden (1990) and syntaxa according to Schaminée *et al.* (1998). A total of 2596 relevé recordings were used in the present study, up to and including 1998. The majority of these were made on Schiermonnikoog where 58 quadrats were studied for 26 years. The total number of recordings was 72 for site 1 and site 2, while all other sites have more than 372. At each study island, the quadrats were positioned over the entire tidal range from low to high marsh. In 1999 the clay thickness was measured in triplicate and averaged per quadrat. We measured elevation of each individual quadrat with respect to mean high tide (MHT). Subsequently, the inundation frequency was calculated following van Wijnen & Bakker (1997).

### *Data analysis*

We tested whether a linear or unimodal multivariate model should be used, and accepted the unimodal model. Thus Canonical Correspondence Analysis (CCA; Jongman *et al.* 1995) was performed to obtain an overview of the major patterns in the 1989 data set. We chose for the year 1989, because after that year a number of quadrats was discarded and this year, therefore, yielded the largest variation. The vegetation data for the start and the end year of quadrats that were followed for more than 20 years were used to calculate the position of these recordings in the ordination diagram, without influencing the ordination. Species data were log-transformed and rare species were down-weighted to reduce their influence on the analysis. Inundation frequency, grazing status, thickness of the clay layer and site were entered as environmental variables.



A Monte Carlo permutation test was used to test the significance of the environmental variables that were selected in the forward selection procedure.

Frequencies of occurrence per plant species were calculated for each treatment and site. The analysis of frequencies was restricted to quadrats that had a constant treatment for more than 20 years. By so doing, bias caused by the fact that quadrats were in transition was minimised. Using a  $\chi^2$ -test, we tested deviations from an even distribution in the untransformed frequencies.

For each relevé, the number of species present was counted. Differences in species number between grazing treatments per year were tested for statistical significance using a paired t-test. The effect of elevation on species number for quadrats in the year 1989 was determined using an Analysis of Covariance (Ancova) with elevation as a co-variable and grazing as a factor.

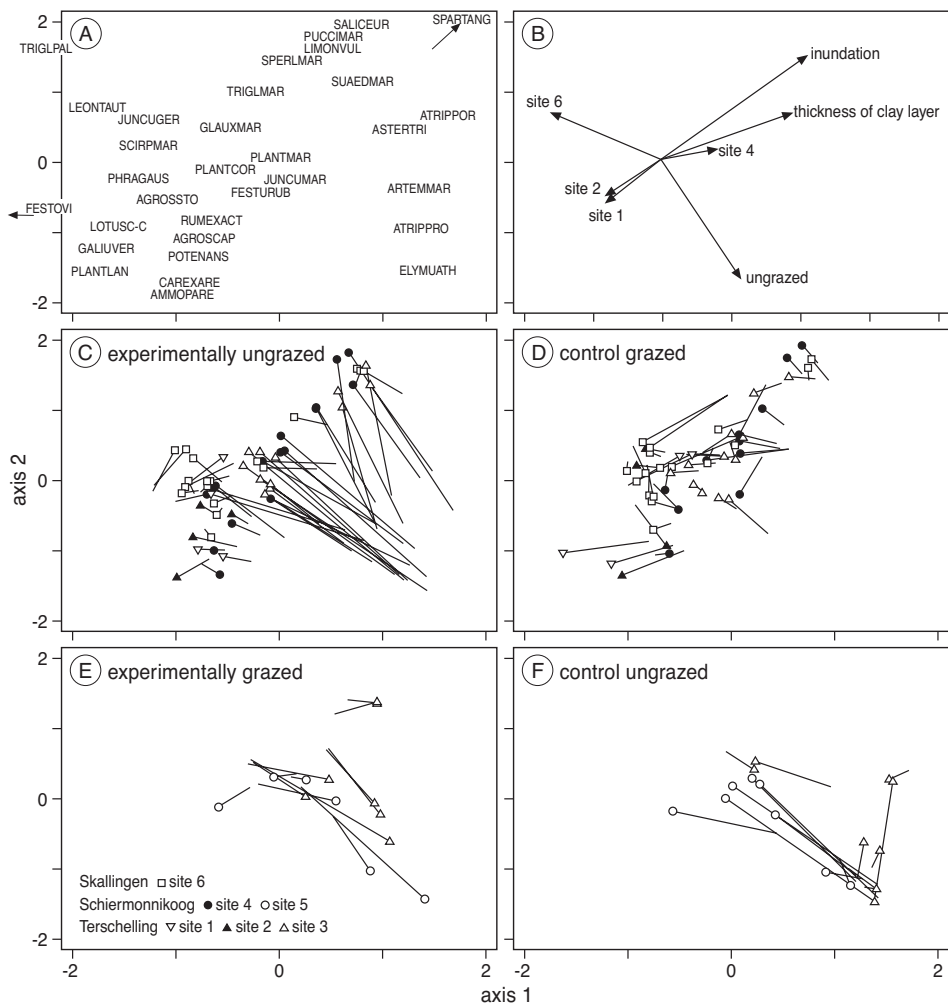
Species-specific responses for the 'experimentally ungrazed' and 'control grazed' treatments over time were analysed using the procedure described by Huisman *et al.* (1993). The best fitting significant model, from a predefined set of five hierarchical models, was selected for each species and treatment. The analysis was restricted to seven species that have particular relevance for grazing by small vertebrate herbivores: *Puccinellia maritima*, *Festuca rubra*, *Triglochin maritima*, *Plantago maritima*, *Artemisia maritima*, *Atriplex portulacoides* and *Elymus athericus*. No extra transformation of data took place. We analysed the developments in the low and high marsh separately and restricted the analysis to quadrats that were followed over the entire experimental period. We separated low and high salt marsh at a level of 50 inundations per year and assigned corresponding pairs of quadrats to these classes, based on the average inundation frequency of the pair. The boundary was arbitrarily drawn based upon the occurrence of plant communities in relation to inundation frequency in our data set. Other authors mention boundaries in the order of 100 inundations per year (Gray & Scott 1967; Erchinger 1985). The models were tested per study island, to assess the generality of the patterns found.

All relevés were identified to association according to Schaminée *et al.* (1998), with support of computer program Salt97 (de Jong *et al.* 1998). Vegetation change at the level of the association was then analysed by summarising the frequency of occurrence of each association in relation to grazing for the final year of study.

## Results

### *Overview of the dataset, interaction of grazing and abiotic conditions*

The relevés were significantly separated along axes correlated to grazing status and inundation frequency in the CCA (Figure 6.1A-F). The total variation explained by the first four hypothetical axes was 22% for the species data and 87% for the species-environment data. Vectors for the environmental variables inundation frequency, clay layer thickness, grazing status and site (Figure 6.1B) yield information about their influence on the vegetation composition; the length of these vectors is a measure of the magnitude of this influence. Clay-layer thickness was positively related to inundation frequency.



**Figure 6.1** Bi-plot of sample- and species-scores from the Canonical Correspondence Analysis (CCA) showing (A) The relative positions of 36 characteristic species, along the first two canonical axes. Species are referred to by the first five letters of the species and the first three letters of the genus name. (B) The vectors of the environmental variables that were significant and (C - F) The change of position in the ordination diagram between the start and the end year of quadrats in the four experimental treatments. (C) experimentally ungrazed, (D) control grazed, (E) experimentally grazed and (F) control ungrazed. The start year of observations is indicated by a symbol that also refers to the study site that the quadrat belongs to. The scale for figure 6.1B was multiplied by 5



Inundation frequency (Permutation test:  $F=11.1$ ,  $P < 0.005$ ,  $\text{LambdaA} = 0.29$ ) and grazing status (Permutation test:  $F= 8.7$ ,  $P < 0.005$ ,  $\text{LambdaA} = 0.22$ ) had the strongest correlations to the first and second canonical axes and were most important in explaining the observed variation. Grazing effects are independent from inundation frequency (the arrows in Figure 6.1B are perpendicular). The identity of four of the sites significantly explained some of the variation (Figure 6.1B,  $\text{LambdaA}$  ranges from 0.08 to 0.18). It is, however, not surprising that vegetation composition differs between sites, as the quadrats were not selected at the start of the study to be equal in this respect. For the purpose of this paper it is important that the patterns in development can be compared.

The lower-right part of the ordination diagrams (Figure 6.1A) is characterised by plants associated with the ungrazed marsh: *Elymus athericus*, *Atriplex prostrata* and *Artemisia maritima*. The plant species that occur at a higher elevation are found in the lower-left corner of the diagrams, e.g. *Festuca ovina* or *Galium verum* (Figure 6.1A). *Spartina anglica*, *Puccinellia maritima* and *Atriplex portulacoides* are species of the low marsh, found in the upper-right corner of figure 6.1A. The quadrats at site 1 and site 2 at Terschelling and some of the quadrats at Skallingen or Schiermonnikoog were positioned at the transition to low dunes (lower left corners of Figure 6.1B-F). At Skallingen and Terschelling, some quadrats harboured *Phragmites australis*, which was lacking in the Schiermonnikoog samples. *Elymus athericus* was never observed in the study quadrats at Skallingen, although the species was present at different locations on the peninsula. Quadrats at Skallingen also featured the occurrence of *Scirpus maritimus*, found in the upper left quadrant of the ordination diagram (Figure 6.1A).

The impact of grazing is very apparent from the trajectories that quadrats followed in the ordination diagram between the start and the end of our observation period. Experimentally ungrazed quadrats (Figure 6.1C) almost all moved to the lower right corner of the diagram, which is characterised by *Elymus athericus* and *Atriplex portulacoides*. Experimentally grazed quadrats (Figure 6.1E) showed exactly the opposite pattern. The ungrazed treatments at Skallingen (Figure 6.1C, open squares) differed in their development from those at Schiermonnikoog (open and closed circles) and at site 3 on Terschelling (open triangles), by the absence of *Elymus athericus*. Low marsh quadrats at Skallingen became dominated by *Atriplex portulacoides*, as occurred elsewhere, but were not invaded by *Elymus athericus* subsequently. At the upper ranges of elevation, the patterns of change were not obviously related to grazing, as quadrats in the lower left corner of figure 6.1C only moved short distances in an inconsistent direction. Some of the control ungrazed quadrats changed considerably over time (Figure 6.1F), indicating that their development had not yet reached a stable state, when the observations started.

### *Grazing management and species richness*

In all, 172 plant species were observed over the years. However, many species were only observed very infrequently. Eighty percent of the species show a higher incidence at grazed than at ungrazed sites with constant treatment for more than 20 years. Of the 30 most frequent species on salt marshes (Table 6.1) only *Artemisia maritima*,

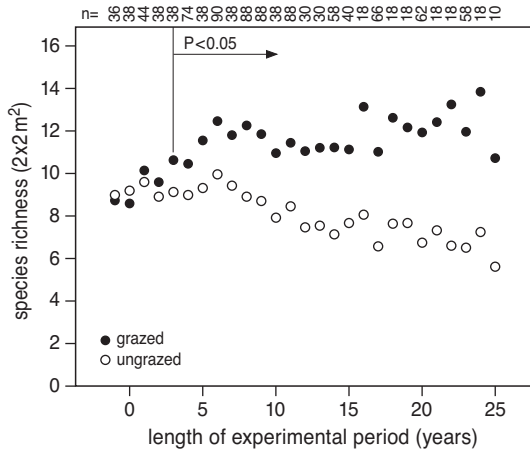
*Atriplex prostrata*, *Elymus athericus* and *Atriplex portulacoides* showed significantly greater incidence without grazing ( $\chi^2$  -test,  $P < 0.05$ ). The differences in species presence between treatments is due to species observed very rarely (i.e. less than 1% of the cases). Observations of species only found in a single treatment happen more often in the grazed than in the ungrazed quadrats (57 versus 16 times, respectively). The total set of observed species in quadrats with constant treatment for more than 20 years contains 21 species on the Red List. Eleven of these do not occur in the ungrazed sites.

**Table 6.1** Frequencies (%) of species occurrence per treatment for the 30 species occurring most frequently. All relevés are included except those in transition for less than 20 years. Species are grouped depending on their response to grazing; For the groups 'higher in grazed' and 'higher in ungrazed', the frequencies deviate significantly from proportionality

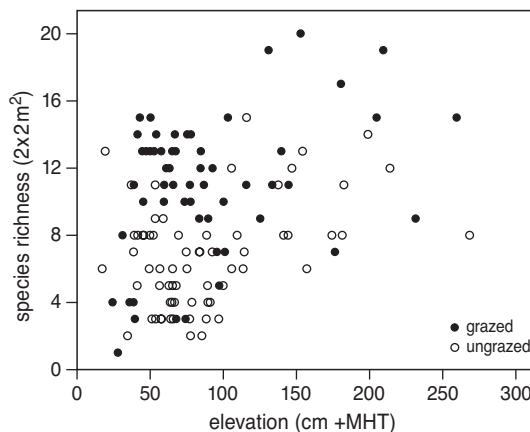
	Species	grazed	ungrazed
higher in ungrazed	<i>Artemisia maritima</i>	43	65
	<i>Atriplex prostrata</i>	19	68
	<i>Elymus athericus</i>	26	52
	<i>Atriplex portulacoides</i>	14	25
no significant difference	<i>Festuca rubra</i>	78	85
	<i>Juncus maritimus</i>	9	10
	<i>Lotus corniculatus</i>	8	10
higher in grazed	<i>Plantago maritima</i>	67	40
	<i>Agrostis stolonifera</i>	53	41
	<i>Juncus gerardi</i>	63	22
	<i>Glaux maritima</i>	58	22
	<i>Triglochin maritima</i>	49	23
	<i>Armeria maritima</i>	46	26
	<i>Puccinellia maritima</i>	43	23
	<i>Spergularia maritima</i>	43	10
	<i>Limonium vulgare</i>	39	12
	<i>Trifolium repens</i>	31	20
	<i>Aster tripolium</i>	36	15
	<i>Poa pratensis</i>	26	19
	<i>Salicornia europaea</i>	35	7
	<i>Suaeda maritima</i>	30	12
	<i>Plantago coronopus</i>	23	2
	<i>Potentilla anserina</i>	14	10
	<i>Agrostis capillaris</i>	15	6
	<i>Carex arenaria</i>	15	6
	<i>Leontodon autumnalis</i>	16	1
	<i>Phragmites australis</i>	14	3
	<i>Plantago lanceolata</i>	11	6
	<i>Ammophila arenaria</i>	10	6
	<i>Spergularia salina</i>	12	2



Plant species richness at the 2 m x 2 m scale was affected by succession and grazing (Figure 6.2). Species number showed a downward trend over time in ungrazed quadrats, whereas it increased in grazed quadrats. In three years, the grazed quadrats had significantly greater species numbers than their paired ungrazed counterparts (Figure 6.2, paired T-test,  $P < 0.05$ ,  $20 < n < 90$ ). With increasing elevation, species richness increased (Figure 6.3, Ancova,  $P < 0.001$ ,  $n = 132$ ). Species richness benefited from grazing with livestock on both the lower and higher salt marsh.



**Figure 6.2** The development of species richness over time in paired grazed and ungrazed permanent quadrats. Sample sizes ( $n$ ) per year since the start of the treatment are indicated in the top of the diagram. After a period of three years the differences between grazing treatments were significant, indicated by the arrow with text " $P < 0.05$ ". Observations for site 4 and 5 started one year before the treatments were installed.



**Figure 6.3** Relationship between elevation with respect to Mean High Tide (MHT) and the species richness in grazed and ungrazed permanent quadrats for the year 1989 (Ancova,  $df = 132$ ,  $R^2 = 0.38$ ,  $P < 0.01$  for the factors grazing and elevation).

Effects of changes in management on important species for geese and hare

Cessation of grazing led to an increased cover of *Elymus athericus* and *Atriplex portulacoides* and a decrease of *Puccinellia maritima* and *Festuca rubra* (Figure 6.4). *Plantago maritima* and *Triglochin maritima* also showed negative trends in the ungrazed quadrats, but their cover was generally very low (Appendix 2). *Artemisia maritima* at first benefitted from cessation of grazing on the low marsh, but later disappeared. Except for Skallingen, *Elymus athericus* quickly invaded the ungrazed high marsh. Even the low marsh of Terschelling and Schiermonnikoog was invaded by *Elymus athericus* after 15 years. *Festuca rubra* significantly declined in the ungrazed high marsh at two of the study islands. Its increase at the ungrazed low marsh of Terschelling was not paralleled at Schiermonnikoog or Skallingen. Cover values for *Elymus athericus*, *Atriplex portulacoides*

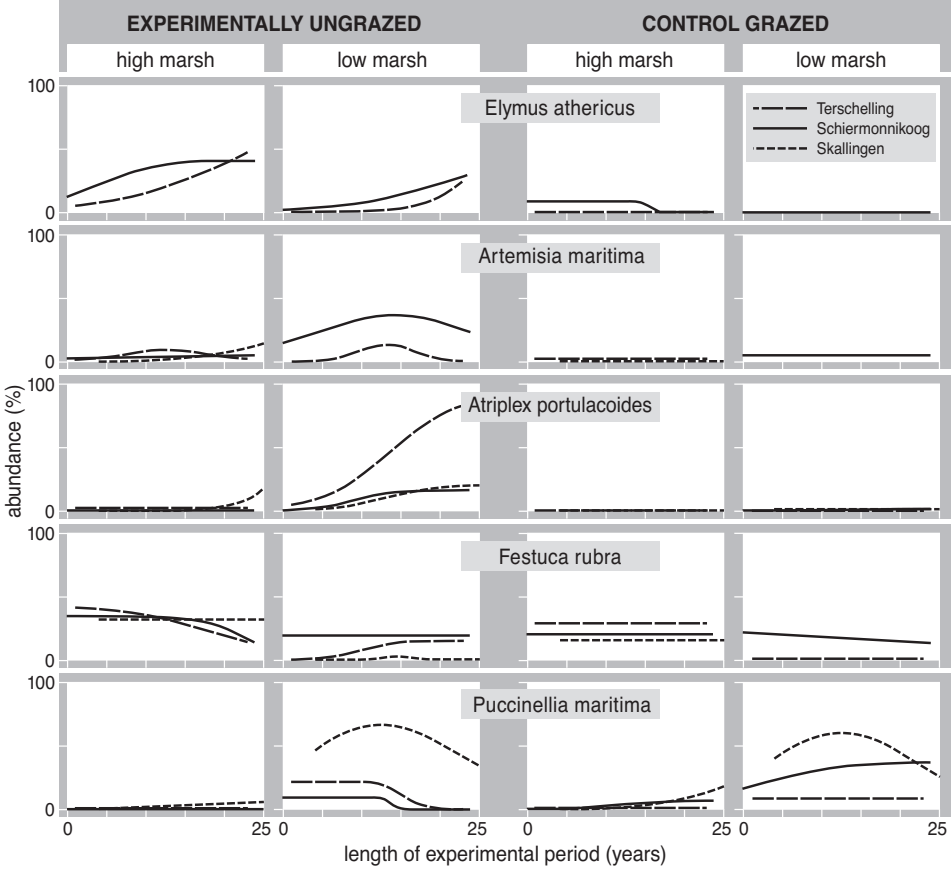


Figure 6.4 Species response curves showing the abundance of a selection of 5 species in relation to the duration of each of the grazing treatments, per study island and per level of inundation. Associated models and sample sizes are given in Appendix 6.2.





and *Artemisia maritima* remained constant and close to zero in the control grazed quadrats. However, at Skallingen, the cover of *Puccinellia maritima* initially increased and decreased again later, parallel to the development in the experimentally ungrazed marsh there. *Puccinellia maritima* increased in cover at the grazed low marsh of Schiermonnik-oog. Species response curves over time (Figure 6.4) showed essentially the same pattern for the three study islands. At Skallingen and at Terschelling, several of our excluded quadrats became dominated by *Scirpus maritimus* and *Phragmites australis* (not shown).

*Effects of grazing at plant community level*

Seven plant associations, as defined by Schaminée *et al.* (1998) occurred more than twice in our data set in the final year (Table 6.2). The Puccinellietum maritimae, Juncetum gerardii, Armerio-Festucetum, Atriplici-Agropyretum pungentis and the Lolio-Potentillion occurred most frequently. The Puccinellietum maritimae and the Juncetum gerardi were found more frequently in the grazed situation ( $\chi^2$ -test,  $P < 0.05$ ) and the Armerio-Festucetum almost significantly so ( $\chi^2$ -test,  $P < 0.10$ ). The Atriplici-Agropyretum pungentis, the Artemisietum maritimae and the Halimionetum portulacoides, associations characterised by *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* were exclusively found in ungrazed treatments. Fifty-eight percent of our ungrazed quadrats were classified to the latter associations.

**Table 6.2** Occurrence of plant communities per treatment in the final year of study (1996-1998). Plant communities are grouped depending on their response to grazing; For the groups 'higher in grazed' and 'higher in ungrazed', the frequencies deviate significantly from proportionality ( $\chi^2$ -test,  $P < 0.05$ ).

	Association	Grazed	Ungrazed
higher in ungrazed	Halimionetum portulacoides		6
	Artemisietum maritimae		7
	Atriplici-Agropyretum pungentis		34
higher in grazed	Puccinellietum maritimae	14	4
	Juncetum gerardii	19	3
no significant difference	Armerio-Festucetum	19	10
	Lolio-Potentillion	16	16
not tested	Other	15	1

## Discussion

### *Developments in grazed and ungrazed salt marsh*

Consistent with other studies (Dijkema 1983a; Roozen & Westhoff 1985; Jensen 1985; Adam 1990; Andresen *et al.* 1990), the ungrazed marsh became dominated by tall growing plants. In all our study islands, *Atriplex portulacoides* cover increased in the ungrazed low marsh (Figures 6.1, 6.4). The ungrazed high marsh became dominated by *Elymus athericus* in many quadrats, except at site 6 (Skallingen) and site 2 (at Terschelling). Fresh water seepage from the dunes at site 2, and from an aquifer connected to the mainland at Skallingen (Christiansen, pers. comm.), favoured the growth of *Phragmites australis* and *Scirpus maritimus* here. *Phragmites australis* may be a very important species locally. It covered up to 100% in some of the ungrazed quadrats there, but only 2% on average in the grazed marsh. The same phenomenon was described by Dijkema (1983a) and observed for brackish marshes (Adam 1990; Esselink *et al.* 2000). *Artemisia maritima* at first increased in abundance after cessation of grazing, but was displaced by *Elymus athericus* later on. Even on low salt-marsh quadrats *Elymus athericus* cover started to increase after two decades of not grazing (Figure 6.4), emphasising the importance of long-term vegetation studies. *Puccinellia maritima*, *Triglochin maritima*, *Plantago maritima* and *Festuca rubra* generally declined in abundance in ungrazed quadrats. These results agree with many studies summarised in Jensen (1985) for *Puccinellia maritima*, *Triglochin palustris*, *Plantago maritima*, *Artemisia maritima* and *Atriplex portulacoides*. *Festuca rubra*, however, is often mentioned to be negatively affected by grazing, according to 12 studies cited in his overview. The adverse effect of grazing in these studies may in part be due to soil compaction due to treading, as was suggested by Jensen (1985). We found a negative effect of cessation of grazing, as it leads to the dominance of *Elymus athericus*, at the expense of *Festuca rubra*.

### *Plant communities*

The changes at the individual level were reflected at the level of the community (Table 6.2). Grazing promotes the Juncetum gerardii (Gray & Scott 1967; Adam 1990), the Puccinellietum maritimae and the Armerio-Festucetum (Dijkema 1983b). Cessation of grazing led to an increase of communities dominated by *Elymus athericus*, *Artemisia maritima* and *Atriplex portulacoides* (see also Figures 6.1C, 6.1F). However, not all of the quadrats studied turned into these communities. In particular the Lolio-Potentillion and the Armerio-Festucetum remain present in the ungrazed situation (Table 6.2). Using vegetation maps, Gettner *et al.* (2000) also observed increased cover of communities dominated by *Artemisia maritima* and *Atriplex portulacoides* at the mainland salt marshes along the coast of Schleswig-Holstein (Germany), after only 3-4 years without grazing. Studies that compared vegetation maps or experiments with exclosures and different stocking rates of cattle and sheep, indicate that the *Elymus athericus* community can become dominant at natural as well as at artificial salt marshes (van Wijnen *et al.* 1997; Bakker *et al.* 2002). Kiehl *et al.* (2000a), however, argue that low sedimentation



rates and waterlogging may hamper this development and lead to a mosaic of different communities in the ungrazed marsh.

### *Species richness*

As in other studies (Adam 1990) we found that the richness of species declined without grazing. None of the species characteristic of salt marshes however, occurred exclusively in only one of the grazing treatments. The differences in species presence between treatments is due to species observed very rarely, and is biased towards the grazed quadrats. This fact in itself may be of importance, because it indicates differences in opportunities for colonisation and establishment. The identity of the species involved may however not be important, because such differences are much more likely to be caused by chance effects. Chaneton & Facelli (1991) and Kiehl (1997) point out that differences in species richness may be dependent on the scale of measurement. They argue that the structure of ungrazed vegetation is more coarse grained, with larger patches dominated by individual species. However, the probability of finding an individual of a certain species increased for most of the plant species found under grazing in this study (Table 6.1), and the number of associations that occurred under grazed conditions was higher than under ungrazed circumstances (data not shown). It is therefore likely that, also at courser scales, species richness will be higher in fixed size quadrats under grazing at these intensities. This is furthermore supported by yet unpublished data on species richness up to a scale of 50 m x 50 m from a variety of marshes along the Dutch Wadden Sea coast (Bos, unpubl. data). Species richness increased with elevation and grazing positively affected richness at low as well as high marsh (Adam 1990, Figure 6.3). This differs from results presented by Bakker (1989), who found lower species richness at the grazed low marsh, due to complete destruction of the top soil.

### *Goose, rabbit and hare grazing*

Geese, hare and rabbits are the most obvious herbivores on marshes whose habitat is affected by changes in vegetation composition. By their own grazing, they may however affect the vegetation themselves as well. Hare grazing, for example, affects plant species composition on salt marshes, but not to the same extent as livestock do (van der Wal *et al.* 2000b). According to the latter study, selective grazing on *Atriplex portulacoides* by hare may delay natural succession by some 40 years, in the low parts of back-barrier marshes. Effects of geese on vegetation composition have been demonstrated for Lesser Snow Geese *Chen caerulescens caerulescens* in La Pérouse Bay, Canada (Bazely & Jefferies 1986; Kotanen & Jefferies 1997). In the marshes we studied however, the impact of geese on succession appears to be low (van der Wal *et al.* 2000a), just like on the Hamburger Hallig, Germany (Kiehl *et al.* 2000b). The main colonisers of ungrazed salt marsh, *Atriplex portulacoides* and *Elymus athericus*, are unpalatable to geese and the geese are not present during the major part of the growing season (Adam 1990). Both plant species increase in abundance during natural succession,

which negatively affects geese, hares and rabbits (van de Koppel *et al.* 1996). Due to natural vegetation succession, Brent geese were shown to loose high quality feeding habitat (van der Wal *et al.* 2000a). By grazing with livestock however, a suitable sward for foraging is maintained which facilitates the smaller herbivores (Cadwalladr *et al.* 1972; Olff *et al.* 1997; Stock & Hofeditz 2000).

### *Management implications*

The stocking rate (Andresen *et al.* 1990), the timing of grazing (Adam 1990) and even the nature of the stock (Gray & Scott 1967; Jensen 1985) mediate the effects of the herbivory. Intensive grazing leads to an impoverishment of the vegetation according to Dijkema (1983b) and Schaminée *et al.* (1998). Kiehl *et al.* (1996) showed that *Atriplex portulacoides* is only very rarely found on intensively grazed marshes. Under extensive grazing though, a mosaic of closely grazed areas and lightly grazed patches develops (van den Bos & Bakker 1990). Depending on the amount of variation that is desired managers should vary the stocking rates (Bakker 1985). Differences between sheep and cattle grazing originate from different ways of grazing (Gettner *et al.* 2000). Cattle tear the grass from the sward, whereas sheep rather bite the grass and are also more selective. Adam (1990) even hypothesised that differences in the response of *Atriplex portulacoides* to grazing, between marshes in west and south-west Britain, may be related to this. Marshes in south-west Britain are primarily cattle grazed, and *Atriplex portulacoides* is equally abundant in grazed and ungrazed areas here, whereas it is limited to areas with restricted access for grazing sheep on the west coast.

The grazing of back-barrier marshes with livestock in this study was shown to enhance the species number in small quadrats with a fixed size, and to promote those plant species and those plant communities that are important forage for waterfowl, rabbit and hare. Other studies demonstrated that the grazing management affects the composition of invertebrate assemblages (Andresen *et al.* 1990; Meyer *et al.* 1995) and those of the breeding birds (Stock *et al.* 1992; Norris *et al.* 1998; Eskildsen *et al.* 2000) via its impact on the vegetation. All of these aspects are relevant to the management of salt marshes, but in certain cases the management objectives are at odds with each other. The basic tenet of this discussion on grazing management, is that grazing or the cessation of grazing is a means to reach previously defined ecological targets, and that long-term ecological monitoring is a prerequisite to judge to which extent these targets are fulfilled (Dijkema 1983b; Stock & Kiehl 2000; Bakker *et al.* 2002).

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## References

- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of Greylag geese *Anser anser* and Barnacle geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. *Z. Ökol. Natursch.* 5: 65-75
- Andresen H, Bakker JP, Brongers M, Heydemann B, Irmiler U (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137-148
- Bakker JP (1985) The impact of grazing on plant communities, plant populations and soil conditions on salt marshes. *Vegetatio* 62: 391-398
- Bakker JP (1989) Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht
- Bakker JP, Bos D, de Vries Y (2002) To graze or not to graze, that is the question. In: Essink, K, van Leeuwe M, Kellerman A & Wolff WJ (eds) Proceedings of the 10th International Scientific Wadden-Sea Symposium. Ministry of Agriculture, Nature Management and Fisheries, The Hague (in press)
- Bazely DR, Jefferies RL (1986) Changes in the composition and standing crop of salt marsh communities in response to the removal of a grazer. *J. Ecol.* 74: 693-706
- Behre KE (1985) Die ursprüngliche Vegetation in den Deutschen Marschgebieten und deren Veränderung durch prähistorische Besiedlung und Meeresspiegelbewegungen. *Verhandlungen der Gesellschaft für Ökologie* 13: 85-95
- Cadwalladr DA, Owen M, Morley JV, Cook RS (1972) Wigeon (*Anas penelope*) conservation and salting pasture management at Bridgwater Bay National Nature Reserve, Somerset. *J. Appl. Ecol.* 9: 417-425
- Chaneton EJ, Facelli JM (1991) Disturbance effects on plant community diversity: spatial scales and dominance hierarchies. *Vegetatio* 93: 143-156
- de Jong DJ, Dijkema KS, Bossinade JH, Janssen JAM (1998) Salt97; een classificatieprogramma voor kweldervegetaties. Rijkswaterstaat & IBN-DLO, Middelburg, pp 1-23
- de Jong F, Bakker JF, van Berkel CJM, Dankers NMJA, Dahl K, Gätje C, Marencic H, Potel P (1999) Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group, Wilhelmshaven
- Dijkema KS (1983a) The saltmarsh vegetation of the mainland coast, estuaries and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 185-269
- Dijkema KS (1983b) Use and management of mainland salt marshes and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 303-312
- Erchinger HF (1985) Dünen, Watt und Salzwiesen. Der Niedersächsische Minister für Ernährung, Landwirtschaft und Forsten, Hannover
- Eskildsen K, Fiedler U, Hälterlein B (2000) Die Entwicklung der Brutvogelbestände auf der Hamburger Hallig. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 61-65
- Esselink P, Zijlstra W, Dijkema KS, van Diggelen R (2000) The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. *Biol. Conserv.* 93: 61-76

- Gettner S, Heinzel K, Kohlhus J (2000) Die Entwicklung der aktuellen Vegetation auf der Hamburger Hallig nach Änderung der Nutzung. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 24-33
- Gray AJ, Scott R (1967) The ecology of Morecambe Bay VII; the distribution of *Puccinellia maritima*, *Festuca rubra* and *Agrostis stolonifera* in the salt marshes. J. Appl. Ecol. 14: 229-241
- Hobohus C (1986) Die Salzwiesen von Sylt. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein und Hamburg 18: 57-99
- Huisman J, Olff H, Fresco LFM (1993) A hierarchical set of models for species response analysis. J. Veg. Sci. 4: 37-46
- Jensen A (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. Vegetatio 60: 37-48
- Jongman RHG, ter Braak CJF, van Tongeren OFR (1995) Data analysis in community and landscape ecology. Cambridge University Press, Cambridge
- Kiehl K (1997) Vegetationsmuster in Vorlandsalzwiesen in Abhängigkeit von Beweidung und abiotischen Standortfaktoren. Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg e.V., Kiel
- Kiehl K, Eischeid I, Gettner S, Walter J (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. J. Veg. Sci. 7: 99-106
- Kiehl K, Gettner S, Heinze C, Stock M (2000a) Langfristige Vegetationsveränderungen im Vorland der Hamburger Hallig und ihre Bedeutung für herbivore Vögel. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 66-73
- Kiehl K, Schröder H, Bredemeier B, Wiggershaus A (2000b) Der Einfluss von Extensivierung und Beweidungsaufgabe auf Artenzusammensetzung und Struktur der Vegetation. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 34-42
- Kotaniemi PM, Jefferies RL (1997) Long-term destruction of sub-arctic wetland vegetation by lesser snow geese. Ecoscience 4: 179-182
- Londo G (1976) The decimal scale for relevés of permanent quadrats. Vegetatio 33: 61-64
- Meyer H, Fock H, Haase A, Reinke HD, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep grazing. Helgoländer Meeresuntersuchungen 49: 563-589
- Neckermann K (1987) Die Salzwiesen Amrums. Kieler Notizen zur Pflanzenkunde in Schleswig-Holstein und Hamburg 19: 110-133
- Norris K, Brindley E, Cook T, Babbs S, Forster Brown C, Yaxley R (1998) Is the density of redshank *Tringa totanus* nesting on saltmarshes in Great Britain declining due to changes in grazing management? J. Appl. Ecol. 35: 621-634
- Olff H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. J. Ecol. 85: 799-814
- Prop J, Deerenberg C (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. Oecologia 87: 19-28
- Ranwell DS (1968) Coastal marshes in perspective. Regional Studies Group Bulletin, University of Strathclyde 9: 1-26
- Roozen AJM, Westhoff V (1985) A study on long-term salt marsh succession using permanent plots. Vegetatio 61: 23-32
- Sanchez JM, Izco J, Medrano M (1996) Relationships between vegetation zonation and altitude in a salt-marsh system in northwest Spain. J. Veg. Sci. 7: 695-702
- Schaminée JHJ, Weeda EJ, Westhoff V (1998) De Vegetatie van Nederland. D1 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitats durch Nonnen- und Ringelgänse. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 43-55

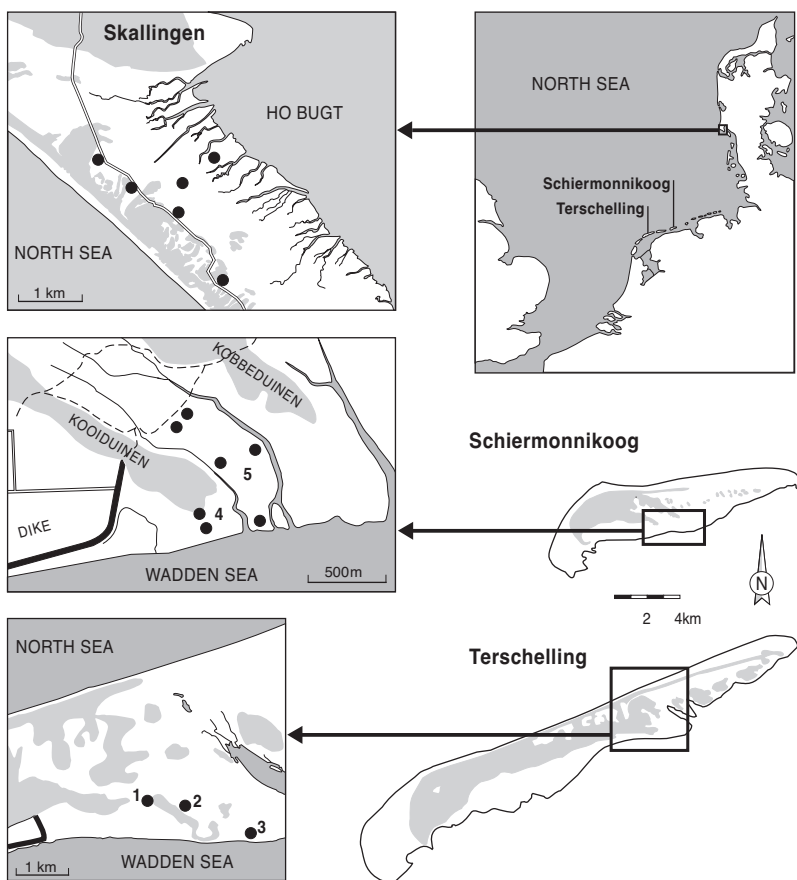




- Stock M, Kiehl K (2000) Empfehlungen zum Salzwiesenmanagement im Nationalpark Schleswig-Holsteinisches Wattenmeer. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 74-77
- Stock M, Teenck G, Grossmann M, Lindemann J (1992) Agricultural management plans on salt marsh islands: What is the breeding bird response? *Vogelwelt* 113: 20-35
- van de Koppel, J. Huisman J, van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745
- van den Bos J, Bakker JP (1990) The development of vegetation patterns by cattle grazing at low stocking density in the Netherlands. *Biol. Conserv.* 51: 263-272
- van der Meijden R (1990) Heukels' Flora van Nederland, 21st edition. Wolters-Noordhoff, Groningen
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000a) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D (2000b) On facilitation between herbivores: How Brent Geese profit from brown hares. *Ecology* 81: 969-980
- van Wijnen H, Bakker JP (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. *J. Coast. Cons.* : 19-26
- van Wijnen H, van der Wal R, Bakker JP (1999) The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia* 118: 225-231
- van Wijnen HJ, Bakker JP, de Vries Y (1997) Twenty years of salt marsh succession on a Dutch coastal barrier island. *J. Coast. Cons.* 3: 9-18
- Westhoff V (1987) Salt marsh communities of three West Frisian islands, with some notes on their long-term succession during half a century. In: Huiskes AHL, Blom CWPM, Rozema J (eds) *Vegetation between land and sea, structure and processes*. Junk Publishers, Dordrecht, pp 16-41
- Westhoff V, van der Maarel E (1973) The Braun-Blanquet approach. In: Whittaker RH (ed) *Ordination and classification of vegetation*. Junk Publishers, The Hague, pp 617-726

Long-term vegetation enclosure on the grazed salt marsh of Schiermonnikoog. Picture taken from the air using a kite in 1999. The enclosure was erected in 1974. (photo J. de Vlas).





**Appendix 6.1** Map showing the geographical positions of the three study sites. Insets depict the positions of the exclosures at the different sites. Geographical names for the sites are: 1) St. Janshoek, 2) Wytdune, 3) Transect, 4) OBK and 5) NBK. Skallingen is site 6.





**Appendix 6.2** Model results for the analysis of species cover in response to time according to Huisman *et al.* (1993). The model type is indicated by Roman numerals, see Huisman *et al.* (1993) for the mathematical model formulation. (+) Indicates an increasing trend, (-) indicates a decreasing trend and (+/-) indicates a trend which decreases after an initial increase. The area below the curve equals the integral over time expressed as a percentage.

Model I	No significant trend in time							
Model II	an increasing or decreasing trend where the maximum is equal to the upper bound							
Model III	an increasing or decreasing trend where the maximum is below the upper bound							
Model IV	increase and decrease by the same rate: symmetrical response curve							
Model V	increase and decrease by different rates: skewed response curve.							
Spec.	Treatment	Zone	Study island	Model	Trend	Sample size	Sign.	Area below the curve (%)
Triglochin maritima	Experimentally ungrazed	high marsh	Terschelling	III	-	192	0.005	0.3
			Schiermonnikoog	III	-	125	0.005	0.1
			Skallingen	I		87	n.s.	0.2
		low marsh	Terschelling	III	-	20	0.01	0.5
			Schiermonnikoog	III	-	182	0.005	0.9
			Skallingen	IV	+/-	19	0.05	0.4
	Control grazed	high marsh	Terschelling	I		172	n.s.	0.8
			Schiermonnikoog	I		125	n.s.	0.2
			Skallingen	I		87	n.s.	0.8
		low marsh	Terschelling	I		20	n.s.	1.4
			Schiermonnikoog	I		181	n.s.	3.3
			Skallingen	III	-	19	0.05	0.1
Puccinellia maritima	Experimentally ungrazed	high marsh	Terschelling	I		192	n.s.	0.8
			Schiermonnikoog	I		125	n.s.	0.0
			Skallingen	III	+	87	0.05	3.1
		low marsh	Terschelling	III	-	20	0.01	15.2
			Schiermonnikoog	III	-	182	0.01	6.3
			Skallingen	V	+/-	19	0.05	60.9
	Control grazed	high marsh	Terschelling	I		172	n.s.	0.6
			Schiermonnikoog	III	+	125	0.01	3.3
			Skallingen	III	+	87	0.01	5.7
		low marsh	Terschelling	I		20	n.s.	9.0
			Schiermonnikoog	III	+	181	0.005	32.5
			Skallingen	IV	+/-	19	0.05	53.5
Plantago maritima	Experimentally ungrazed	high marsh	Terschelling	III	-	192	0.005	2.3
			Schiermonnikoog	II	-	125	0.05	1.4
			Skallingen	III	-	87	0.01	3.0
		low marsh	Terschelling	I		20	n.s.	0.5
			Schiermonnikoog	III	-	182	0.05	1.9
			Skallingen	IV	+/-	19	0.05	0.6
	Control grazed	high marsh	Terschelling	III	-	172	0.01	7.1
			Schiermonnikoog	I		125	n.s.	1.3
			Skallingen	I		87	n.s.	4.2
		low marsh	Terschelling	I		20	n.s.	1.7
			Schiermonnikoog	III	-	181	0.005	1.2
			Skallingen	IV	+/-	19	0.01	0.1

## Appendix 6.2 Continued

Spec.	Treatment	Zone	Study island	Model	Trend	Sample size	Sign.	Area below the curve (%)
Festuca rubra	Experimentally ungrazed	high marsh	Terschelling	III	-	192	0.05	33.4
			Schiermonnikoog	III	-	125	0.05	34.4
			Skallingen	I		87	n.s.	34.5
		low marsh	Terschelling	III	+	20	0.05	10
			Schiermonnikoog	I	-	182	n.s.	21.5
			Skallingen	IV	+/-	19	0.01	0.5
	Control grazed	high marsh	Terschelling	I		172	n.s.	31.7
			Schiermonnikoog	I		125	n.s.	21.3
			Skallingen	I		87	n.s.	16.2
		low marsh	Terschelling	I		20	n.s.	1.1
			Schiermonnikoog	III	-	181	0.01	19
			Skallingen	Species is absent				
Elymus athericus	Experimentally ungrazed	high marsh	Terschelling	III	+	192	0.005	23.8
			Schiermonnikoog	III	+	125	0.005	35.1
			Skallingen	Species is absent				
		low marsh	Terschelling	III	+	20	0.005	4.6
			Schiermonnikoog	III	+	182	0.005	12.4
			Skallingen	Species is absent				
	Control grazed	high marsh	Terschelling	I		172	n.s.	1.8
			Schiermonnikoog	III	-	125	0.05	6.5
			Skallingen	Species is absent				
		low marsh	Terschelling	Species is absent				
			Schiermonnikoog	I		181	n.s.	0.1
			Skallingen	Species is absent				
Atriplex portulacoides	Experimentally ungrazed	high marsh	Terschelling	I		192	n.s.	2.3
			Schiermonnikoog	I		125	n.s.	0.1
			Skallingen	III	+	87	0.005	2.6
		low marsh	Terschelling	II	+	20	0.005	43.3
			Schiermonnikoog	III	+	182	0.01	10.7
			Skallingen	III	+	19	0.05	12.9
	Control grazed	high marsh	Terschelling	I		172	n.s.	0.1
			Schiermonnikoog	III	+	125	0.05	0.1
			Skallingen	I		87	n.s.	0.2
		low marsh	Terschelling	III	+	20	0.05	0.6
			Schiermonnikoog	III	+	181	0.01	0.8
			Skallingen	I		19	n.s.	0.7
Artemisia maritima	Experimentally ungrazed	high marsh	Terschelling	IV	+/-	192	0.01	5.7
			Schiermonnikoog	III	+	125	0.05	4.7
			Skallingen	III	+	87	0.05	4.5
		low marsh	Terschelling	IV	+/-	20	0.01	6.2
			Schiermonnikoog	IV	+/-	182	0.01	31.6
			Skallingen	Species is absent				
	Control grazed	high marsh	Terschelling	I		172	n.s.	1.7
			Schiermonnikoog	I		125	n.s.	0.7
			Skallingen	I		87	n.s.	0.1
		low marsh	Terschelling	Species is absent				
			Schiermonnikoog	I		181	n.s.	5.2
			Skallingen	Species is absent				



## Utilisation of Wadden Sea salt marshes by geese in relation to livestock grazing

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### Abstract

To Arctic breeding geese, the salt marshes of the international Wadden Sea are important spring staging areas. Many of these marshes have always been grazed with livestock (mainly cattle and sheep). To evaluate the influence of livestock grazing on composition and structure of salt-marsh communities and its consequences for habitat use by geese, a total of 17 pairs of grazed and ungrazed marshes were visited both in April and May 1999, and the accumulated grazing pressure by geese was estimated using dropping counts. We also collected such data for hare. Observed grazing pressure was related to management status and to relevant vegetation parameters.

The intensity of livestock grazing influences the vegetation on the marsh. Salt marshes that are not grazed by livestock are characterised by stands with a taller canopy, a lower cover of grasses palatable for geese, and a higher cover of plants that are unpalatable.

Overall goose dropping densities are significantly lower in ungrazed marshes compared to marshes grazed by livestock. Some ungrazed marshes had comparatively high goose grazing pressure, and these were all natural marshes on a sandy soil, or artificial mainland marshes with a recent history of intensive livestock-grazing. Goose grazing is associated with a short canopy. The plant communities with short canopy, dominated by *Agrostis stolonifera*, *Festuca rubra* and *Puccinellia maritima*, respectively, together account for 85% of all goose droppings in our data.

The sites that were not visited by geese differed very little from those that were visited, in the parameters we measured. This might indicate that there was no shortage of available habitat for spring staging geese in the Wadden Sea, in the study period.

## Introduction

### *Goose grazing, natural succession and salt-marsh management*

Salt marshes in the international Wadden Sea serve as feeding grounds for spring staging geese, preparing for migration to breeding areas in the Arctic. Barnacle Geese *Branta leucopsis* utilise the marshes mainly from February to April, with an increasing number present during May (Stock & Hofeditz 2000, Engelmoer *et al.* 2001), while Brent Geese *Branta b. bernicla* are mainly present from March until the end of May (Ebbing *et al.* 1999). Feeding conditions during this period are crucial for future reproductive success, as reproductive output of geese is strongly related to the amount of fat and protein reserves accumulated during spring (de Boer & Drent 1989, Ebbing 1989, Prop & Black 1997). To a large extent, these feeding conditions will be determined by the vegetation composition and canopy height of the marsh, because plant species and plant parts differ in their palatability for geese. Vegetation composition is strongly related to the management of salt marshes, for example grazing with livestock (Beefink 1977, Jensen 1985, Bakker 1989, Esselink *et al.* 2000, Gettner *et al.* 2000).

Under ungrazed conditions, salt-marsh vegetation changes due to natural succession (Jensen 1985, Roozen & Westhoff 1985, Adam 1990, Westhoff & van Oosten 1991, Bakker *et al.* 1993, Kiehl *et al.* 2000b). Continual input of nitrogen by sedimentation is put forward as the major force driving natural succession (van Wijnen & Bakker 1997). Increasing availability of nitrogen favours the growth of the later successional tall grass *Elymus athericus* at high marsh elevation and the tall forb *Atriplex portulacoides* at the lower marsh (Olf *et al.* 1997, van Wijnen & Bakker 1997). Both plant species are unpalatable to geese and outcompete the preferred forage species *Plantago maritima*, *Triglochin maritima*, *Puccinellia maritima* and *Festuca rubra* (Prop & Deerenberg 1991, van der Wal *et al.* 2000b). Subsequently, goose grazing decreases when marshes become too productive (van de Koppel *et al.* 1996). Grazing by hare *Lepus europaeus* has been shown to affect vegetation succession (van der Wal *et al.* 2000b) to a certain extent. Hare utilise the salt-marsh habitat year-round, and retard natural succession by grazing on the woody stems of *Artemisia maritima* and *A. portulacoides* in winter. Hare thus temporarily provide more suitable habitat for geese (van der Wal *et al.* 2000b). On the natural, livestock-ungrazed salt marsh of Schiermonnikoog it has nonetheless been observed that densities of both geese and hare decline as natural succession proceeds (van de Koppel *et al.* 1996).

Most of the salt marshes in the Wadden Sea have traditionally been grazed by livestock (Esselink 2000). Cattle and sheep grazing prevents accumulation of biomass. They create a short canopy and high cover of plant species that are palatable for geese and hare (Bakker *et al.* 1993, Olf *et al.* 1997), thus positively affecting the feeding conditions for geese (Aerts *et al.* 1996). Depending on the intensity of grazing a homogeneous sward results, dominated by few species, or a diverse vegetation pattern with alternating patches of short and tall swards (Dijkema 1983, Aerts *et al.* 1996, Berg *et al.* 1997, Kiehl 1997). In the past decade however, there has been a reduction in agricultural use along the coast of Niedersachsen, Germany (Potel & Südbeck 1994) and live-



stock grazing was stopped at 42% of the mainland marshes in Schleswig-Holstein, Germany (Stock & Kiehl 2000), as a result of policies promoting natural development of the marsh ecosystem (Kempf *et al.* 1987, Stock *et al.* 1997, Stock & Kiehl 2000). In the Netherlands and Denmark about 40% and 10% of the salt marsh area is livestock-ungrazed, respectively (Kempf *et al.* 1987, de Jong *et al.* 1999).

### *Differences between marsh types*

The rate of vegetation succession, and possibly the final stages of the succession, differ between artificial mainland marshes and the natural marshes on the barrier islands of the Wadden Sea, as they differ in soil composition. The barrier marshes, or barrier-connected marshes according to de Jong *et al.* (1999), have a relatively thin layer of clay on top of a sandy sub-soil. In contrast, the artificial mainland marshes with sedimentation fields feature a thick layer of clay. This has important consequences for the availability of nitrogen and drainage. Marsh type is thus an important source of variation for vegetation composition and maybe also for the feeding conditions of small vertebrate herbivores, such as geese and hare.

### *Objective*

In this study we will evaluate the importance of livestock grazing in explaining variability in goose utilisation relative to other sources of variation. Our basic hypothesis is that livestock grazing affects the habitat choice of Brent and Barnacle Geese. Evidence to support this hypothesis has been derived from local studies (Aerts *et al.* 1996, Stock & Hofeditz 2000), but the validity has not been generalised. We expect food availability to be important for the distribution of geese and we will indirectly assess food availability using parameters of vegetation composition, canopy height and tiller density. Other sources of variation that will be examined are the availability of freshwater, disturbance, the presence of hare and marsh dimensions.

## **Methods**

We established 63 transects, divided over 38 study sites (see Appendix 7.1), based on the following criteria: The marsh in which the transect was placed, should have a stable and clearly defined management for at least six consecutive years. Only marshes with sufficiently large area ( $> 5$  ha), such that a flock of geese could land without inhibition, were included. The sites were distributed over the entire Danish ( $n = 11$ ), German ( $n = 17$ ) and Dutch ( $n = 10$ ) Wadden Sea. Twenty-two sites harboured transects in marshes with at least two different grazing regimes. Seventeen sites with paired transects were visited twice, once in April and once in May 1999, and so were some of the unpaired transects (Appendix 1). The remainder was only visited once. Several transects were known to have had a relatively recent change in management from

intensively grazed to ungrazed (< 10 years before), and these transects were treated separately. Management was subdivided in >long term ungrazed= (> 10 years), 'short-term ungrazed' (6 - 10 years), 'extensively grazed' ( $\leq 4.5$  sheep ha<sup>-1</sup> or > 1 cow ha<sup>-1</sup>) and 'intensively grazed'. Grazed marshes were classified as being sheep- or cattle grazed. The transects on barrier marshes in our study are, with one exception, only visited by Brent Geese, while most transects on mainland marshes are utilised by Brent and Barnacle Geese.

For each management regime at each site, 1 transect was placed perpendicular to the seawall and the coastline. At fixed intervals, small plots of 4 m<sup>2</sup> were located. Twenty replicate plots per transect were sampled, equally divided over the length of the transect. The accumulated number of goose and hare droppings in these plots were counted. Goose dropping densities are a good measure of grazing intensity, as geese defecate very regularly (Owen 1971). Dropping densities and grazing pressure by hare are also correlated (Langbein *et al.* 1999). We did not discriminate between droppings of Brent or Barnacle Geese. Hare droppings were distinguished from rabbit faeces by shape and size. Transects from which results were likely to have been affected by flood during the preceding 14 days, which was assessed using tide tables and observations in the field, are not included in our dataset. The vegetation at each plot was classified to a plant community using a key that was based upon the salt-marsh typology from de Jong *et al.* (1998, see Appendix 7.2). Nomenclature of species follows van der Meijden (1990). Vegetation composition was described using five parameters: (1) percentual cover of palatable grasses (*Lolium perenne*, *Poa* spp., *A. stolonifera*, *Puccinellia maritima* and *F. rubra*), (2) percentual cover of tall plant species (*E. athericus*, *A. portulacoides*, *A. maritima*, *Spartina anglica* and standing dead remnants of *Aster tripolium*), (3) joint abundance of *Plantago maritima* and *T. maritima* (absent, present and abundant (> 3% cover)) and (4) canopy height. Canopy height was measured five times per plot to the nearest 0.5 cm using a polystyrene disc (20 cm Ø, 24 g), sliding along a graduated stick, that was randomly dropped on the vegetation. Finally, we measured (5) tiller-density in the *F. rubra* and *Puccinellia maritima* communities using a quadrat of 25 cm<sup>2</sup>. A tiller was defined as a group of leaves with one meristem, often surrounded by senescing leaves. Additional plots were randomly placed in *F. rubra* and *Puccinellia maritima* communities at each transect (when present), and sampled for the parameters mentioned above, to arrive at a minimum sample size of five for these communities. For each transect, an index of disturbance was assessed covering three classes. This index was based on the distance to nearest roads, towns and recreational pressure (see Appendix 7.1). Distance to a fresh water source (km) was assessed in the field, aided by a topographical map.

### Statistical analyses

Observed dropping densities were related to factors at two levels of explanation and two levels of aggregation. On the one hand, we averaged the dropping density and vegetation parameters over the 20 plots per transect and related them to livestock grazing regime, salt-marsh type (mainland versus barrier marsh) and month of sampling



as fixed factors in a General Linear Model (GLM). In the analysis of dropping densities, we limited the selection of transects to those sites where two contrasting management regimes were sampled in either month. Transect length was included as a covariate, while site and the interaction between month of sampling and grazing regime were included as factors. Dropping density was also directly related to vegetation parameters (vegetation composition, canopy height, tiller density and combined abundance of *Plantago maritima* and *T. maritima*) using multiple regression. At a lower level of aggregation, all data were pooled per plant community and per transect, and differences between plant communities were tested. The additional plots that we had sampled were included in these analyses. Within the plant communities dominated by *Puccinellia maritima* and *F. rubra*, we also studied the effect of livestock grazing regime, salt-marsh type and month of sampling in a General Linear Model. For the analyses of dropping densities at the plant community level, only those sites were selected where geese or hare had been observed in any of the months.

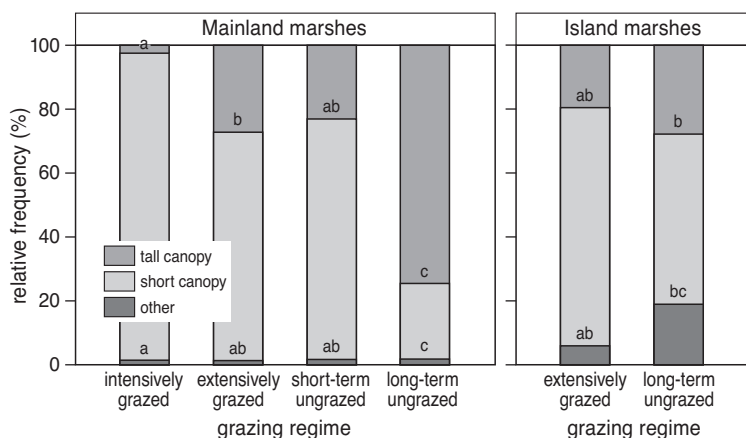
The relative frequency of plant communities per transect (%) was calculated as the proportion of observations of each community on the total of 20 plots sampled. Canopy height and dropping density at the plot level were related to distance from the seawall for each grazing regime separately, while correcting for site, using General Linear Modelling. Arcsine and log-transformations were used for percentage values and canopy height respectively (Zar 1996). Non-parametric tests were employed where appropriate.

## Results

### *Effects of livestock grazing on marsh vegetation*

The vegetation composition was significantly related to livestock grazing on mainland marshes (Figure 7.1), but these differences were less pronounced on barrier marshes. Incidence of communities characterised or dominated by short grasses (*Puccinellia maritima*, *F. rubra*, *A. stolonifera* and *Juncus gerardi*) was higher at intensively grazed marshes and decreased with reduced stocking rates (GLM factor grazing,  $F_{3,58} = 23.9$ ,  $P < 0.001$ ). The incidence of communities dominated by tall unpalatable plants (*E. athericus*, *A. portulacoides* and *A. maritima*) increased with lower stocking rates of livestock (GLM factor grazing,  $F_{3,58} = 19.7$ ,  $P < 0.001$ ).

The vegetation parameters canopy height, cover of edible grasses, cover of structural elements and tiller density were strongly and significantly correlated to each other at all levels of aggregation (Pearson's correlation, all  $P < 0.01$ , Table 7.1). For this reason only the data for canopy height will further be presented. The canopy height of marsh vegetation strongly differed between communities (Figure 7.2A, K-W test,  $\chi^2 = 75.4$ ,  $P < 0.001$ ). Communities dominated by *Puccinellia maritima*, *F. rubra* and *A. stolonifera* had significantly lower canopy than communities dominated by *E. athericus*, *A. portulacoides* and *A. maritima*. But even within plant communities, a relationship was found between livestock grazing and relevant habitat parameters for



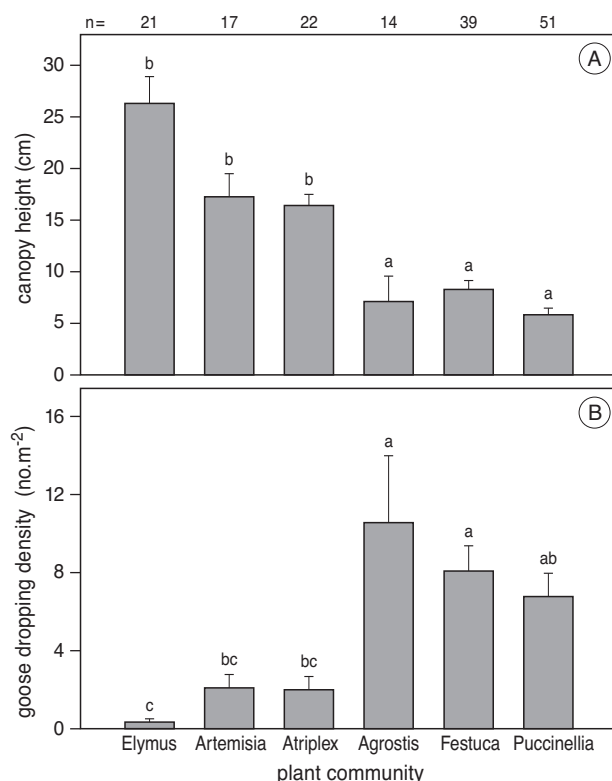
**Figure 7.1** Incidence of communities on salt marshes, grouped by height of the canopy, in relation to livestock grazing regime and marsh type. The group with short canopy includes the communities of *Puccinellia maritima*, *Limonium vulgare*, *J. gerardi*, *A. stolonifera* and *F. rubra*. The group with tall canopy includes the communities of *E. athericus*, *A. portulacoides* and *A. maritima*. See Appendix 2 for a key to identification of the communities in the field. Grazing regimes that do not share the same letter within a class of communities are significantly different from each other ( $P < 0.05$ ).

small herbivores. Under ungrazed circumstances, the communities dominated by *Puccinellia maritima* and *F. rubra* on mainland marshes, had taller canopy (Figure 7.3A, GLM,  $F_{3,84} = 21.3$ ,  $P < 0.001$ ). Barrier marshes had a lower canopy height for a given livestock grazing regime (Figure 7.3A, GLM,  $F_{1,84} = 5.4$ ,  $P = 0.022$ ). The index of combined abundance of *Plantago maritima* and *T. maritima* was higher for barrier marshes (K-W test  $\chi^2 = 9.3$ ,  $P < 0.005$ ) than for mainland marshes. We were not able to detect differences in the vegetation parameters studied for the two species of livestock (sheep or cattle). Canopy height significantly increased with distance from the seawall in 33% of the marshes (GLM interaction of distance and site significant), while in 54% there was no relationship. These proportions did not differ significantly between grazing regimes (contingency test,  $\chi^2 = 10.3$ , n.s.).

**Table 7.1** Pearson correlation coefficients for vegetation parameters at the community level. All correlations are significant at the 0.01 level.

	TP	PG	CH	TD
Cover of tall plants (TP)		-0.67	0.86	-0.30
Cover of palatable grasses (PG)			-0.61	0.39
Canopy height (CH)				-0.39
Tiller density (TD)				

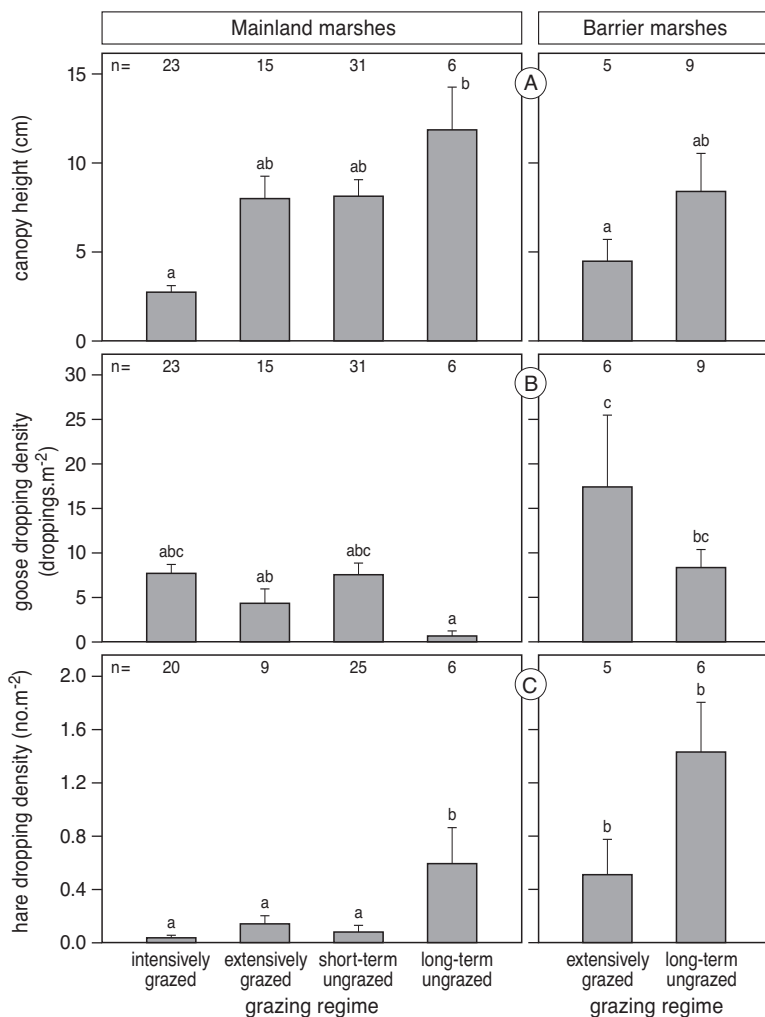




**Figure 7.2** A) Canopy height of salt marsh vegetation for the six plant communities that were most frequent in the dataset. Data refer to all transects. B) Grazing pressure of geese per plant community. Only data for sites that were visited by geese are used. Bars that do not share the same letter are significantly different from each other ( $P < 0.05$ ).

### Goose grazing

Grazing pressure by geese at the transect level increased significantly with the intensity of livestock grazing regime (Figure 7.4, GLM,  $F_{3,60} = 5.7$ ,  $P = 0.002$ ), while transect length, month of sampling, marsh type nor the interaction between grazing regime and month of sampling significantly explained any variation. Nonetheless, when testing for the effect of marsh type separately within ungrazed transects, we found that long-term ungrazed transects on the mainland had much lower dropping densities than long-term ungrazed transects on barrier marshes ( $0.3 \pm 0.2$  versus  $5.2 \pm 0.7$ ; T-test,  $t = 2.7$ ,  $P = 0.03$ ). In April, goose dropping densities at the transect level did not differ between grazing regimes (GLM,  $F_{3,21} = 1.7$ , n.s.), while in May, livestock grazed marshes had significantly higher dropping densities than ungrazed marshes (GLM  $F_{3,19} = 9.2$ ,  $P = 0.001$ ). This finding still holds when the dataset is further limited to the 17 sites with paired transects that were visited both periods or to



**Figure 7.3** The relation of livestock grazing regime and marsh type with A) canopy height, B) grazing pressure by geese and C) hare grazing pressure. Data represent the communities dominated by *Puccinellia maritima* and *F. rubra* for all sites that were visited by geese (A & B), respectively hare (C). Bars that do not share the same letter within a marsh type are significantly different ( $P < 0.05$ ) from each other. Effects of marsh type were significant for all three parameters.

the sites ( $n = 14$ ) that are known to be visited by both species of geese. There were no significant differences in dropping densities by geese between transects that were grazed by cattle or sheep.

A classification into plant communities significantly explained variation in goose grazing pressure (Figure 7.2B, K-W test,  $\chi^2 = 38.1$ ,  $P < 0.001$ ). The communities dominated by *Puccinellia maritima*, *F. rubra* and *A. stolonifera*, have higher utilisation by

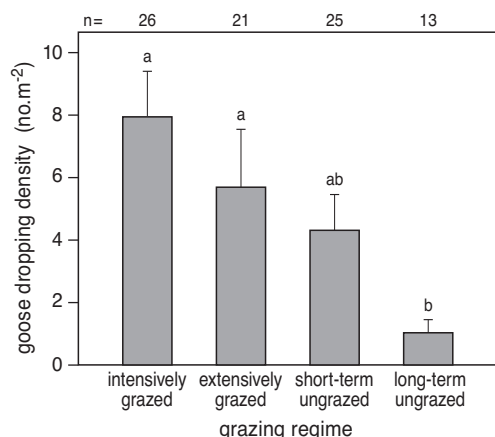


Figure 7.4 Average goose grazing pressure at the transect level in relation to livestock grazing regime for all transects that were paired within the same site. Bars that do not share the same letter are significantly different from each other ( $P < 0.05$ ).

geese. These communities together account for 85% of all goose droppings in our data. Within plant communities, still some differences exist between levels of livestock grazing (Figure 7.3B). In the communities of *F. rubra* and *Puccinellia maritima*, the communities for which we tested these relationships, higher dropping densities were found with increased intensity of livestock grazing (GLM,  $F_{3,85} = 3.6$ ,  $P < 0.017$ ), with higher dropping densities at the barrier connected marshes (GLM,  $F_{1,85} = 14.1$ ,  $P < 0.001$ ) than at the mainland marshes.

Per transect, we summed the cover of all plant communities that are characterised by short canopy and grasses that are palatable for geese (the communities *Puccinellia maritima*, *Limonium vulgare*, *J. gerardi*, *A. stolonifera* and *F. rubra*, see Appendix 7.2 and Figure 7.1). This variable was positively related to goose dropping densities at the transect level (Figure 7.5, linear regression  $R^2 = 0.1$ ,  $P = 0.037$ ). Goose dropping densities at the transect level were negatively related to average canopy height ( $F_{1,45} = 5.0$ ,  $P = 0.029$ ) and positively related to the combined index of abundance of *Plantago maritima* or *T. maritima* ( $F_{1,45} = 6.9$ ,  $P = 0.012$ ). Within transects, dropping densities were negatively related to distance from the seawall in 27% of the marshes (GLM interaction of distance and site significant), but in 67% of the cases there was no relation. These proportions did not differ between grazing regimes (contingency test:  $\chi^2 = 10.7$ , n.s.). A visual inspection of dropping data in relation to distance from the seawall did not yield indications of a threshold level in any of the transects.

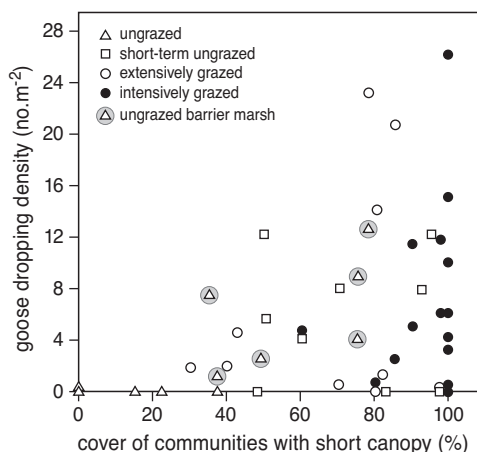


Figure 7.5 The relationship between average accumulated goose grazing pressure and the incidence of communities with a short canopy (the communities of *Puccinellia maritima*, *Limonium vulgare*, *J. gerardi*, *A. stolonifera* and *F. rubra*, see Appendix 7.2)

### Sites without signs of geese

Out of the 38 sites we visited, 11 sites (29%), had no goose droppings at all. This frequency did not differ significantly between island and mainland (contingency test:  $\chi^2 = 3.2$ , n.s.) nor between marsh type (contingency test:  $\chi^2 = 1.1$ , n.s.). Twenty-three percent of the transects were not visited by geese at all, and these were all positioned at the 11 sites mentioned above. The frequency of transects that were visited by geese was independent from livestock grazing regime (contingency test:  $\chi^2 = 0.033$ , n.s.). The height of the canopy is 3.1 cm higher ( $F_{1,57} = 5.1$ ,  $P = 0.027$ ) and tiller density is 35% lower on average (Figure 7.6,  $F_{1,63} = 6.8$ ,  $P = 0.01$ ) at these sites that are not visited by geese, after controlling for grazing regime (Figure 7.6,  $F_{3,63} = 6.5$ ,  $P = 0.001$ ). Mean grass cover, mean cover of tall plants, community composition, transect length and our indices of disturbance and freshwater availability, were not significantly different between sites that were visited by geese and sites that were not. The latter finding also held when only the sites with the highest dropping densities ( $>10$  droppings.m<sup>-2</sup>) were compared to sites that were not visited by geese.

### Distribution of hare

Hare droppings were found in average densities that were much lower than those of geese. First of all, many more sites had no hare droppings at all (47%). These sites were found on barrier marshes as well as on mainland marshes with frequencies that did not differ significantly with marsh type (contingency test:  $\chi^2 = 0.025$ , n.s.). More than 40% of the transects were without hare droppings, independent from livestock

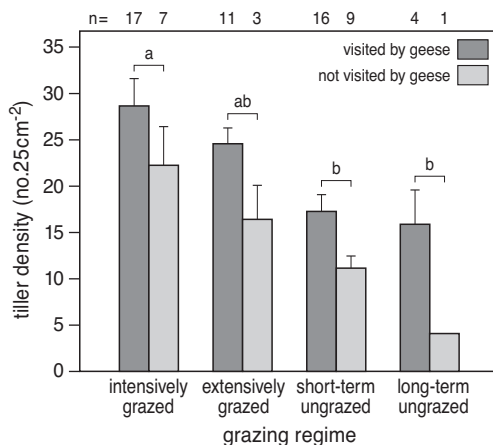


Figure 7.6 The relationship between tiller density and grazing regime in communities of *F. rubra* and *Puccinellia maritima* on the mainland marsh. Averages for sites that were visited by geese are given separately from those that did not receive any grazing pressure in our sample.

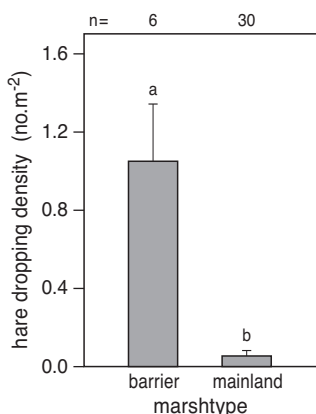


Figure 7.7 Average grazing pressure by hare at the transect-level in relation to marsh type (spring 1999 all transects)

grazing regime (contingency test:  $\chi^2 = 0.043$ , n.s.). Average dropping densities of hare were more than ten times higher at barrier marshes than at mainland marshes (Figure 7.7, K-W test,  $\chi^2 = 4.11$ ,  $P = 0.043$ ), and independent from month of sampling or livestock grazing regime. Hare grazing pressure was significantly higher in the communities of *F. rubra* and *Puccinellia maritima* at the mainland marsh, compared to the other plant communities there (K-W test,  $\chi^2 = 12.6$ ,  $P = 0.027$ ), but the magnitude of the differences was small (0.1 droppings.m<sup>-2</sup>). Within the barrier marshes no significant differences in hare grazing pressure were found between plant communities (K-W test,

$\chi^2 = 4.5$ , n.s.). The communities of *F. rubra* and *Puccinellia maritima* have higher hare dropping densities at barrier marshes than at the mainland for a given grazing regime (Figure 7.3C, Mann Whitney U test,  $P < 0.001$ ), and ungrazed versions of these communities at the mainland have significantly more hare droppings than grazed ones (Figure 7.3C, K-W test,  $\chi^2 = 9.9$ ,  $P = 0.019$ ). In the multiple regression analysis for hare dropping densities, only the combined index of abundance of *Plantago maritima* or *T. maritima* was selected as a significant variable at the transect level. We did not find a correlation between dropping densities of hare and geese, neither at the transect-, nor at the community level.

## Discussion

### *Livestock grazing and vegetation composition*

Natural vegetation succession and succession after cessation of livestock grazing on salt marshes often leads to the dominance of a few tall growing species (Jensen 1985, Andresen *et al.* 1990, Westhoff & van Oosten 1991, Aerts *et al.* 1996, Olff *et al.* 1997, van Wijnen & Bakker 1997, Bakker *et al.* 2002). Studies from barrier marshes show that succession will lead towards a vegetation dominated by *A. portulacoides* on the low marsh or *E. athericus* on the high salt marsh, while the latter may even invade the low marsh if sufficient nitrogen is available (van Wijnen & Bakker 1997, Bakker *et al.* 2002). These changes take place over periods of decades. Based on comparisons of vegetation maps over time in long-term ungrazed mainland marshes, Bakker *et al.* (2002) conclude that also on mainland marshes *E. athericus* can get dominant, though areas with low sedimentation rates or influence of fresh water are exceptions to that general pattern. Ungrazed transects in the present study, had a higher incidence of communities dominated by *A. portulacoides*, *A. maritima* or *E. athericus* (Figure 7.1) than grazed transects, but were nevertheless not entirely dominated by them. The six long-term ungrazed transects on the mainland were covered with tall communities for 75% on average against 28% on average for the barrier marshes. For some of these transects at barrier marshes (Griend, Rottumeroog, Schiermonnikoog, Terschelling), this may be due to the fact that the age of the marsh was low, and hence the productivity (Westhoff & van Oosten 1991, van der Wal *et al.* 2000a). The transects on Langli, however, appear to be an exceptional case. Langli has a well established old salt marsh that has not been cattle grazed for several decades, but which is nonetheless covered for 75% with communities dominated by short grasses. Langli is characterised by high densities of hare (Madsen pers. comm.) and is also inhabited by below-ground grazing waders *Arvicola terrestris* (pers. obs., not mentioned by van Laar (1981)). The combined impact of these species of small herbivores in this case may be strong enough to halt the vegetation succession.

The effects of livestock grazing regime were also detectable in terms of significant differences in average canopy height, cover of palatable grasses and cover of tall plants on the transects. Even within the communities of *Puccinellia maritima* and *F. rubra*, we observed differences between grazing regimes (Figure 7.3A), with stands of the same community having a taller canopy at ungrazed marshes. The short-term ungrazed



marshes in our study are already different from their grazed counterparts in most of the vegetation parameters we studied (e.g. Figure 7.3A), although the plant communities were still the same. This is in agreement with data for the *Puccinellia maritima* community at the mainland marsh of the Hamburger Hallig (Kiehl *et al.* 2000b).

Kiehl *et al.* (1997, 2000a) argue that heterogeneity in abiotic conditions in space and time will prevent absolute dominance of a single community in the absence of livestock grazing. Waterlogging in undrained mainland marshes, for example, may render parts of the marsh unsuitable for *E. athericus* and *A. portulacoides*, and may be a reason why the results of studies on well-drained sandy barrier marshes only have limited value for mainland marshes. Results of Esselink (2000) indeed indicate that a lack of drainage, although in interaction with goose and cattle grazing, affects vegetation composition substantially at the brackish marshes of the Dollard. Some of the short-term livestock-ungrazed marshes along the coast of Schleswig-Holstein are subject to neglect of the drainage system since about ten years and have high goose grazing pressure. For the present, it remains an open question to what extent the geese may be able to maintain suitable habitat within these areas, in the absence of livestock.

### Goose grazing pressure

Goose grazing pressure was found to be closely correlated to canopy height. This is consistent with observations by several authors (Summers & Critchley 1990, van de Koppel *et al.* 1996, van der Wal *et al.* 1998). Canopy height is a good indicator of forage quality, because short canopies refer to homogeneous swards with shortly grazed tillers and a favourable leaf/stem ratio. In spring, shortly grazed tillers are of high food quality. Low canopy height coincides with the plant communities characterised by the forage species of geese. We found a positive relation between the cover of communities with a short canopy and the dropping density at the transect level (Figure 7.5). Decreased intensity of livestock grazing leads to a decrease in the cover of communities with a short canopy (Figure 7.1) and lower grazing pressure by geese (Figure 7.4, Figure 7.5). The magnitude of this effect is considerable, as long-term ungrazed marshes have only 12 % of the dropping density found at intensively grazed marshes. However, the effect of livestock grazing is not absolute, as the ungrazed marshes at Griend, Rottumeroog, Schiermonnikoog and Terschelling stand out with high goose dropping densities. The results for these barrier marshes are consistent with the course of vegetation succession at these young marshes with low productivity (van de Koppel *et al.* 1996). Van der Wal *et al.* (2000a) in fact showed that the ungrazed barrier marsh of Schiermonnikoog had an optimal vegetation composition, for small vertebrate herbivores, at an age between 20 and 50 years, and a decrease in goose numbers became apparent after succession had proceeded for longer periods of time. Goose dropping densities at the short-term ungrazed marshes on the mainland are intermediate to those on intensively grazed and ungrazed marshes in our study.

Besides canopy height, goose grazing pressure was also related to our index of combined abundance of *Plantago maritima* or *T. maritima*. This relationship may be

interpreted as a direct causal link, as Prop & Deerenberg (1991) have shown that the rate of accumulation of fat in spring staging Brent Geese is contingent upon the amount of these plant species in the diet. It might, however, also be interpreted as a pseudo-correlation, since *Plantago maritima* and *T. maritima* were found to be associated with barrier marshes. It is a general result, that the sandy soils of barrier marshes are a suitable habitat for *Plantago maritima* and *T. maritima* (Schaminée *et al.* 1998) and barrier marshes may have more benefits to Brent Geese such as lower experienced levels of predation and disturbance. Barnacle Geese do not occur in reasonable numbers on the barrier marshes that were included in this study, except for Schiermonnikoog.

In April, the differences in goose dropping densities between livestock grazing regimes were not statistically significant, while differences were apparent in the combined dataset and the data for May. Similarly, we found that in April three out of eleven of the short-term ungrazed transects had higher droppings than their grazed counterpart, while in May all short-term ungrazed transects had lower dropping densities than the grazed transect at the same site. This may be related to a difference in the presence of the two goose species, as in April the Barnacle Geese are still present together with the Brent Geese, and the two species differ in the selection of habitat to some extent (chapter 3). In May, the majority (> 75%) of the Barnacle Geese had departed to the breeding grounds. Other reasons might be that the differences between salt marshes with different livestock grazing regimes become more pronounced during the growing season, or that higher primary production in combination with lower numbers of geese allows the geese to be more selective in their choice of habitat.

We are aware of only a few published studies that have explicitly considered the effects of livestock grazing at salt marshes on feeding conditions of waterfowl. Detailed studies at the Hamburger Hallig and Westerhever so far give results that are not directly in line with our data. No, or only very small effects of cessation of grazing on goose dropping densities were detected here in spring, not even after 9 years without grazing. Over this period, the prevailing *Puccinellia maritima* community did not transform into another community, but only the canopy became taller. In autumn, the differences in goose dropping densities between grazed and short-term ungrazed parts of the marsh were, however, very pronounced (Stock & Hofeditz 2000). Work at the mainland marshes of the Leybucht and the Dollard, revealed a quick change in the vegetation composition after cessation of grazing, followed by an almost immediate strong reduction in grazing pressure by geese in autumn and spring (Aerts *et al.* 1996, Bergmann & Borbach-Jaene 2001). Cadwalladr (1972) demonstrated that grazing pressure by Wigeon *Anas penelope* was higher in sheep grazed swards, compared to swards that were left ungrazed. Results presented by Boudewijn & Ebbinge (1994) indicate that the ungrazed barrier marsh at Terschelling, in spite of a relatively young age (less than 50 years), had somewhat lower goose grazing pressure at the end of the 1970s than the grazed marsh. The positive effects of livestock on goose grazing conditions are a result of their long-term effect on the vegetation composition, as livestock is not yet present on the marshes in spring. Within a season, grazing by livestock may also affect goose feeding conditions positively by maintaining a short sward, thus preventing





a decrease in forage quality due to ageing of leaves (Holmes 1989, Riddington *et al.* 1997). Vickery *et al.* (1997) found a positive correlation between livestock grazing intensity and Brent Goose grazing pressure within a series of coastal swards that were all livestock grazed, but had very similar vegetation composition.

About 20% of the sites sampled did not show signs of goose grazing. These sites differed from those that were visited by geese in taller canopy height (by 3 cm) and in higher tiller density (35% on average). The small difference in canopy height is likely a result of the geese grazing themselves. The same may apply for the observed differences in tiller density (Bazely & Jefferies 1989), but the differences can also be an inherent to the sites themselves. The importance of this finding remains obscure, but within the selection of transects that were visited by geese tiller density was not found to be related to dropping density. Madsen *et al.* (1990) mention that the narrow Danish mainland marshes are less suitable for the Brent Geese than the wide mainland marshes along the coast of Schleswig-Holstein due to their dimensions (depth), but we did not find evidence for such a relationship in our sample. So, apart from the unexplained difference in tiller density between sites that were visited by geese and sites that were not, it appears that there was no shortage of available habitat for spring staging geese in the Wadden Sea, during our study period, as was also suggested by Madsen *et al.* (1990) and Rösner & Stock (1994).

### *Hare grazing*

Presence and absence of hare on the barrier marshes is contingent upon the chances for colonisation, and can often directly be traced back to introduction by man. In total, twenty-three of the 42 islands in the chain of barrier-islands bordering the Wadden Sea, were reported to harbour hares (van Laar 1981). Hare dropping densities were not significantly related to livestock grazing regimes at the transect level, but marsh type significantly explained variation as there were a few barrier marshes with high densities of hare. Hare droppings correlated to the index of combined abundance of *Plantago maritima* or *T. maritima*. These plant species do occur in the diet of hare, though in low quantities (van der Wal *et al.* 2000b) and had higher abundance at barrier marshes. We hypothesise however, that barrier marshes are better suitable habitat for hare compared to mainland marshes for other reasons. Maybe flooding of the marsh has a disproportionate effect on hare mortality at mainland marshes in comparison to barrier marshes, due to difference in geomorphology. Elevated areas such as dunes, that provide refuge during flooding, may be reached directly on barrier marshes without a need to cross gullies or ditches. The seawall bordering mainland marshes can, however, often only be reached over land, via small dams. Above that, foxes are absent from the large majority (39) of Wadden Sea islands (van Laar 1981). There are no large differences in hare dropping densities between the mainland marshes of the Netherlands and Denmark, where hunting for hare is practised, and marshes along the German coast, where there is no hunting. Hunting of hare is prohibited in the barrier marshes we sampled.

At the community level, within the communities dominated by *Puccinellia maritima* and *F. rubra*, we observed higher hare dropping densities under ungrazed conditions at the mainland (Figure 7.3C). Hare live in the marsh year-round and have a different digestive strategy than geese. The diet of hare mainly consists of *F. rubra* (70%) in spring and summer, but in winter half of it is *A. portulacoides* (van der Wal *et al.* 2000b). Hare can digest food more effectively than geese and may thus accept forage of lower quality, which is often associated with higher biomass. We also suggest that the rate of intake for hare at low canopy heights is constrained more than the rate of intake for geese, due to a difference in morphology of the mouth. In a field experiment where a choice between patches with high and low biomass was offered, hare consistently selected the swards with higher canopy (Stahl 2001). Hare furthermore require cover for themselves and their young (Lange 1994) and such cover is more readily available under extensive or ungrazed conditions.

There is no correlation between dropping densities of geese and hare at the scales that we sampled. This suggests that the facilitative effect of hare grazing on geese, which was observed at the barrier marsh of Schiermonnikoog (van der Wal *et al.* 2000b), is not of overriding importance in the Wadden Sea as a whole, under current conditions.

### *Consequences for management*

Arctic breeding geese are dependent on the Wadden Sea for fattening up during spring staging (Madsen *et al.* 1999). Natural succession on salt marshes leads to a declining suitability of the marsh as a feeding habitat for geese. To a certain extent the geese may be able to feed in alternative habitat, such as agricultural grassland, but this has financial and maybe ecological disadvantages. Salt-marsh habitat appears to be preferred by the geese over agricultural grassland (Ebbinge 1992, Vickery *et al.* 1995), and a comparative study by Prop & Black (1997) suggests that staging in agricultural habitat may have negative consequences for the reproductive performance of the birds. Long-term data on individual reproductive success of Brent Geese presented by Spaans & Postma (2001) do not support the latter suggestion. Seagrass *Zostera* spp. is not an important food source in spring for Brent Geese (Ebbinge *et al.* 1999), as its occurrence in the Wadden Sea is low since the 1930s (den Hartog 1987, Reise *et al.* 1989, Landesamt für den Nationalpark Schleswig Holsteinisches Wattenmeer 1998).

Coastal protection works along the Wadden Sea shore, reduce the natural dynamics within the marshes and prevent a landward expansion of the marsh area. However, as a result of enhanced sedimentation within brushwood groynes, the coastal protection measures also contribute to the creation of new and young salt marsh that is not dominated by unpalatable plants. New and young salt marsh also arises on barrier islands as part of the natural build-up and breakdown (de Jong *et al.* 1999). Since the cessation of grazing in large areas leads to an ageing of the vegetation, Esselink (2000) proposed to maintain sufficient area under livestock grazing, as the grazing by large herbivores maintains the marsh vegetation at a younger successional stage. So far we do not have indications that the species of livestock used for this purpose is of crucial importance.



Livestock grazing on salt marshes has been demonstrated to affect more than just the vegetation and the feeding conditions of waterfowl, but also the relative abundance of entomofauna (Andresen *et al.* 1990, Meyer *et al.* 1995) and breeding birds (Norris *et al.* 1997, Esselink 2000, Eskildsen *et al.* 2000). We support the view that nature management of salt marshes should not be guided by the needs of a single species, but rather aim at maintaining the characteristic communities of salt marshes. Establishing variation in the grazing intensity over large areas will lead to this objective. It is recommended to specify the ecological targets, to consider to what extent livestock grazing is a suitable tool for reaching these targets, and to monitor the developments in the field.

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## References

- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of Greylag geese *Anser anser* and Barnacle Geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. *Z. Ökol. Natursch.* 5: 65-75
- Andresen H, Bakker JP, Brongers M, Heydemann B, Irmiler U (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137-148
- Bakker JP (1989) Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht
- Bakker JP, Bos D, De Vries Y (2002) To graze or not to graze, that is the question. In: Proceedings of the 10th International Scientific WaddenSea Symposium (eds K Essink, M van Leeuwe, A Kellerman, WJ Wolff): Ministry of Agriculture, Nature Management and Fisheries, Groningen (in press)
- Bakker JP, de Leeuw J, Dijkema KS, Leendertse PC, Prins HHT, Rozema J (1993) Salt marshes along the coast of the Netherlands. *Hydrobiologia* 265: 73-95
- Bazely DR, Jefferies RL (1989) Leaf and shoot demography of an Arctic stoloniferous grass *Puccinellia phryganodes* in response to grazing. *J. Ecol.* 77: 811-822
- Beeftink WG (1977) The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. In: Ecosystems of the World. Wet coastal ecosystems (ed VJ Chapman): Elsevier Scientific Publishing Company, Amsterdam

- Berg G, Esselink P, Groeneweg M, Kiehl K (1997) Micropatterns in *Festuca rubra*-dominated salt marsh vegetation induced by sheep grazing. *Plant Ecology* 132: 1-14
- Bergmann HH& Borbach-Jaene J (2001) Abschlussbericht des Forschungsprojektes Auswirkungen von Bewirtschaftungsänderungen auf die Habitatwahl, Raumnutzung und das Verhalten von Nonnengans und Ringelgans am Beispiel der Leybucht im Nationalpark Niedersächsisches Wattenmeer. Universität Osnabrück, Osnabrück
- Boudewijn TJ, Ebbinge BS (1994) General review. In: van Nugteren J (ed) Brent Geese in the Wadden Sea. Dutch society for the preservation of the Wadden Sea, Harlingen pp 39-49
- Cadwalladr DA, Owen M, Morley JV, Cook RS (1972) Wigeon (*Anas penelope*) conservation and salting pasture management at Bridgwater Bay National Nature Reserve, Somerset. *J. Appl. Ecol.* 9: 417-425
- de Boer WF, Drent RH (1989) A matter of eating or being eaten? The breeding performance of Arctic geese and its implications for waders. *WSG Bull.* 55: 11-17
- de Jong DJ, Dijkema KS, Bossinade JH, Janssen JAM (1998) Salt97; een classificatieprogramma voor kweldervegetaties. Rijkswaterstaat & IBN-DLO, Middelburg
- de Jong F, Bakker JF, van Berkel CJM, Dankers NMJA, Dahl K, Gätje C, Marencic H, Potel P (1999) Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group, Wilhelmshaven
- den Hartog C (1987) "Wasting disease" and other dynamic phenomena in *Zostera* beds. *Aquatic Botany* 47: 21-28.
- Dijkema KS (1983) Use and management of mainland salt marshes and Halligen. In: KS Dijkema, WJ Wolff (eds) *Flora and vegetation of the Wadden Sea islands and Coastal areas*. Stichting Veth tot steun aan Waddenonderzoek, Leiden pp 303-312
- Ebbinge BS (1989) A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. *Ibis* 131: 196-204
- Ebbinge BS (1992) Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla* on spring staging sites. *Ardea* 80: 203-228
- Ebbinge BS, Berrevoets C, Clausen P, Ganter B, Guenther K, Koffijberg K, Mahéo M, Rowcliffe JM, St.Joseph A, Süßbeck P, Syroechkovski EE, Jr. (1999) Dark-bellied Brent Goose *Branta bernicla*. In: J Madsen, G Cracknell, AD Fox (eds) *Goose populations of the Western Palearctic. A review of status and distribution*. Wetlands International, Wageningen. National Environmental Research Institute, Rønde pp 284-297
- Engelmoer M, Taal J, Wymenga E, Kuipers R (2001) Aantalsafname bij de Rotgans *Branta bernicla* langs de Friese waddenkust. *Limosa* 74: 41-56
- Eskildsen K, Fiedler U, Hälterlein B (2000) Die Entwicklung der Brutvogelbestände auf der Hamburger Hallig. In: M Stock, K Kiehl (eds) *Die Salzwiesen der Hamburger Hallig*. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning pp 61-65
- Esselink P (2000) Nature management of coastal marshes. Interactions between anthropogenic influences and natural dynamics. PhD thesis, University of Groningen, Groningen
- Esselink P, Zijlstra W, Dijkema KS, van Diggelen R (2000) The effects of decreased management on plant-species distribution patterns in a salt marsh nature reserve in the Wadden Sea. *Biol. Conserv.* 93: 61-76
- Gettner S, Heinzel K, Kohlus J (2000) Die Entwicklung der aktuellen Vegetation auf der Hamburger Hallig nach Änderung der Nutzung. In: M Stock, K Kiehl (eds) *Die Salzwiesen der Hamburger Hallig*. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning pp 24-33
- Holmes W (1989) *Grass*. Blackwell Scientific, Oxford
- Jensen A (1985) The effect of cattle and sheep grazing on salt-marsh vegetation at Skallingen, Denmark. *Vegetatio* 60: 37-48.
- Kempf NJL, Lamp J, Prokosch P (1987) Salzwiesen: geformt vom Küstenschutz, Landwirtschaft oder Natur? Internationale Fachtagung zu Perspektiven für Schutz und Pflege von Salzwiesen im Wattenmeer. Umweltstiftung WWF-Deutschland, Husum
- Kiehl K (1997) Vegetationsmuster in Vorlandsalzwiesen in Abhängigkeit von Beweidung und abiotischen Standortfaktoren. Arbeitsgemeinschaft Geobotanik in Schleswig-Holstein und Hamburg e.V., Kiel



- Kiehl K, Gettner S, Heinze C, Stock M (2000a) Langfristige Vegetationsveränderungen im Vorland der Hamburger Hallig und ihre bedeutung für herbivore Vögel. In: M Stock, K Kiehl (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning pp 66-73
- Kiehl K, Schröder H, Bredemeier B, Wiggershaus A (2000b) Der Einfluss von Extensivierung und Beweidungsaufgabe auf Artenzusammensetzung und Struktur der Vegetation. In: M Stock, K Kiehl (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning pp 34-42
- Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (1998) Umweltatlas Wattenmeer. Bd. 1 Nordfriesisches und Dithmarscher Wattenmeer. Ulmer, Stuttgart
- Langbein J, Hutchings MR, Harris S, Stoate C, Tapper SC, Wray S (1999) Techniques for assessing the abundance of Brown Hares *Lepus europaeus*. *Mammal Rev.* 2: 93-116
- Lange R, Twisk P, van Dijk W (1994) Zoogdieren van West-Europa. Stichting Uitgeverij van de Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Madsen J, Cracknell G, Fox AD (1999) Goose populations of the Western Palearctic. A review of the status and distribution. Wetlands International, Wageningen. National Environmental Research Institute, Rønde
- Madsen J, Frikke J, Laursen K (1990) Occurrence of and habitat utilisation by the Dark-bellied Brent Goose (*Branta bernicla bernicla*) in Denmark, with special reference to the Danish Wadden sea. *Danske Vildtundersøgelser* 45: 195-216
- Meyer H, Fock H, Haase A, Reinke HD, Tulowitzki I (1995) Structure of the invertebrate fauna in salt marshes of the Wadden Sea coast of Schleswig-Holstein influenced by sheep-grazing. *Helgoländer Meeresuntersuchungen* 49: 563-589
- Norris K, Cook T, O' Dowd B, Durdin C (1997) The density of redshank *Tringa totanus* breeding on the salt-marshes of the Wash in relation to habitat and its grazing management. *J. Appl. Ecol.* 34: 999-1013
- Olf H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, De Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814
- Owen M (1971) The selection of feeding site by white fronted geese at the new grounds, Slimbridge. *J. Appl. Ecol.* 9: 385-398
- Potel P, Südbeck P (1994) Dark-bellied Brent Geese in Niedersachsen: a review of numbers, trends and distribution. In: van Nugteren J (ed) Brent Geese in the Wadden Sea. Dutch Society for the Preservation of the Wadden Sea, Harlingen pp 87-96
- Prop J, Black JM (1997) Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. In: F Mehlum, JM Black, J Madsen (eds) Proceedings of the Svalbard Goose symposium. Norsk-Polarinstitut, Oslo pp 175-193
- Prop J, Deerenberg C (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28
- Reise K, Herre E, Sturm M (1989) Historical changes in the benthos of the Wadden Sea around the island of Sylt in the North Sea. *Helgoländer Meeresuntersuchungen* 43: 417-433
- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153-160
- Roozen AJM, Westhoff V (1985) A study on long-term salt marsh succession using permanent plots. *Vegetatio* 61: 23-32
- Rösner H-U, Stock M (1994) Numbers, recent changes, seasonal development and spatial distribution of Dark-bellied Brent Geese in Schleswig-Holstein. In: van Nugteren J (ed) Brent Geese in the Wadden Sea. Dutch Society for the Preservation of the Wadden Sea, Harlingen pp 69-85
- Schaminée JHJ, Weeda EJ, Westhoff V (1998) De Vegetatie van Nederland. DI 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440

- Stahl J (2001) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD thesis, University of Groningen, Groningen
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitates durch Nonnen- und Ringelgänse. In: M Stock, K Kiehl (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning pp 43-55
- Stock M, Kiehl K (2000) Empfehlungen zum Salzwiesenmanagement im Nationalpark Schleswig-Holsteinisches Wattenmeer. In: M Stock, K Kiehl (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning pp 74-77
- Stock M, Kiehl K, Reinke HD (1997) Salt marsh protection in the Schleswig-Holstein Wadden Sea area. Umweltbundesamt, Berlin.
- Summers RW, Critchley CNR (1990) Use of grassland and field selection by Brent Geese *Branta bernicla*. J. Appl. Ecol. 27: 834-846.
- van de Koppel J, Huisman J, van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. Ecology 77: 736-745.
- van der Meijden R (1990) Heukels' Flora van Nederland, 21st edition. Wolters-Noordhoff, Groningen
- van der Wal R, van de Koppel J, Sagel M (1998) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. Oikos 82: 123-130
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000a) Are spring staging brent geese evicted by vegetation succession? Ecography 23: 60-69
- van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D (2000b) On facilitation between herbivores: How Brent Geese profit from brown hares. Ecology 81: 969-980
- van Laar V (1981) The Wadden Sea as a zoogeographical barrier to the dispersal of terrestrial mammals. In: CJ Smit, J den Hollander, WKRE van Wingerden, WJ Wolff (eds) Terrestrial and freshwater fauna of the Wadden Sea area. Stichting Veth tot steun aan Waddenonderzoek, Leiden pp 231-266
- van Wijnen H, Bakker JP (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. J. Coast. Cons. : 19-26
- Vickery JA, Sutherland WJ, O'Brien M, Watkinson AR, Yallop A (1997) Managing coastal grazing marshes for breeding waders and overwintering geese: Is there a conflict? Biol. Conserv. 79: 23-34
- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. Oecologia 103: 499-508
- Westhoff V& van Oosten MF (1991) De Plantengroei van de Wadden eilanden. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Zar JH (1996) Biostatistical Analysis. Prentice-Hall, Inc., N.J.



Maarten Loonen maintains an overall view (photo J. Stahl).





Appendix 7.1 An overview of the selected sites. I = Intensive, SU = Short-term Ungrazed, E = Extensive and LU = Long-term Ungrazed

No	Location	Marsh-type	Grazing regime	Species of livestock	dropping density (no.m <sup>-2</sup> )			Cover of communities with short canopy(%)	Disturbance class
					Goose April	Goose May	Hare		
1	Skallingen	Barrier	E	Cattle	0.0	.	0.0	50	Undisturbed
1	Skallingen	Barrier	LU	-	0.0	.	0.0	17	Undisturbed
2	Langli	Barrier	LU	-	12.7	.	1.5	78	Undisturbed
3	Vilslev	Mainland	I	Sheep	0.0	.	0.0	100	Undisturbed
4	Kammerslusen	Mainland	I	Sheep	0.8	.	0.0	80	Undisturbed
5	Mandø	Barrier	E	Cattle	0.0	0.0	0.3	80	Undisturbed
5	Mandø	Mainland	E	Sheep	1.9	2.0	0.1	40	Undisturbed
5	Mandø	Mainland	LU	-	0.3	0.0	0.3	23	Undisturbed
6	Råhede	Mainland	E	Sheep	0.0	0.0	0.0	63	Undisturbed
7	Rejsby	Mainland	I	Sheep	0.0	.	0.0	100	Undisturbed
8	Brøns	Mainland	I	Sheep	0.0	.	0.0	100	Undisturbed
9	Astrup	Mainland	I	Sheep	2.6	.	0.0	85	Moderate
10	Rømø	Mainland	E	?	1.0	.	0.0	100	Moderate
11	Ballum Enge	Mainland	I	Sheep	2.5	9.8	0.0	98	Undisturbed
12	Marienkoog	Mainland	I	Sheep	0.0	0.0	0.0	93	Undisturbed
12	Marienkoog	Mainland	SU	-	0.0	0.0	0.0	100	Undisturbed
13	Grøde	Mainland	E	Cattle/sheep	16.0	30.6	0.0	78	Undisturbed
13	Grøde	Mainland	SU	-	6.1	18.5	0.0	40	Undisturbed
14	Sönke Nissenkoog	Mainland	I	Sheep	11.7	8.5	0.0	100	Undisturbed
14	Sönke Nissenkoog	Mainland	SU	-	0.0	0.0	0.0	98	Undisturbed
15	Hamburger Hallig	Mainland	I	Sheep	9.8	14.0	0.0	98	Moderate
15	Hamburger Hallig	Mainland	E	Sheep	1.4	0.0	0.0	70	Undisturbed
15	Hamburger Hallig	Mainland	SU	-	5.0	6.5	0.0	50	Undisturbed
16	Nordstrand	Mainland	I	Sheep	0.1	0.0	0.0	100	Undisturbed
16	Nordstrand	Mainland	SU	-	0.0	0.0	0.0	83	Undisturbed
17	Norderheverkoog	Mainland	SU	Sheep	0.0	.	0.1	90	Undisturbed
18	Westerhever	Mainland	I	Sheep	3.8	8.7	0.0	100	Undisturbed
18	Westerhever	Mainland	SU	-	9.7	6.6	0.0	70	Undisturbed
19	Friedrichskoog	Mainland	I	Sheep	5.6	3.1	0.0	100	Undisturbed
19	Friedrichskoog	Mainland	SU	-	0.1	0.0	0.0	98	Undisturbed
20	Dieksanderkoog Nord	Mainland	I	Sheep	2.1	4.5	0.0	100	Moderate
20	Dieksanderkoog Nord	Mainland	SU	-	13.7	2.4	0.1	93	Moderate
21	Dieksanderk Sud	Mainland	I	Sheep	16.6	13.9	0.0	100	Moderate
21	Dieksanderk Sud	Mainland	SU	-	19.2	5.4	0.0	95	Undisturbed
22	Berensch	Mainland	I	Sheep	0.0	.	0.0	100	Undisturbed
22	Berensch	Mainland	SU	-	0.0	.	0.0	95	Undisturbed
23	Wremen	Mainland	I	Cattle	0.0	.	0.0	100	Undisturbed
24	Langwarder Außengroden	Mainland	SU	-	0.0	.	0.0	55	Undisturbed
25	Elisabeth Außengroden	Mainland	LU	-	0.0	.	0.0	30	Moderate
26	Harlesiel	Mainland	E	Cattle	0.6	0.0	0.2	98	Undisturbed
26	Harlesiel	Mainland	SU	-	0.0	0.0	0.6	48	Undisturbed
27	Neßmersiel	Mainland	E	Cattle	0.0	.	0.0	90	Undisturbed
27	Neßmersiel	Mainland	SU	-	0.0	.	0.0	30	Undisturbed
28	Leybucht	Mainland	I	Cattle	20.3	32.3	0.0	100	Undisturbed
28	Leybucht	Mainland	SU	-	4.0	4.9	0.0	60	Undisturbed
29	Rottumeroog	Barrier	LU	-	6.1	9.0	0.0	35	Undisturbed
30	Noordpolderzijl	Mainland	I	Sheep	.	4.8	0.1	60	Moderate
30	Noordpolderzijl	Mainland	LU	-	.	0.0	0.0	0	Undisturbed
31	Groningen coast	Mainland	I	Sheep	15.5	7.5	0.0	90	Moderate
31	Groningen coast	Mainland	E	Sheep	7.5	1.8	0.0	43	Moderate
32	Groningen coast	Mainland	I	Sheep	3.0	7.3	0.0	90	Moderate
32	Groningen coast	Mainland	LU	-	2.4	0.2	0.1	38	Moderate
33	Groningen coast	Mainland	E	Sheep	3.8	0.1	0.1	30	Undisturbed
33	Groningen coast	Mainland	LU	-	0.0	0.0	0.0	38	Undisturbed
34	Schiermonnikoog	Barrier	E	Cattle	16.1	12.4	1.4	80	Moderate
34	Schiermonnikoog	Barrier	LU	-	3.7	1.6	1.5	49	Undisturbed
35	Noord Friesland Buitendijks	Mainland	I	Cattle	5.7	6.8	0.0	100	Undisturbed
35	Noord Friesland Buitendijks	Mainland	E	Cattle	1.5	1.3	0.0	82	Undisturbed
35	Noord Friesland Buitendijks	Mainland	LU	-	0.1	0.2	0.0	15	Undisturbed
36	Terschelling	Barrier	E	Cattle/horses	.	20.8	0.1	85	Undisturbed
36	Terschelling	Barrier	LU	-	.	4.2	1.6	75	Undisturbed
37	Texel	Barrier	LU	-	0.3	.	0.0	0	Undisturbed
38	Griend	Barrier	LU	-	9.0	.	0.0	75	Undisturbed





## Appendix 7.2 Key to the classification of plant communities on saltmarshes. A globalisation of the classification by de Jong et al, 1998. Follow the key from above to below:

There are four salt-marsh zones: The pioneer zone, the low marsh, and the middle to high marsh. First decide on the zone, based on the underlined decision rules. Then choose the first option that fits the plot.

### If total cover > 1% and pioneer species > species of low marsh:

- Sa - *Spartina* *Spartina anglica* > *Salicornia* and *Suaeda maritima*  
Q - *Salicornia* *Salicornia* and/or *Suaeda maritima* > *Spartina anglica*

### If Pioneer species < species of low marsh > species of high and middle marsh:

- Ap - *Atriplex* *Atriplex portulacoides* > 25% cover or (*Atriplex portulacoides* > 15% and *Limonium vulgare* < 15% cover)  
Pm - *Puccinellia* Other low marsh

### If (Pioneer species + species of low marsh) < species of high and middle marsh:

- Am - *Artemisia* *Artemisia maritima* > 15% cover and *A. Maritima* > *F. rubra*  
Ap - *Atriplex* *Atriplex portulacoides* > 15% cover  
Lv - *Limonium* *Limonium vulgare* > 15% cover  
Jg - *Juncus gerardi* *Juncus gerardi* > *Festuca rubra*  
Jm - *Juncus maritimus* *Juncus maritimus* > 10% cover  
Gm - *Glaux* *Glaux maritima* dominant  
EA - *Elymus* *Elymus* sp. + *Atriplex prostrata* + *Atriplex lanceolata* > 25% cover  
As - *Agrostis* *Agrostis stolonifera* dominant  
Fr - *Festuca* Other middle high marsh  
D - Dune  
O - No vegetation / Other

### Pioneer species:

*Spartina anglica*, *Salicornia* sp. and *Suaeda maritima*

### Species of the low marsh:

*Puccinellia maritima*, *Atriplex portulacoides*, *Cochlearea anglica*, *Aster tripolium*, *Spergularia* sp., *Triglochin maritima*, *Limonium vulgare*, *Plantago maritima*, *Parapholis* spp., *Atriplex pedunculata*.

### Species of the middle marsh:

*Artemisia maritima*, *Armeria maritima*, *Juncus gerardi*, *Glaux maritima*, *Festuca rubra*

### Species of the high marsh:

*Potentilla anserina*, *Trifolium* spp., *Poa* spp., *Lolium* spp., *Elymus* spp., *Lotus corniculatus*, *Plantago coronopus*

*Limonium vulgare* on a young livestock-ungrazed salt marsh (photo J. Stahl).





# 8

CHAPTER

## Capacity of Wadden Sea coastal grasslands for Dark-bellied Brent Geese

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### Abstract

We have compiled information on vegetation composition, grazing management and spatial distribution of Dark-bellied Brent Geese along the coast of the entire Wadden Sea in May 1995-98. Brent Goose distribution was clumped, with relatively high numbers in Schleswig-Holstein and the Netherlands. Brent Goose densities were highest on the Halligen, followed by barrier marshes and then by mainland marshes. There is large variation in bird numbers between counting areas, part of which could be attributed to vegetation composition, grazing regime, soil type and numbers of Brent Geese in the region. Livestock grazing positively affected the occurrence of vegetation that is dominated by short grasses, which are palatable for geese. We predicted the potential number of geese for relevant categories of marsh, based on vegetation composition and independent estimates of potential goose density per plant community. These predictions enabled us to identify marshes that are apparently under-utilised in May in the current situation, and to predict the effect of large-scale changes in livestock grazing management on the capacity of salt marshes for geese. We infer that grazing with livestock enhances the capacity of Wadden Sea salt marshes by a factor of three to eight.

## Introduction

### *Spatial distribution of Brent Geese*

Migrating Brent *Branta b. bernicla* and Russian Barnacle Geese *Branta leucopsis*, of the East Atlantic Flyway spend a large part of the spring staging period in the International Wadden Sea. During this period they depend to a large extent on salt marshes to accumulate fat reserves for migration and breeding (Ebbing 1989; Ebbing & Spaans 1995) and several factors have been identified that affect the spatial distribution of geese. Understanding the patterns of distribution is essential for the estimation of the capacity of salt marshes and the evaluation of salt-marsh management.

Potentially, livestock grazing on marshes is one of the main factors affecting the geese, via its impact on vegetation composition. Local studies indicate that geese spend more time on grazed than on ungrazed salt marshes (Boudewijn & Ebbing 1994; Aerts *et al.* 1996; Bergmann & Borbach-Jaene 2001), but this effect is not found on young marshes with a sandy soil, e.g. Trischen (Guenther *et al.* 1998). It is also less apparent on marshes where livestock grazing was stopped less than a decade ago (Potel & Südbeck 1994; Stock & Hofeditz 2000), although Bergmann & Borbach Jaene (2001) already found a very strong effect after 5 years of no grazing. Livestock grazing favours plant communities dominated by short grasses that are palatable for geese, such as *Festuca rubra* and *Puccinellia maritima* (Dijkema 1983c; Adam 1990). In the absence of livestock, tall unpalatable plants, such as *Elymus athericus* and *Atriplex portulacoides* invade the marsh at the expense of these grasses (Olf *et al.* 1997; van Wijnen & Bakker 1997; Gettner *et al.* 2000; Bakker *et al.* 2002). Barrier marshes, or 'barrier-connected marshes' in the definition of de Jong *et al.* (1999), have originated on a sandy substrate and have soils with a thinner layer of clay than more sheltered mainland salt marshes (Dijkema 1983b). Olf *et al.* (1997) showed that the pool of nitrogen is positively related to the thickness of the clay layer and ongoing sedimentation thus leads to a continual increase in nutrient availability. Olf and co-workers concluded that succession on barrier marshes is mainly caused by this process. Age of the marsh is thus an important determinant of the successional stage and suitability of the marsh for geese, in interaction with the grazing regime.

Until the last decades of the 20<sup>th</sup> century, most of the marshes along the mainland of the Wadden Sea were grazed with cattle, sheep and horses. This situation has changed over the 1990s with a reduction in agricultural use along the coast of Niedersachsen (DE) (Potel & Südbeck 1994) and the cessation of grazing on 42% of the mainland marshes in Schleswig-Holstein (DE) (Stock & Kiehl 2000). In the Netherlands, the grazing intensity had already declined along the mainland coast from the 1980s onwards and currently about 60% of the total marsh area is grazed here. About 85% of the marshes in the Danish part of the Wadden Sea are livestock grazed. Today, about 60% of all marshes in the International Wadden Sea are grazed by domestic animals.

In addition to the large herbivores, the most important vertebrate grazers of the Wadden Sea marshes are the Brent and Barnacle Geese, hares *Lepus europaeus* and to some extent rabbits *Oryctolagus cuniculus* (van Laar 1981). These small vertebrate herbi-



vores may directly interfere with Brent Geese, or indirectly affect the amount and quality of available food (van der Wal *et al.* 1998; van der Wal *et al.* 2000b). Barnacle Geese are suggested to prevent Brent Geese from foraging in certain locations in early spring (Rösner & Stock 1994; Ebbinge & Spaans 1995; Engelmoer *et al.* 2001), but Stahl *et al.* (2001b) showed that there might also be a facilitative effect. They showed that previous experimental grazing by Barnacle Geese in April enhanced forage quality for Brent Geese following in the grazing sequence. For Barnacle Geese, the Wadden Sea is a primary staging area in autumn, winter and early spring. When population size was still small in the 1970s, almost all Barnacle Geese would leave the Wadden Sea area in March, and move to the Baltic area (Gotland (SE) and Estonia), the key spring staging area in April and the first half of May for Russian Barnacle Geese. The smaller Brent Geese winter much further to the south, primarily along the coasts of England and France, and the majority does not return to the Wadden Sea until late March, to stage there until late May. In the 1970s, when both populations were much smaller, there was an almost complete temporal separation in the spring distribution of both species, with only a small overlap in March in the Wadden Sea. After an almost five-fold increase in population size for both species, a considerable number of Barnacle Geese extended their spring stay in the Wadden Sea until late April, whereas Brent Geese also started to use the western part of the Wadden Sea as a wintering area. In this paper we, therefore, also include data on Barnacle Geese in trying to explain the habitat use in spring of Brent Geese. Thus far, there is no evidence for a strong direct effect of grazing by geese on vegetation composition, but hares were shown to retard vegetation succession for up to 40 years by grazing on *Atriplex portulacoides* in winter (van der Wal *et al.* 2000b), thus facilitating exploitation by geese.

Other factors potentially affecting goose distribution are related to safety, fresh drinking water availability and group- or social processes. The perceived safety of marshes depends upon the lack of predators and human disturbance (Stock & Hofeditz 1996), and foxes *Vulpes vulpes* for example, were only reported to occur at three of the 42 barrier islands in the Wadden Sea (van Laar 1981). Brent Geese were shown to be more tolerant to salt stress than Barnacle Geese (Stahl *et al.* 2001a), and therefore the two goose species are likely to respond differently to a lack of fresh water for drinking. Finally, there is a strong element of tradition in site choice by geese (Ganter & Ebbinge 1996). Many individual birds are faithful to their staging sites, but some are nomadic.

### *Capacity of salt marshes*

Carrying capacity represents the population size which the resources of the environment can maintain without a tendency to either increase or decrease (Caughley 1979; Begon *et al.* 1990). Sutherland & Goss-Custard (1991) and Goss-Custard (1985), suggest that for birds wintering on estuaries, it is useful to use the term carrying capacity for those cases where the addition of a further individual would lead to the emigration or death of another. However, the term has been given more and often contradictory meanings, such that some have suggested to abandon it (Dhondt 1988). The size of

natural populations are not determined by simple carrying capacities, since there is a suite of factors affecting individuals, and resource availability not only affects density, but is affected by density as well. Besides, there are unpredictable environmental fluctuations (Begon *et al.* 1990), and in systems dominated by stochastic events, the concept of carrying capacity loses validity (McLeod 1997). In the case of migratory animals, population numbers might be regulated to a large extent in other places than the ones that are considered. Equilibrium population size, the population number at which recruitment is equal to mortality, can be well below the estimated values of local carrying capacity due to this (Sutherland 1996). Recruitment and mortality are assumed to be related to population size through 'density dependent' processes. One very important density dependent process appears to be operating in the breeding areas, where a limited number of safe nesting sites constrains the breeding output (Ebbinge & Spaans 2002). Recruitment in Brent Geese is also strongly affected by the amount of fat reserves that are accumulated during spring, and feeding conditions during the spring staging period thus potentially affect reproduction and hence the population size (Ebbinge *et al.* 1982; Ebbinge & Spaans 1995). Calculation of the number of individuals that a site will contain in the equilibrium situation, requires tackling the problem in two stages (Sutherland 1996); first it is necessary to consider the total population size that will result from interaction of all density-dependent and density-independent mortality and recruitment in all breeding sites and all non-breeding sites. The second stage is to consider how the individuals will be distributed between the sites. The number of individuals in a given site then depends upon the interaction between these two stages. We will here ignore the relationship with equilibrium population size and define local capacity to be the potential grazing density, as a function of resource availability, over the time period of interest (McLeod 1997). For the current study this is the month of May. Our aim is to illuminate the factors that are most important in determining local capacity and to give an approximate estimate of the capacity for different types of marsh and livestock grazing regime using this information.

Some authors estimated carrying capacity of a particular site directly, assuming that peak numbers in high quality preferred sites would rise to a ceiling value (Ebbinge 1992; Ganter & Ebbinge 1996; Esselink 2000; van der Wal *et al.* 2000a). Massé *et al.* (2001) estimated capacity from the net aboveground primary production in relevant plant communities. We will in this paper, deduce estimates of potential goose density in May from independent sources, for relevant plant communities on the marsh. Subsequently, we will predict the potential numbers of geese that could forage in different goose count units using vegetation maps, and examine the validity of this approach by comparing the results with observed values. First we will describe the spatial distribution of Brent Geese during the month of May, for a large number of goose count units in relation to the vegetation composition, and assess the relative importance of livestock grazing regime, soil type, the interaction with Barnacle Geese, human disturbance, availability of fresh drinking water and marsh dimensions. We focus our analysis on the end of spring because this is the period that Brent Geese numbers peak in this area (Ebbinge





*et al.* 1999). By May the majority of Barnacle Geese has left the Wadden Sea.

## Methods

### *Goose data*

On a regular basis, goose numbers are assessed along the entire coastline of the international Wadden Sea (Melfo *et al.* 1994; Rösner & Stock 1994; Rösner *et al.* 1994; Poot *et al.* 1996; Koffijberg *et al.* 1997). Most of these counts are based upon observations from the ground, but for Denmark we used data that were obtained from aerial surveys (Madsen *et al.* 1990). The count units used in this study are in most cases identical to the most detailed geographical areas used in the field when counting the geese for the Netherlands (SOVON,  $n = 110$ ), Niedersachsen (NLÖE,  $n = 122$ ), and Schleswig-Holstein (Hälterlein *et al.* 1991,  $n = 105$ ). For the Danish Wadden Sea we aggregated the 65 field units used during the surveys (Madsen *et al.* 1990) to 42 count units in order to be able to attribute geese to a specific area of marsh unambiguously. We used the data from 1995 - 1998 and calculated the average number of Brent and Barnacle Geese observed per count unit, for the months of April and May. For Brent Geese we have chosen to use the May counts, because in early May peak numbers occur in the Wadden Sea, and Ebbsing (1992) showed that for the islands of Terschelling and Texel these May peak numbers were highly correlated with the total number of Brent Goose-days spent over the months April and May. Data for April are included to obtain a better insight in the distribution of Barnacle Geese. For Denmark, an absence of counts in some of these months forced us to use data from 1991-95 for May and 1989-94 for April. The mean of the monthly averages over these years were used in this study, as a measure of the use of the count unit by each goose species. The mean value was highly correlated to the maximum (Pearson  $r = 0.97$ ,  $P < 0.001$ ) or the minimum value (Pearson  $r = 0.86$ ,  $P < 0.001$ ) for the same years. The choice for this specific set of years is determined by the availability of data at sufficient level of detail. The years 1995-98 are a period of decline in Brent Goose population numbers, from over 300,000 in the beginning of the 1990s to about 250,000 in 1995 (Ebbsing *et al.* 2002). Barnacle Goose numbers in the Wadden Sea have increased considerably in the past decades, from 20,000 in 1960 to over 260,000 in 1997 and were still rising during our study period (Ganter *et al.* 1999).

### *Vegetation data*

Vegetation information was derived from detailed vegetation maps of salt marshes, that were available in digital format (see Appendix 8.1). The maps were all derived from interpretation of aerial photographs in combination with a field survey. Scale of mapping varied between 1:5,000 and 1:10,000. Date of mapping varies between 1988 and 1995 (see Appendix 8.1). The maps for Schleswig-Holstein (Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning) and the Netherlands (Monitoring programme RIKZ, Meetkundige Dienst, Delft) contained information on the vegetation composition at a detailed level, with over 200 legend units following Gettner

(unpubl.) and de Jong *et al.* (1998) respectively. These legends strongly adhere to the classification by Schaminée *et al.* (1998). For Niedersachsen a map of 'biotope-types' was available. Biotope types are abstract units, based on vegetational and structural characteristics (Hecker 1995). The classification key for biotopes in Niedersachsen was made by Ringot (1993). In order to harmonise the available vegetation maps we converted the existing legends to plant communities at the association level. In this grouping, we followed the botanical logic by Schaminée *et al.* (1998) and de Jong *et al.* (1998) (see Appendix 8.2) Nomenclature of taxa following van der Meijden (1990). For the Danish Wadden Sea only the areal extent of marshes was available, but no information on the vegetation composition. Using a Geographic Information System (GIS), we established the total area of salt-marsh vegetation and the area covered by each plant community per count unit. For the count units for which no vegetation maps were available, we obtained the total area of marsh from Kempf *et al.* (1987). Count units were classified as marsh if salt marsh was present ( $> 1$  ha) and contain 150 ha ( $\pm 150$  ha s.d.) of marsh vegetation on average. In only a few count units there was a combination of artificial grassland and marsh and, to prevent bias, these were excluded from the analyses when relationships between goose distribution and salt-marsh vegetation were analysed. In total, there were 358 count units with goose observations, of which 203 were classified as marsh.

### *Additional information*

Per count unit we compiled information on salt-marsh management (livestock grazing regime), marsh-dimension (width in km), indications of disturbance level and distance to fresh or brackish drinking water. Grazing management was classified as 'long-term ungrazed' ( $> 10$  years), 'short-term' ungrazed ( $\leq 10$  years), 'grazed' or combinations of these when the count unit contained marshes with different management regimes. Marshes were classified into marsh-types following de Jong *et al.* (1999) and further combined into groups of marshes with a sandy soil (barrier marshes and green beaches) or marshes with a clay soil (estuarine, mainland and foreland marshes as well as Halligen). Note, however, that Hallig marshes may differ from other clay marshes in soil nutritional status and drainage characteristics, as they have mixed layers of clay-sediments and shell fragments. For each count unit we estimated the potential importance of human disturbance, for the habitat use of the Brent Geese in that unit in three classes: undisturbed, lightly disturbed or heavily disturbed. We assessed whether a fresh or brackish water source was available in the count unit, within 2.5 km of the boundary of the count unit or further away. We subdivided the Wadden Sea into 29 counting regions (following Meltøfte *et al.* 1994) and calculated the average number of geese per region for the months of April and May, in order to obtain insight in the distribution on a larger scale. The average monthly count results per count unit were summed for each species per region per year, and averaged over the years 1995-1998. Missing values were replaced by the average value of the count units for that month over these years.





### *Potential grazing density*

We compiled observed values of Grazing Density (GD, no.ha<sup>-1</sup>.d<sup>-1</sup>) from literature and our own field studies, to arrive at an estimate of Mean Potential Grazing Density (MPGD, no.ha<sup>-1</sup>.d<sup>-1</sup>). Grazing Density in this study is defined as the average number of Brent and Barnacle Geese that can forage daily on a unit of marsh at a given time during the season. MPPGD refers to the Mean Potential Grazing Density that can be realised for the month of May, for relevant plant communities on the marsh and for different types of marsh. It is estimated from the upper values of reported Grazing Density that are valid for the specified category of marsh. Grazing Density is calculated from observed numbers ( $GD = N \times A^{-1}$ ), from reported goose days ( $GD = I \times t^{-1}$ ), from accumulated droppings ( $GD = D \times 10,000 \times P^{-1} \times t^{-1}$ ) and from dropping rates ( $GD = R \times 10,000 \times P^{-1}$ ). Here, N (no) refers to observed numbers, A (ha) to the area considered, I (goose day.ha<sup>-1</sup>) to grazing intensity reported in goose days, t (day) to the time interval over which the data are collected, D (no.m<sup>-2</sup>) to dropping density, P (no) to the daily number of droppings produced per goose, and R (no.m<sup>-2</sup>.d<sup>-1</sup>) to dropping rates. All the data collected refer to the spring period (but with varying time intervals) and to Brent and/or Barnacle Geese. For the calculations, we assumed a total foraging time of 10 hours per day and dropping intervals (sec.dropping<sup>-1</sup>) of 280 s for Brent Geese, 243 s for Barnacle Geese (Bruinzeel *et al.* 1997) and 260 s when droppings were produced by a combination of both species. To express variation in Potential Grazing Density due to climatic fluctuation between years and environmental heterogeneity, we also estimated a range over which the MPPGD is assumed to vary, based on the collected information.

### *Analysis*

Statistical analyses were restricted to all sites that were classified as ‘marsh’. We related average Brent Goose numbers to the area of relevant plant communities per count unit in a General Linear Model (GLM). In addition, we tested for the effects of live-stock grazing regime, soil-type, the presence of Barnacle Geese in April and May, the regional number of Brent in May, marsh dimensions, availability of fresh water and human disturbance. We also tested for significance of the interaction between area of each plant community included and grazing regime. Any non-significant contributions were removed from the model. The effects of grazing regime and soil-type on the relative cover of plant communities was determined using non-parametric (Kruskal-Wallis) tests. For count units with clearly defined management regime (grazed or long-term ungrazed), and for which we had a complete vegetation map, we predicted the number of geese that could potentially graze there in spring. For this, we multiplied the area of each plant community (ha) with the MPPGD (no.ha<sup>-1</sup>.d<sup>-1</sup>) that was estimated for that community, and summed them over the communities present. Upper

and lower predicted values were calculated in the same way, using the range over which the MPGD was assumed to vary. We assessed the average vegetation composition of salt marshes per grazing regime and soil type and made a prediction of Potential Grazing Density for each of these combinations per unit area. Given these figures, and the area of marsh in each count unit, we then extrapolated the estimates to predicted potential bird numbers per count unit. In this extrapolation we assumed an average vegetation composition per soil type and grazing regime and we will thus refer to it as the prediction based on soil type and grazing regime. We also assumed that the short term ungrazed marsh would feature the vegetation composition of a long-term ungrazed marsh, because they are in transition towards that stage.

## Results

### *Vegetation composition*

A total area of more than 30,000 ha. of marsh vegetation fringes the Wadden Sea, two thirds of which is on the mainland (Figure 8.1). We were able to obtain an estimate of the vegetation composition for 75% of the total marsh area. Half of this could be attributed to a specific management regime and differences between these grazing regimes are illustrated in Figure 8.2. Livestock grazing positively affected the occurrence of the *Armerio-Festucetum* and the *Puccinellietum*, communities dominated by the short grasses *Festuca rubra* and *Puccinellia maritima*, respectively. Stocking rates in this study vary between count units, but are generally in the order of 0.5 - 1.2 Livestock Units (LU) ha<sup>-1</sup> for mainland marshes and 0.5 LU ha<sup>-1</sup> for barrier marshes. One LU refers to

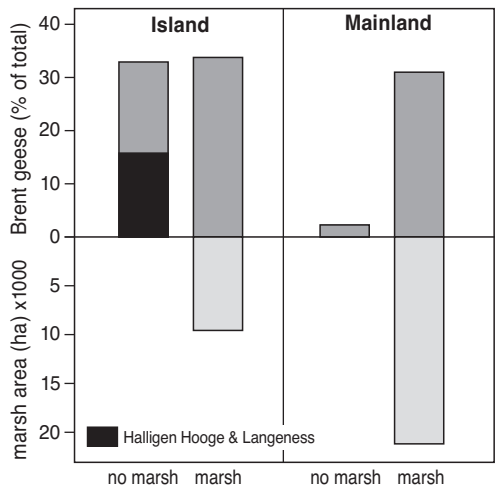
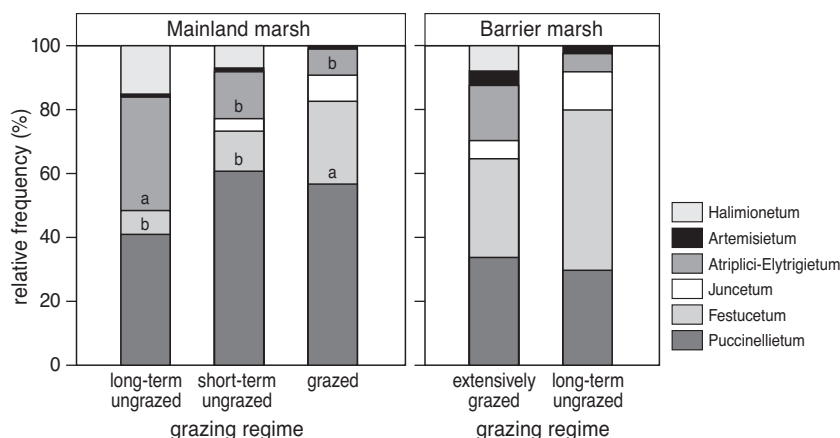


Figure 8.1 Distribution of Brent Geese (%) and marsh vegetation (ha) over islands (barrier islands and Halligen) and mainland.



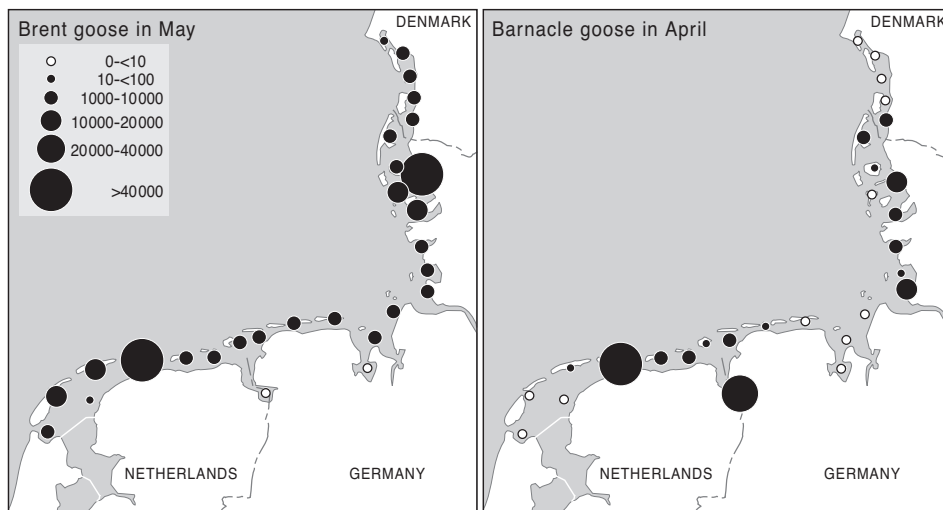
**Figure 8.2** The relative cover of the main salt marsh plant communities above the pioneer zone, in relation to grazing regime and marsh type (see Appendix 2 for a description of the communities). Significant differences in relative cover of a plant community within a marsh type, are indicated with different letters ( $P < 0.05$ ).

one adult cow or 10 sheep. On ungrazed marshes, the Atriplici Elytrigietum and the Halimionetum, communities dominated by tall *Elymus athericus* and *Atriplex portulacoides*, respectively, covered a larger proportion of the area under study. The effect of not grazing was most pronounced and significant ( $P < 0.05$ ) at mainland marshes, where almost 50% was covered by tall vegetation in the long-term ungrazed situation against only 10% in the grazed situation (Figure 8.2).

### Distribution of geese

#### REGIONAL SCALE

On average, 205,000 Brent Geese staged in the Wadden Sea during the months of May 1995-1998. Additionally some 20,000 Barnacle Geese were present in the same period in the same area. The largest share of the Brent Geese were observed in counting areas classified as marsh (64%, see Figure 8.1), but a substantial number was observed on the Halligen Hooe and Langeness (16%), which had not been classified as marsh (following Dijkema (1983a) and Kempf *et al.* (1987)) or the polder areas on the Dutch barrier islands (15%). The Brent Goose distribution was highly clustered, with only 3 regions harbouring more than 50% of the birds (Figure 8.3). These regions were the north-coast of Friesland including Ameland (region 25), and two regions in the Halligen area in Schleswig-Holstein (regions 8 & 9). Some regions were not visited at all in May, such as the Dollard and the Jadebusen. At the regional level, there was nevertheless a significant positive correlation between the total area of marsh (including the area of the Halligen Hooe and Langeness, 1492 ha) and average goose numbers for Brent in May (Pearson  $r = 0.478$ ,  $P = 0.01$ ,  $n = 28$ ) and for Barnacle Goose in



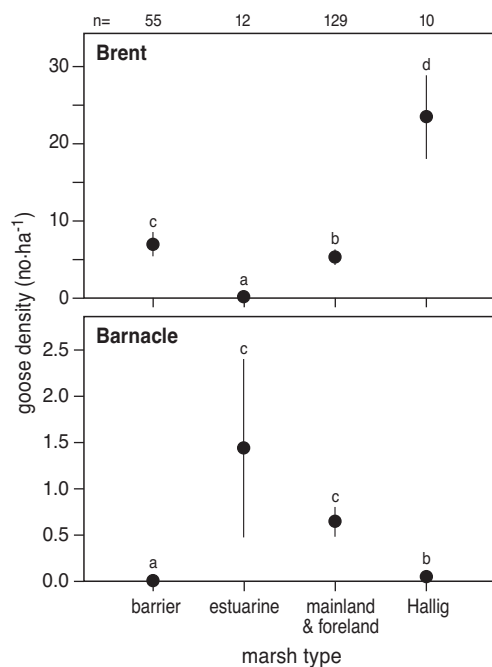
**Figure 8.3** Map of the distribution of Brent (in May) and Barnacle Geese (in April) at the regional level. Regions are defined by Meltofte *et al.* (1994).

April (Pearson  $r = 0.533$ ,  $P = 0.003$ ,  $n = 28$ ). Brent Goose numbers in May were positively correlated to Barnacle Goose numbers in April (Pearson  $r = 0.646$ ,  $P < 0.001$ ,  $n = 28$ ) and May (Pearson  $0.612$ ,  $P < 0.001$ ,  $n = 28$ ), at the regional level of scale.

#### LOCAL SCALE (COUNT UNITS)

In May, the marshes on islands generally have higher Brent Goose densities than on the mainland (Figure 8.4, Mann-Whitney U-test,  $n = 200$ ,  $P < 0.001$ ). The Hallig marshes have an exceptionally high number of Brent Geese given their size, while estuarine marshes stand out low. Barnacle Goose densities in May were generally low and highest at marshes on the mainland (Figure 8.4). Barnacle Goose densities in April were higher on mainland marshes than on island marshes ( $7.3 \pm 1.3$  s.e. versus  $0.3 \pm 0.2$  s.e., Mann-Whitney U-test,  $n = 206$ ,  $P < 0.001$ ), with 12.5 % of the Barnacle Geese on estuarine mainland marshes and 85 % on other mainland marshes.

The average number of Brent Geese was positively related to the area of the Puccinellietum, within the grazed marshes (Table 8.1, GLM: interaction grazing regime (GR) x Area of Puccinellietum (AP),  $F_{4,141} = 4.3$ ,  $P = 0.002$ ). Soil type significantly explained some of the variation: sandy marshes have about double the amount of Brent Geese, as compared to the clay marshes of the mainland, controlling for the area of Puccinellietum and the other factors. The regional number of Brent Geese in May, as well as the number of Barnacle Geese that was present in the count unit in April, had a positive relation to the average number of Brent Geese observed in May in a count unit. Barnacle Goose numbers in May explained no extra variation, but were positively correlated to Brent Goose numbers in May in a separate bi-variate correlation. Marsh dimensions did not explain any variation in this model, but were correlated



**Figure 8.4** The average density of Brent and Barnacle Geese (no.ha<sup>-1</sup>.d<sup>-1</sup>) in May between 1995 and 1998, for the different types of salt marsh that are most relevant. Different letters indicate significant differences ( $P < 0.05$ ).

**Table 8.1** Differences in the average observed number of Brent Geese in May between count units, as a function of the Area of Puccinellietum (ha), the grazing regime, soil type (clay or sand), the population number in the region and the use of the count unit by Barnacle Geese in April. GLM results,  $R^2 = 0.544$ .

Source of variation	df	F	P
Area of Puccinellietum (AP)	1	5.9	0.016
Grazing regime (GR)	4	1.8	0.130
GR x AP	4	4.3	0.002
Soil type	1	6.8	0.010
Regional Brent goose number	1	41.1	0.000
Barnacle goose number in April	1	16.6	0.000
Error	141		

to several of the other variables, such as the regional number of Brent Geese (Pearson  $r = 0.50$ ,  $P < 0.001$ ,  $n = 152$ ) and the area of Puccinellietum (Pearson  $r = 0.51$ ,  $P < 0.001$ ,  $n = 152$ ) in a separate test. Mainland marshes are significantly narrower in Niedersachsen with  $0.6 \text{ km} \pm 0.5$  (s.d.), against  $0.8 \text{ km} \pm 0.5$  in Denmark,  $1.1 \text{ km} \pm 0.9$  in Schleswig-Holstein and  $1.4 \text{ km} \pm 1.1$  in the Netherlands. Five marsh areas were identified where human disturbance was assumed to be 'high' and 47 marshes where disturbance was 'light', but the factor disturbance did not explain variation in this model. Drinking water availability was strongly associated to geographical position in the tidal basin (island versus mainland, contingency-test:  $\chi^2 = 31.1$ ,  $n = 125$ ,  $df = 4$ ,  $P < 0.001$ ), with 55% of the count units on islands having no fresh or brackish water nearby, against only 12% at the mainland. Drinking water availability thus highly correlated to soil-type (Pearson  $r = 0.65$ ,  $n = 86$ ,  $P < 0.001$ ), and hence it was not included in the model. Brent Goose densities were higher on the sandy marshes, and thus appear not dependent on the availability of fresh or brackish drinking water (K-W test:  $\chi^2 = 25$ ,  $df = 4$ ,  $P < 0.001$ ).

The results of the statistical analysis are to be treated with some caution, because the factors 'grazing regime' and 'soil type' are highly confounded. The data file included only three count units on barrier marshes that were grazed versus a limited sample of five long-term ungrazed marshes on the mainland. Furthermore, we had insufficient information to test for the effect of fertilisation, while some of the count units with the highest Brent Goose numbers, at the north coast of Friesland, were known to receive artificial fertiliser regularly (Engelmoer 1998).

### *Independent estimates of potential grazing density*

#### LIVESTOCK GRAZED

A variety of estimates of grazing density (GD) is available in the literature for the Puccinellietum and the Armerio-Festucetum (Table 8.2). These plant communities are important for geese as they are characterised by the highest abundance of preferred food plants. For the grazed Puccinellietum, high grazing densities based on dropping counts were reported for the Hallig Langeness ( $50 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{day}^{-1}$  in spring, (Prokosch 1979)). On the intensively grazed mainland marsh of the Hamburger Hallig, the average goose grazing intensity was  $42 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$  over spring in the years 1998-99 (mainly Barnacle Geese (Stock & Hofeditz 2000)). At Noord Friesland Buitendijks (NFB), which is sometimes fertilised, van der Graaf *et al.* (2002) measured  $54 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$  in May and Aerts *et al.* (1996) observed an average density of  $33 \text{ Barnacle Geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$  in spring in the Dollard. Van der Graaf *et al.* (2002) also report a grazing density of  $32 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$  in May for the livestock-grazed Puccinellietum on the barrier marsh of Schiermonnikoog and measured a local density of  $65 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$  for the fertilised and livestock-grazed Puccinellietum in May on the barrier marsh of Ameland. Livestock-grazed communities of *Agrostis* and *Festuca* appear to have slightly higher maximal reported values of grazing density for the different marsh types compared to the Puccinellietum, with locally  $69 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$  in spring on the Hallig Süderoog,  $50 \text{ geese} \cdot \text{ha}^{-1} \cdot \text{d}^{-1}$



**Table 8.2** Upper and lower Grazing Densities from literature and estimates of Mean Potential Grazing Density (MPGD, no.ha<sup>-1</sup>) per marsh type, plant community and grazing regime. The term 'short palatable' refers to the plant communities characterised by the forage species of geese, the Puccinellietum and the Armerio-Festucetum (see Appendix 8.2). All data refer to assessments based on dropping counts. Sources: 1 (Aerts *et al.* 1996), 2 (ch. 7), 3 (ch. 4), 4 (chapter 5), 5 (Ebbinge & Boudewijn 1984), 6 (Engelmoer *et al.* 2001), 7 (Esselink 2000), 8 (Madsen 1989), 9 (Madsen *et al.* 1990), 10 (Olff *et al.* 1997), 11 (Prokosch 1979), 12 (Prokosch 1991), 13 (Rösner & Stock 1994), 14 (Spaans & Postma 2001), 15 (Stock & Hofeditz 2000), 16 (Prop 1991), 17 (Stock *et al.* 1995).

Marsh type	Grazing status	Plant community	range		MPGD	Sources
			Lower	Higher		
Sandy marsh	grazed	Short palatable	8	45	30	2,3,5
	ungrazed	Short palatable	4	30 <sup>1</sup>	15	2,3,5,8,9,16
Clay marsh	grazed	Short palatable	8	50	30	1,2,3,6,11,13,15,17
	ungrazed	Short palatable	0.5	5	5	2
all	all	Juncetum	0	10 <sup>2</sup>	2	2,3
		Artemisietum	0	4	2	2,3
		Halimionetum	0	5	2	2,3
		Salicornietum	0	2	2	2
		Spartinetum	0	5	2	2
		Atriplici-Elytrigietum	0	3	2	2,3

<sup>1</sup> Locally, values up to 90 geese.ha<sup>-1</sup> were found: sources 8,9 and 16

<sup>2</sup> Locally values up to 30 geese.ha<sup>-1</sup> were found: source 3

in spring on the foreland of Föhr (Prokosch 1979) and 30-40 geese.ha<sup>-1</sup>.d<sup>-1</sup> in spring on the barrier marsh of Terschelling (Ebbinge & Boudewijn 1984). Along the mainland coast of Groningen we observed a density of 20 geese.ha<sup>-1</sup>.d<sup>-1</sup> in May (chapter 4). We estimate a MPGD for grazed communities characterised by palatable grasses (Armerio-Festucetum and Puccinellietum, see Appendix 2), to be in the order of 30 geese.ha<sup>-1</sup>.d<sup>-1</sup> in May, which is conservative for the marshes with a clay soil.

#### LIVESTOCK UNGRAZED

High values of grazing density were found for the ungrazed Puccinellietum at the barrier marshes of Langli (26 to 90 geese.ha<sup>-1</sup>.d<sup>-1</sup> in May (Madsen 1989)), and on the young successional stages of this community at Schiermonnikoog (40-60 geese.ha<sup>-1</sup>.d<sup>-1</sup> (Prop 1991)). Other estimates for this community, from different locations on Terschelling and Schiermonnikoog, range from 5-10 geese.ha<sup>-1</sup>.d<sup>-1</sup> (Ebbinge & Boudewijn 1984; Olff *et al.* 1997; chapter 4). This large variation is caused by large differences in vegetation composition that exist within the ungrazed Puccinellietum. With ongoing vegetation succession, the suitability of the Puccinellietum as a foraging area

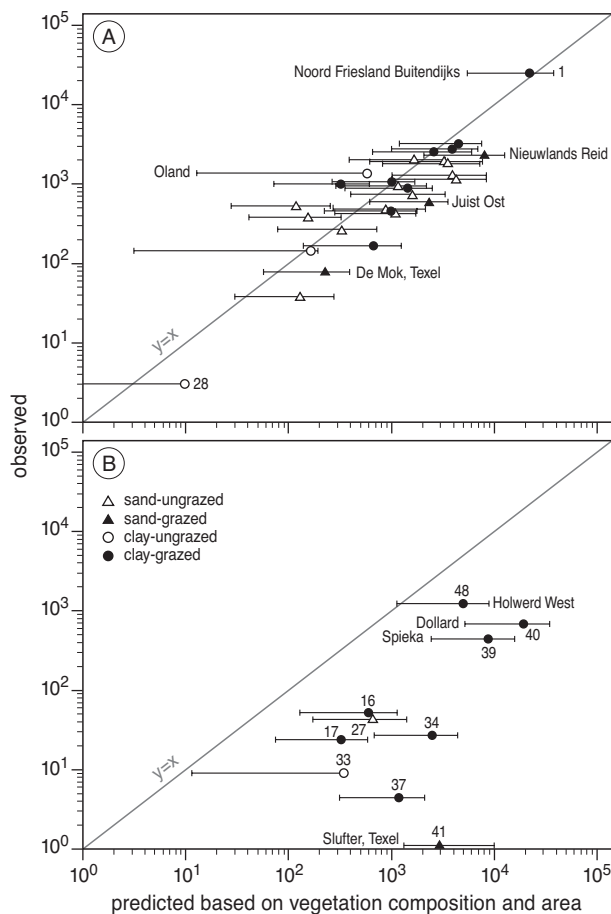
first increases to decrease again later (Oloff *et al.* 1997; van der Wal *et al.* 2000a). The grazing density at ungrazed Armerio-Festucetum on Schiermonnikoog was estimated to be 14 geese.ha<sup>-1</sup>.d<sup>-1</sup> over spring in 1977 (Ebbinge & Boudewijn 1984), while a grazing density of 25 geese.ha<sup>-1</sup>.d<sup>-1</sup> was observed in May 1986, on the young successional stages of this community (Prop 1991). Somewhat lower values (5-8 geese.ha<sup>-1</sup> were found in 1998 in May by van der Graaf *et al.* (2002) in a sample that also included older successional stages of this community. Estimates of grazing density for ungrazed Armerio-Festucetum and Puccinellietum on marshes with a clay soil, and plant communities other than Puccinellietum and Armerio-Festucetum were scarce. In a transect survey on accumulated grazing pressure in salt marshes in the Wadden Sea (chapter 7), grazing density was observed to be low in ungrazed Puccinellietum and Armerio-Festucetum at the mainland clay marsh (see Table 8.2). The most important other communities in terms of area are the Atriplici-Elytrigietum and the Juncetum community (Figure 8.2), which generally have very low grazing density of about 2 geese.ha<sup>-1</sup>.d<sup>-1</sup>. Locally, however, high grazing density (30 geese.ha<sup>-1</sup>.d<sup>-1</sup>) was found in the Juncetum at Schiermonnikoog, whenever the associated plant species *Puccinellia maritima* or *Plantago maritima* were abundant (Bos unpubl. data), or in the *Elymus repens* community in the Dollard (17 geese.ha<sup>-1</sup>.d<sup>-1</sup>, (Aerts *et al.* 1996)). We estimate a MPGD for ungrazed communities characterised by palatable grasses (Armerio-Festucetum and Puccinellietum) to be in the order of 15 geese.ha<sup>-1</sup>.d<sup>-1</sup> in May for marshes with a sandy soil, and for this we ignore the higher estimates of Prop (1991) and Madsen (1989). For ungrazed communities characterised by palatable grasses on marshes with a clay soil, we estimate a MPGD of 5 geese.ha<sup>-1</sup>.d<sup>-1</sup>, while it is 2 geese.ha<sup>-1</sup>.d<sup>-1</sup> in all other communities.

### Extrapolation

#### ACCORDING TO MAPPED VEGETATION COMPOSITION

Using the estimated values of Mean Potential Grazing Density (MPGD) in Table 8.2, we predicted the number of birds (Brent or Barnacle Geese) that could potentially feed in each count unit with known grazing regime and vegetation composition (Figure 8.5). For reasons of graphical illustration and reduction of noise, we then grouped count units belonging to the same grazing regime and geographical location (as defined in the hierarchical coding system of count units for all countries, except Denmark, see Appendix 8.3). The correlation between observed goose number in May and the predicted potential number for a selection of locations ( $n = 28$ ) with high goose numbers (Figure 8.5A), gives some support for the approach. The grazed marshes with a clayey soil and the ungrazed barrier marshes, that had high observed numbers of geese are on the line  $y = x$ , or scattered around this line. There are three valid estimates for grazed barrier marshes, the Nieuwlands Reid (rank number 5; number refers to the rank order in Figure 8.5A), Juist Ostheller (rank number 17) and Texel, de Mok (rank number 26). They are higher than the observed values. It is, however, true that these observed averages have high coefficients of variation and additional count information indicates that





**Figure 8.5** The predicted potential number of geese, based on vegetation composition and area, versus the observed average number in May. Over 90 % of the observed birds are Brent Geese. Only those count units are included with known vegetation composition, a valid estimate of average observed goose numbers and a clearly defined management regime, (long term ungrazed (mostly barrier marshes) or livestock-grazed (mostly mainland marshes)). When multiple count units with identical grazing regime are present at one location, these count units are grouped. (A) the selection of groups of count units ('locations') that are assumed to be used by geese at densities 'close' to capacity. Individual data points can be identified based on their rank number (1-28, ordered from high to low observed values), that corresponds to the location that they belong to as given in Appendix 8.3. (B) the selection of groups of count units that appear under-utilised in May. The label numbers directly refer to the locations that a data point belongs to, as mentioned in the text, or as given in Appendix 8.3.

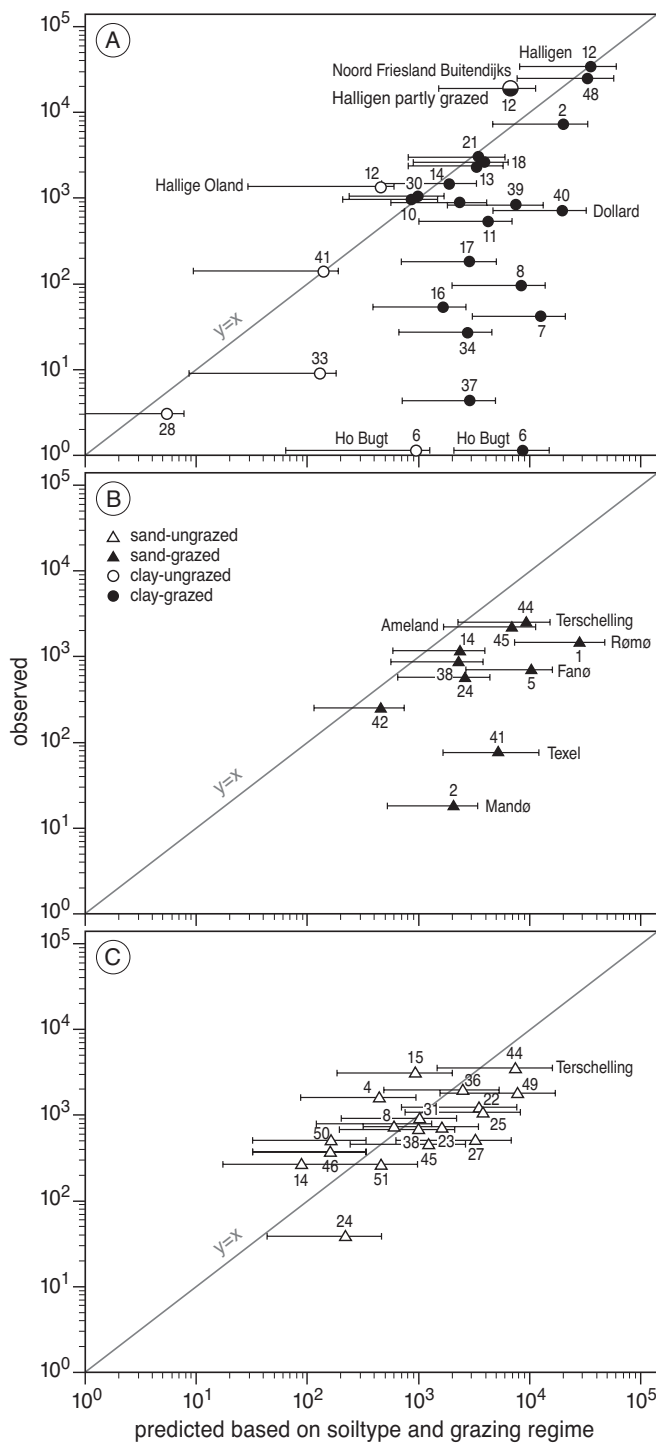
there is reason to assume that the observed values are in fact under estimates. Figure 8.5B presents the complementary selection of count units ( $n = 10$ ), whose observed average goose numbers deviate strongly from the predicted values. This can be caused by a strong over-estimation of the predicted value or because the count units are under-utilised in May. The most important deviations are found for the Slufter on Texel (41, numbers refer to the identifier used in Figure 8.5B), Horumersiel Vorland (34), Spieka Vorland (39), the Dollard (40) and Holwerd West (48). The Slufter was not at all visited by geese in May, which is likely related to its odd geographical position amongst dunes close to the North Sea. Horumersiel Vorland is a very narrow strip of marsh (0.25 km), the Dollard consists of estuarine marsh and Holwerd West is only grazed at very low stocking rate ( $0.3 \text{ LU ha}^{-1}$ ), with an *Aster tripolium* dominated Puccinellietum in spring. For Spieka Vorland and the other locations in Figure 8.5B we are not aware of any peculiarities that could potentially explain the discrepancy.

ACCORDING TO SOIL TYPOLOGY AND GRAZING REGIME

Given the average vegetation composition of salt marshes with different soil-type and grazing regime (Figure 8.2), we extrapolated the estimated values of Mean Potential Grazing Density (MPGD) per community (Table 8.2) to an estimate of potential grazing density for the average marsh of a certain type on a per hectare basis (Table 8.3). This yields  $10 \text{ geese.ha}^{-1}.\text{d}^{-1}$  for ungrazed barrier marshes, while ungrazed marshes with a clay soil would support  $3 \text{ geese.ha}^{-1}.\text{d}^{-1}$ . Grazed barrier marshes are predicted to support  $23 \text{ geese.ha}^{-1}.\text{d}^{-1}$ , and grazed marshes with a clay soil  $20 \text{ geese.ha}^{-1}.\text{d}^{-1}$ . The estimate for marshes with a clay soil is lower because, according to our sample, these marshes have a larger proportion of pioneer zone ( $22 \% \pm 2.2 \text{ s.e.}$  versus  $7\% \pm 1.3 \text{ s.e.}$ ).

**Table 8.3** Potential Grazing Densities (PGD,  $\text{no.ha}^{-1}$ ) for marshes with different soil type and grazing regime. Predictions are based upon average vegetation composition (Figure 8.2) and Mean Potential Grazing Density (MPGD,  $\text{no. ha}^{-1}$ ) per plant community (Table 8.2). Empirical estimates of potential goose density ( $\text{no.ha}^{-1}$ ) from the literature are indicated (Sources: see caption Table 8.2).

Soil type	Grazing status	Prediction based on vegetation-composition and MPGD (table 8.2)		Literature estimates					
				based on counts			based on droppings		
		PGD	Range	Lower	Higher	Sources	Lower	Higher	Sources
Sandy	grazed	23	(6-37)	13	33	5,13	12	85	3,5,10,13
	ungrazed	10	(2-21)	13	36	5,13	2	95	3,8,9,10,16
Clay	grazed	20	(5-35)	15	50	5,7,12,13	7	50	5,6,7,9,11,15,17
	ungrazed	3	(0.2-4)	0	1	this study	0	3	2
Agricultural grassland		80	(60-240)	60	75	4,14	26	240	3,4,5,9,14

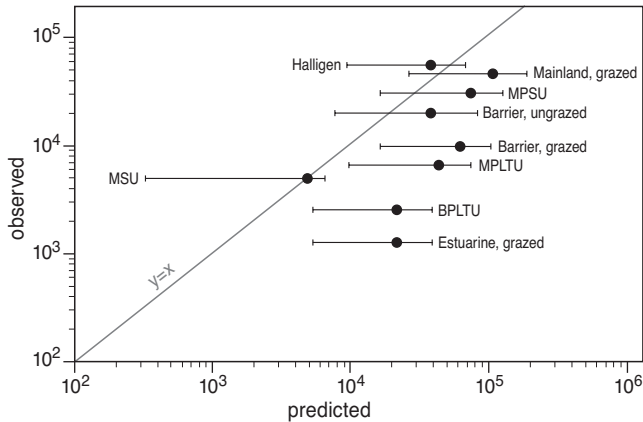


**Figure 8.6** The predicted potential number of geese based on soil composition and livestock-grazing regime versus the observed average number in May. Over 90 % of the observed birds are Brent Geese. Only count units with a clearly defined management regime (long-term ungrazed (mostly barrier marshes) or livestock-grazed (mostly mainland marshes)) are plotted, but for partly-grazed Halligen an exception was made. A) Grazed and ungrazed marshes with a clay soil. B) Sand-grazed marshes. C) Sand-ungrazed marshes. The label numbers directly refer to the locations that a data point belongs to, as mentioned in the text, or as given in Appendix 8.3.

Table 8.3 also indicates observed values for these types of marsh based on counts, for comparison. The predictions were subsequently applied to our count units, which were again grouped per location, and compared to the average observed number of geese (Figure 8.6). Especially the locations with sandy-grazed marsh (Figure 8.6B) have consistently lower goose numbers than predicted, but among the sandy-ungrazed (Figure 8.6C) and the clay-grazed locations there are some that fluctuate around  $y = x$ . The clay marshes in the Danish Wadden Sea, and again the estuarine marshes of the Dollard, stand out with low numbers of geese in May, relative to the predicted potential (Figure 8.6A, locations 2,6,7,8,40), whereas the Halligen (12) and Noord Friesland Buitendijks (48) have relatively high observed numbers of geese. In this calculation, the Halligen Hooze and Langeness have been included. Long-term ungrazed marshes with a clay soil are still rare, and the few that are present are mostly small. All have low goose numbers, except for the foreland marsh at Oland (12), but here the count results appear to be biased by one exceptional high count. Among the sandy-grazed marshes (Figure 8.6B), the observed values for Ameland (45) and Terschelling (44) deviate less from the prediction than, for example, Rømø (1), Mandø (2), Fanø (5) and Texel (41, in particular de Slufter). Count unit Rømø North (location 1, 1000 ha) has by far the largest deviation (22,000 birds predicted but only 884 birds observed), but is also exceptional in the sense that it is a military training area. The sandy ungrazed marshes of Trischen (15, Figure 8.6C) and Langli (4) have exceptionally high observed numbers of geese, relative to other marshes of the same type, while some of the long-term ungrazed barrier marshes in Niedersachsen and the Netherlands had lower observed goose numbers than what was predicted (for example the count unit with the 100 year old ungrazed marsh on Schiermonnikoog (part of location 49), where observed values were a factor three below the prediction).

In Figure 8.7 the results of the extrapolation based on soil type and grazing regime are summarised for the main categories of marsh in our database, including those categories where the boundaries of the management regime did not exactly overlap those of the count units, or where management had changed in the last decade. Grazed mainland marshes are predicted to sustain the highest number of geese, but this potential is only realised for 40% in May. About 15% of the predicted potential goose numbers was observed on grazed barrier marshes, while the long-term ungrazed barrier marshes harboured 50% of the predicted potential. The combined Halligen have an observed number of geese in May which is 37% above the predicted number. Brent Geese are hardly observed on estuarine marshes.

There is a significant relation between observed and predicted values at the regional scale, using the regional classification of Meltøfte (1994) (linear regression  $R^2 = 0.769$ ,  $n = 26$ ,  $P < 0.001$ ). The observed values for the Danish regions are, however, not related to the predictions (interaction country  $\times$  predicted value,  $F_{3,20} = 5.5$ ,  $P = 0.009$ ), mainly because in region 4 (Rømø, Mandø and Ballum Vorland) many more birds were expected. The average width of marshes had no significant contribution in explaining variation.



**Figure 8.7** Observed average goose numbers for the major categories of marsh in the Wadden Sea versus the predicted potential numbers. Categories that are ‘partly grazed’ contain goose counting units of which the boundaries did not exactly coincide with those of the grazing regime. ‘Short-term grazed’ and ‘Long-term ungrazed’ indicate no live-stock-grazing for less than ten years or more then ten years, respectively. MSU = Mainland short-term ungrazed, MPSU = Mainland partly short term ungrazed, MPLTU = Mainland partly long-term ungrazed, BPLTU = Barrier partly long-term ungrazed.

## Discussion

### Overview

Brent Goose distribution in the Wadden Sea was clustered with concentration areas in the Netherlands and Schleswig-Holstein (Figure 8.3). The birds appear to favour marshes on barrier islands and Halligen over the mainland, and were hardly found in the estuarine marshes (Figure 8.4). There was large variation in average Brent Goose numbers between individual count units, but some of this could be attributed to the area of an abundant plant community in the Wadden Sea, the Puccinellietum. We will contrast this observed pattern to predicted potential goose numbers for relevant categories of marsh in May, meanwhile evaluating the validity of our extrapolations and the relative importance of livestock grazing, marsh type and other factors studied.

### *Independent estimates of grazing density*

A literature review in combination with own field observations, yielded independent estimates of grazing density by geese and revealed that livestock-grazed swards of *Armerio-Festucetum* and *Puccinellietum*, potentially have the highest goose densities. For Brent, as well as for Barnacle Geese, high observed values of grazing density were found for both communities, and given the amount of variation, there were no strong indications that one community could harbour more geese than the other. The infor-

mation available indicated that these plant communities generally support lower goose grazing density when they are not grazed by livestock (Ebbinge & Boudewijn 1984), but exceptions to this were found for the young successional stages at the ungrazed barrier marshes on Schiermonnikoog (Prop 1991) and Langli (Madsen 1989). The results of a transect survey at 38 locations along the Wadden Sea (chapter 7) indicated that Puccinellietum and Armerio-Festucetum ungrazed by livestock, at the mainland had lower densities than the same communities on barrier marshes. All other plant communities are generally estimated to have low goose grazing densities in May. The observed ranking of the plant communities in terms of grazing density can be explained from the relative cover of food plants, that differs strongly between plant communities, but also varies with soil type and grazing regime within plant communities (see below). A second important process is the primary productivity, which determines the maximum amounts of food that could potentially be removed over a certain period. It is to be predicted that given a specific plant community marshes with a thicker layer of clay should be able to sustain higher goose densities because of higher primary production. Evidence for this effect between marsh types though, was not strong in our review of grazing density (Table 8.2, Table 8.3). We did, however, find that productive artificial grassland had the highest reported values of goose grazing density for all communities studied (Spaans & Postma 2001). The productivity in this habitat is so high, that the suitability of the sward would deteriorate without these high grazing intensities, and the birds are observed to aggregate to keep up with the production (Spaans & Postma 2001; chapter 5).

#### *Vegetation composition in relation to soil type and grazing regime*

Livestock grazing favours communities with grasses that are tolerant to grazing, such as the Puccinellietum, Armerio-Festucetum and Juncetum (Dijkema 1983c; Bakker 1989; Andresen *et al.* 1990; Bakker *et al.* 2002). Especially the Puccinellietum and the Festucetum are characterised by the forage species of geese, *Puccinellia maritima*, *Festuca rubra*, *Plantago maritima* and *Triglochin maritima*. Undisturbed succession on salt marshes, however, favours communities like the Atriplici-Elytrigietum and the Halimionetum, dominated by tall plant species that are unpalatable for geese, especially *Elymus athericus* and *Atriplex portulacoides* (Olf *et al.* 1997; van Wijnen & Bakker 1997; Bakker *et al.* 2002). For sandy barrier marshes this process takes several decades, as the succession is dependent on the input of nitrogen via sedimentation (Olf *et al.* 1997). The data presented in this study are consistent with these results (Figure 8.2), as long-term ungrazed marshes have higher cover of communities dominated by *Elymus athericus* and *Atriplex portulacoides* than other marshes. The effect of livestock grazing is stronger on mainland as compared to barrier marshes, which is due to the fact that the group of long-term ungrazed barrier marshes is diverse in age. It includes relatively young marshes on islands that are 'moving', such as Trischen (Stock *et al.* 1997), Mellum (Kuhbier 1987) and Schiermonnikoog (van der Wal *et al.* 2000a) or where marsh had established recently for other reasons. On Terschelling for example, the creation of an artificial sand dike has led to the rapid development of salt marsh on the Boschplaat



in the past fifty years (Westhoff & van Oosten 1991). An illustration of the effect of age on relative cover of the different communities can be derived from the comparison of vegetation composition in three count units on the long-term ungrazed marsh on Schiermonnikoog. The successional age of this vegetation differs between the three count units due to eastward expansion of the island, as is illustrated by van der Wal *et al.* (2000a). The relative cover of the communities dominated by tall *Elymus athericus* and *Atriplex portulacoides* strongly increases from 19% of all vegetation above the pioneer zone at an age of 0-25 years, to 50% at an age of 50-100 years. The western part of the ungrazed marsh on Schiermonnikoog is one of the oldest known ungrazed barrier marsh in the Wadden Sea, and the estimated vegetation composition of long-term ungrazed barrier marsh presented in Figure 8.2 is thus biased towards relatively young age. The vegetation composition at Langli is characterised by an unexpectedly high cover of *Puccinellietum* and *Festucetum* (75%, chapter 7), given the fact that the marsh has not been grazed by livestock for many decades. It is hypothesised that the combined impact of hare and below-ground grazing water voles *Arvicola terrestris*, may be strong enough to retard the vegetation succession.

Within plant communities, the relative abundance of the different species is also dependent on grazing regime and soil type. Intensively grazed salt marsh tends to be dominated entirely by *Puccinellia maritima*, *Festuca rubra* or *Agrostis stolonifera* (Dijkema 1983b; Kiehl *et al.* 1996). With lower livestock grazing intensity, the relative cover of other marsh species is higher. On the sandy marshes, this is especially *Limonium vulgare*, while on marshes with a clay soil *Aster tripolium* becomes prevalent, in addition to species such as *Artemisia maritima*, *Elymus athericus* and *Atriplex portulacoides*, that are less strictly related to a particular soil type (Schaminée *et al.* 1998).

### *Spatial distribution of Brent Geese*

The information obtained from vegetation maps and the independent estimates of grazing density per plant community, allowed us to predict potential goose numbers per count unit. The observed values fit the predicted values rather well for some of the ungrazed barrier marshes and grazed mainland marshes (Figures 8.5A & 6). The predictions allowed us to identify count units, marsh types and regions with lower observed goose numbers than the predicted potential. Discrepancies between observed and predicted potential numbers are either caused by a fundamental over estimation of the potential numbers for a given marsh type, a situation of 'under-utilisation', or errors in the estimation of average goose numbers and vegetation composition. An example of the latter sort of error comes from the type of vegetation map that was used to estimate the vegetation composition for Niedersachsen. This map was produced with a different precision and with an entirely different legend than those for the Netherlands and Schleswig-Holstein. It is not unlikely that this has resulted in an overestimation of the relative amount of the *Puccinellietum*, and thus an overestimation of the potential goose numbers in this areas, due to the decision rules we followed during reclassification (see Appendix 8.2). Similarly, we assumed that the vegetation composition on the



Halligen would resemble the other marshes with a clay soil, because we had no suitable vegetation maps available for this marsh type. Halligen, however, have an entirely different origin from that of man-made mainland marshes, as they have accreted on the remains of flooded former polders (Dijkema 1983b), without the support of brushwood groynes. Halligen have a somewhat lower clay content in the soil, a natural drainage system and there is likely to be a lower share of pioneer zone, than on man-made mainland marshes. To what extent these differences lead to an over- or underestimation of potential goose numbers on the Halligen remains unclear.

#### VARIATION BETWEEN MARSH TYPES

The Hallig marshes stand out with the highest densities of Brent Geese in May (Figure 8.4) and the observed numbers are even above the predicted values (Figure 8.7). Hallig marshes are only fertilised by some farmers with liquid manure or dung, and differ especially from mainland marshes in the fact that they are inhabited and that they are islands. Most sandy barrier marshes are islands as well. Observed Brent Goose numbers are on average a little higher on barrier marshes than on the mainland (Figure 8.4), also for a given area of *Puccinellietum*. Together, these observations point at the existence of a preference which is not related to soil-type, but rather to one of the characteristics associated with islands. Examples of such characteristics are the more natural morphology, lower experienced levels of predation/disturbance and generally an absence of Barnacle Geese. We hypothesise that the relative isolation and presumed lower levels of disturbance of the Halligen and barrier marshes, enable the geese to graze the swards in a more efficient way. Lower levels of disturbance enable a slower rate of digestion (Prins & Ydenberg 1985; Prop & Vulink 1992) and a possibility to concentrate the grazing intensity (see chapter 5), thus manipulating the suitability of the sward. The Halligen are furthermore very attractive staging areas in autumn, as they are surrounded by huge seagrass fields at that time. The reason that it is especially Brent Geese that use the Halligen and the barrier marshes might be found in the hypothesis that Barnacle Geese are more sensitive to salt stress. Barnacle Geese were shown to have smaller salt glands than Brent Geese. They respond negatively to experimental spraying of the vegetation with salt water, whilst Brent Geese do not (Stahl *et al.* 2001a). Finally, we suggest that the presence of nearby mudflats that are suitable for supplementary feeding (on algae, Rowcliffe *et al.* 2001) and invertebrates such as *Nereis* spp., RD pers. obs.), may explain preference for certain marsh types.

We assume that a large proportion of variation between observed and predicted goose numbers within the ungrazed barrier marshes is related to the successional stage of the vegetation. Within the *Puccinellietum*, there may be large differences in vegetation composition leading to large differences in goose grazing density (Table 8.2). In spite of this, there is a general agreement between observed and predicted values for this marsh type (Figures 8.5A & 8.6). For ungrazed marshes with a clay soil and grazed barrier marshes, the validity of the approach can hardly be evaluated, due to a limited sample size of these types. The present data suggest that the predictions are on the high side for the grazed barrier marshes (Figure 8.6).





#### 'POTENTIAL GOOSE AREAS' WITHOUT GEESE

Using our 'shot-gun' approach we have identified some salt-marsh areas in the Wadden Sea that appear to be under-used during the month of May (Figures 8.5B & 8.6). Many of these locations or count units have already specifically been mentioned above (in the results section), but the general pattern appears to be that, especially on the mainland, several count units can harbour more geese in May than they did so far. There are count units, such as the estuarine marshes in the Dollard, where very few Brent Geese were observed in May during the study period, but where considerable numbers of Barnacle Geese stage during early spring. Other count units, such as the Slufter on Texel, the Horumersiel Vorland, North-Rømø and the estuarine marshes in the Ho-Bugt have identifiable characteristics (geographical position, marsh width, disturbance, agricultural activity) that might explain lower than expected numbers. However, there is also a group of count units, for example some of the grazed mainland and barrier marshes in Denmark or Niedersachsen, that have low numbers of both species without a clear reason. It should, in this context, be mentioned that Brent Geese are very site faithful, although they may have knowledge of other areas, and we assume that tradition plays a major role in the observed distribution patterns. However, before concluding that a particular area may harbour more geese during spring staging we need to be cautious, and carefully examine on a site-specific basis whether other factors, such as disturbance, plant phenology or the lack of nearby alternative feeding areas, may constrain its use.

#### INTERACTION WITH BARNACLE GEESE

We did not find any statistical indication of a negative association between Brent and Barnacle Geese in our data-set, neither in April nor in May. Clearly, the barrier islands and Halligen are almost exclusively used by Brent Geese, while estuarine marshes are mainly occupied by Barnacle Geese. But, as there are a large number of mainland count units where the two species co-occur in high numbers, there is no negative correlation between them at this scale and in this time frame. This does not deny the existence of a competitive interaction between the two species of geese, causing a negative association in space, as the effects may be expressed at a smaller level of scale (Stock *et al.* 1995; Engelmoer *et al.* 2001). Another reason may of course be that food was not limiting the number of geese during the years of study.

Facilitative and competitive effects may operate simultaneously, as the removal of food positively affects forage quality (Stahl *et al.* 2001b). To evaluate the relative importance of the two processes one needs to experimentally manipulate the presence of the two species independently within an area. Alternatively, one could compare the patterns of utilisation of areas that differ in the presence of these species in space or in time. It remains essential to continue investigating to what extent food-competition between Brent and Barnacle Geese occurs, because the numbers of Barnacle Geese are still increasing (Ganter *et al.* 1999) and the effects may become apparent at higher population levels or in periods of low food-availability.

## CLUSTERING AT THE REGIONAL SCALE

The distribution of Brent Geese along the shore of the Wadden Sea was clumped, with only a few regions harbouring the majority of birds. The Danish marshes had low average numbers of Brent Geese in this study. However, they compare well with data presented by Meltofte *et al.* (1994), and the general pattern was similar in their study, with the largest concentrations of Brent Geese in Schleswig-Holstein and the Netherlands (Meltofte *et al.* 1994). At the scale of the Wadden Sea, these concentration areas are widely separated, and it is therefore unlikely that climatological differences are causally related to the observed clustering. The two regions with highest average numbers of Brent Geese, the Halligen (region 8, DE) and the coast of Friesland (region 25, NL), are also the regions where large numbers are predicted based on marsh area, soil type and grazing regime in this study. The most parsimonious explanation for the clustering is thus found in a greater availability of suitable marsh in the regions mentioned. Region 4 though, encompassing Rømø, is an important exception with observed numbers that are much lower than expected.

## Management implications

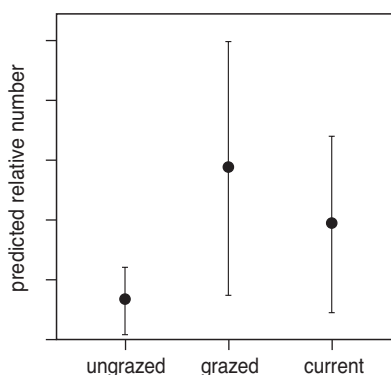
Brent Geese are dependent on young or livestock grazed salt marsh for feeding in spring (Ebbinge & Boudewijn 1984; Olff *et al.* 1997; van der Wal *et al.* 2000a; chapter 4; chapter 7). Currently, 64% of the area of mainland marsh in the Wadden Sea is grazed, and approximately 20% had been grazed until the 1990s and still appears to be in successional transition (Gettner *et al.* 2000; Stock & Hofeditz 2000). Barrier marshes require many decades before succession leads to a vegetation dominated by tall *Elymus athericus* and *Atriplex portulacoides*, and appear to be of optimal value for geese up to an age of approximately 50 years (van der Wal *et al.* 2000a). We are only aware of a few ungrazed barrier marshes that had an undisturbed development for more than 50 years, and the average marsh vegetation on barrier marshes is thus likely to age further. There is a small new input of young barrier marsh, as some of the barrier marshes in the Wadden Sea are 'wandering'. Along the mainland coast, new marsh is formed within the shelter of coastal protection works. In the Leybucht for example, 200 ha of pioneer marsh is expected to develop before 2006, due to engineered changes in hydrology (Bergmann & Borbach-Jaene 2001). Along the mainland coast of Schleswig-Holstein 700 ha of new marsh developed between 1988-96 (Stock *et al.* 2001). However, coastal protection also constrains rejuvenation of the marsh, as coastal regression or large scale erosion are prevented. Without management measures to enhance sedimentation along the foreshore (Esselink 2000), or de-embankment (de Jong *et al.* 1999), the relative share of young stages of salt-marsh succession on the total area of marsh declines.

## TWO EXTREME SCENARIOS OF GRAZING MANAGEMENT

Given a total area of 30,000 ha of salt-marsh, and an average vegetation composition for the different soil types and grazing regimes as estimated in Figure 8.2, we calculated the predicted potential number of geese that could forage on salt marshes in the



Wadden Sea in May when 1) there would be no livestock grazing at all, 2) when all marshes would be grazed, or 3) in the current situation (Figure 8.8). The upper and lower estimates are derived from the estimated range in MPGD as presented in Table 8.2. We present the data in Figure 8.8 as relative numbers, since we are convinced for several reasons that it would be unwise to draw heavily on the absolute values of the predictions. First, the data only reflect predictions for the potential grazing density of geese in May, while constraints on the amounts of forage may be more prevalent during the month of April, when primary production is lower and Barnacle Geese are present in higher numbers. Moreover, we feel that the role of several factors, like salinity (Wolff *et al.* 1967), the presence of suitable roosts, but especially that of disturbance, requires more scrutinous examination. The removal of sources of disturbance may lead to rather unexpected increases in the numbers of waterfowl utilising particular staging areas (Madsen *et al.* 1998; chapter 3). The difference between the two extreme scenarios of livestock grazing management on salt marshes in the Wadden Sea is nonetheless clearly illustrated in Figure 8.8, and lies in the order of hundreds of thousands of birds, with approximately 4 times as many geese in an all-grazed scenario as compared to a scenario without livestock grazing. The difference is caused by the compound effect of a change in the abundance of suitable plant communities and lower goose grazing pressure for livestock-ungrazed versions of plant communities that are characterised by palatable plant species. So, under a scenario of ‘no grazing’, the marshes are ultimately predicted to loose most of their value as goose feeding



**Figure 8.8** Predictions of potential relative goose numbers (Brent or Barnacle Geese) on salt marshes in the Wadden Sea in May (lower, higher) for the current livestock grazing situation, and for two extreme scenarios of livestock grazing management, in which all marshes are either grazed or not by livestock. Calculations (see text) are made using the Potential Grazing Density that was estimated for relevant categories of marsh (Table 8.3), using reported values of dropping counts (Table 8.2). The upper and lower estimates (the range) was based on the upper and lower estimates of Potential Grazing Density specified in Table 8.2. For the current situation it is assumed that short-term ungrazed marshes are characterised by the average vegetation composition of long-term ungrazed marsh.

ground and we conservatively estimate a loss of capacity of approximately 75% compared to a scenario where all marsh would be grazed. The intensity of livestock grazing is here an important variable. Intensive grazing removes the majority of the primary production each year, and results in homogeneous swards, with a vegetation composition that is most suitable for waterfowl (Dijkema 1983b; Kiehl *et al.* 1996; Aerts *et al.* 1996). More extensive grazing results in a vegetation pattern with shortly grazed patches alternating with patches of taller canopy (Bakker 1989). Data from the mainland salt marsh at the Hamburger Hallig did only show a minor difference in goose usage between moderately grazed marshes and marshes that were abandoned since ten years, but which were formerly intensively grazed (Stock & Hofeditz 2000). At the other Halligen goose numbers have not dropped, although the grazing intensity has been reduced over the last 10 years by down to 50% (Rösner & Stock (1994), unpubl. data). The information we have until now is, however, insufficient to further quantify the effects of extensive grazing on goose distribution and salt-marsh capacity.

The relative importance of eelgrasses (*Zostera* spp.) as a feeding source for Brent Geese is low in spring, but still considerable in autumn in Denmark and Schleswig-Holstein, where the largest eelgrass beds occur (Reise 2001). In the past *Zostera* feeding has been very common and still, it is highly relevant in other staging areas along the flyway (Ebbinge *et al.* 1999; Rowcliffe *et al.* 2001). Restoration of traditional eelgrass habitat seems realistic (van Katwijk 2000), and extensive eelgrass beds are likely to enhance the capacity of the Wadden Sea region for Brent Geese in autumn. However, we doubt whether it could become important in spring, after being depleted in autumn, as production starts relatively late in spring (van Katwijk 2000). If natural systems of the Wadden Sea would fall short in providing sufficient resources to the Brent population, a system could be considered in which the birds can temporarily feed on inland reserves. The effectiveness of such a reserve, consisting of artificial and fertilised grassland, was studied on the barrier island of Texel where it attracted large numbers of Brent Geese (Spaans & Postma 2001). However, in a study of Barnacle Geese, the accumulation of body reserves on such inland pastures was different from the performance on salt marshes and the food on the pastures seemed inadequate in providing all nutrients required for balanced body reserves (Prop & Black 1997). Spaans & Postma were not able to detect differences in fitness parameters between birds feeding most of the time in pasture habitat throughout spring, compared to birds foraging in salt marshes, but it is uncertain to what extent additional forage was gathered on nearby salt marshes and intertidal flats by the pasture-feeding birds. We suggest that the creation of such inland reserves should only be a solution on a restricted scale to alleviate local agricultural problems.

The information presented here suggests that an extreme scenario of no-livestock grazing at all would lower the potential number of geese grazing at marshes in the Wadden Sea. Moreover, we have ignored the phenomenon that the equilibrium population size may be well below the local capacity (Sutherland 1996). Authorities in charge of the management of salt marshes are well aware of their responsibilities for protecting geese and their habitat (Stock & Kiehl 2000) and the role of livestock gra-



zing in this respect, but balance these objectives against other ecological targets such as the diversity in plant species, entomofauna and breeding birds. It remains, however, necessary to continue monitoring the current developments, and to study the interactions between the different herbivores and the vegetation, within the framework of the life-cycle of geese. Our knowledge on vegetation development remains limited, especially for short-term ungrazed salt marshes where artificial drainage is no longer maintained and still high densities of geese are grazing. Furthermore, we need to better understand the role of the staging areas in determining the population demography, as has for example been attempted by Pettifor *et al.* (2000) and the importance of human disturbance as a constraint on the use of potential feeding areas (chapter 3).

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## References

- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of Greylag geese *Anser anser* and Barnacle geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. *Z. Ökol. Natursch.* 5: 65-75
- Andresen H, Bakker JP, Brongers M, Heydemann B, Irmiler U (1990) Long-term changes of salt marsh communities by cattle grazing. *Vegetatio* 89: 137-148
- Bakker JP (1989) Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht
- Bakker JP, Bos D, de Vries Y (2002) To graze or not to graze, that is the question. In: Essink, K, van Leeuwe M, Kellerman A & Wolff WJ (eds) Proceedings of the 10th International Scientific Wadden-Sea Symposium. Ministry of Agriculture, Nature Management and Fisheries, The Hague (in press)
- Begon M, Harper JL, Townsend CR (1990) Ecology: Individuals, Populations and Communities. Blackwell Scientific Publications, Oxford
- Bergmann HH, Borbach-Jaene J (2001) Abschlussbericht des Forschungsprojektes Auswirkungen von Bewirtschaftungsänderungen auf die Habitatwahl, Raumnutzung und das Verhalten von Nonnengans und Ringelgans am Beispiel der Leybucht im Nationalpark Niedersächsisches Wattenmeer. University of Osnabrück, Osnabrück
- Boudewijn TJ, Ebging BS (1994). General review In: van Nugteren J (ed) Brent Geese in the Wadden Sea. The Dutch society for the preservation of the Wadden Sea, Harlingen, pp 39-49

- Bruinzeel L, van Eerden MR, Drent RH, Vulink JT (1997) Scaling metabolisable energy intake and daily energy expenditure in relation to the size of herbivorous waterfowl: limits set by available foraging time and digestive performance. In: van Eerden MR (ed) Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. PhD thesis University of Groningen, Groningen pp 111-132
- Caughley G (1979) What is this thing called carrying capacity? In: Boyce MS, Harden-Wing LD (eds) North American Elk: ecology, behaviour and management. Univ. of Wyoming, Laramie (WY), pp 2-8
- de Jong DJ, Dijkema KS, Bossinade JH, Janssen JAM (1998) Salt97; een classificatieprogramma voor kweldervegetaties. Rijkswaterstaat & IBN-DLO, Middelburg pp 1-23
- de Jong F, Bakker JF, van Berkel CJM, Dankers NMJA, Dahl K, Gätje C, Marencic H, Potel P (1999) Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group, Wilhelmshaven
- Dhondt AA (1988) Carrying capacity: a confusing concept. *Acta Oecol. Gen.* 9: 337-346
- Dijkema KS (1983a) Landscape and vegetation map of the Wadden Sea islands and mainland coastal areas. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 85-136
- Dijkema KS (1983b) The saltmarsh vegetation of the mainland coast, estuaries and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 185-269
- Dijkema KS (1983c) Use and management of mainland salt marshes and Halligen. In: Dijkema KS, Wolff WJ (eds) Flora and vegetation of the Wadden Sea islands and Coastal areas. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 303-312
- Ebbinge B, StJoseph A, Prokosch P, Spaans B (1982) The importance of spring staging areas for arctic-breeding geese, wintering in western Europe. *Aquila* 89: 249-258
- Ebbinge BS (1989) A multifactorial explanation for variation in breeding performance of Brent Geese *Branta bernicla*. *Ibis* 131: 196-204
- Ebbinge BS (1992) Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla bernicla* on spring staging sites. *Ardea* 80: 203-228
- Ebbinge BS, Berrevoets C, Clausen P, Ganter B, Guenther K, Koffijberg K, Mahéo M, Rowcliffe JM, StJoseph A, Südbeck P, Syroechkovski EE, Jr. (1999) Dark-bellied Brent Goose *Branta bernicla bernicla*. In: Madsen J, Cracknell G, Fox AD (eds) Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International, Wageningen. National Environmental Research Institute, Rønde pp 284-297
- Ebbinge BS, Boudewijn T (1984) Richtlijnen voor het beheer van rotganzen in het Nederlandse wadden-gebied, rapport 84/4. Rijksinstituut voor Natuurbeheer, Leersum
- Ebbinge BS, Heesterbeek JAP, Ens BJ, Goedhart PW (2002) Density dependent population limitation in dark-bellied brent geese. *Avian Science* (in press).
- Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. *J. Avian Biol.* 26: 105-113
- Ebbinge BS, Spaans B (2002) How do Brent Geese (*Branta b. bernicla*) cope with evil? Complex relationships between predators and prey. *J. Ornithol.* 143:33-42
- Engelmoer M (1998) Pleisterende ganzen en zwanen langs de Friese Waddenkust - seizoen 1997/98. Altenburg & Wymenga Ecologisch Onderzoek, Veenwouden
- Engelmoer M, Taal J, Wymenga E, Kuipers R (2001) Aantalsafname bij de Rotgans *Branta bernicla* langs de Friese waddenkust. *Limosa* 74: 41-56
- Esselink P (2000) Nature management of coastal marshes. Interactions between anthropogenic influences and natural dynamics. PhD thesis University of Groningen, Groningen
- Ganter B, Ebbinge BS (1996). Salt marsh carrying capacity and the effect of habitat loss on spring staging brent geese: two case studies using marked individuals. In: Goss-Custard JD, Rufino R, Luis A (eds). Effect of habitat loss and change on waterbirds. ITE, Wetlands International, London





- Ganter B, Larsson K, Syroechkovskiy EV, Litvin KE, Leito A, Madsen J (1999) Barnacle Goose *Branta leucopsis*. In: Madsen J, Cracknell G, Fox AD (eds) Goose populations of the Western Palearctic. A review of status and distribution. Wetlands International, Wageningen. National Environmental Research Institute, Rønde, pp 271-283
- Gettner S, Heinzel K, Kohlus J (2000) Die Entwicklung der aktuellen Vegetation auf der Hamburger Hallig nach Änderung der Nutzung. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 24-33
- Goss-Custard JD (1985) Foraging behaviour of wading birds and the carrying capacity of estuaries. In: Sibly RM, Smith RH (eds) Behavioural Ecology: ecological consequences of adaptive behaviour. Blackwell Scientific, Oxford, pp 169-188
- Guenther K, Stock M, Rösner H-U (1998) Ringelgänse im Wattenmeer. In: Umweltatlas Wattenmeer. Bd. 1 Nordfriesisches und Dithmarscher Wattenmeer. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Ulmer, Stuttgart, pp 126-127
- Hälterlein B, Fleet DM, Rösner H-U (1991) Gebietsdefinitionen für Brut- und Rastvogelzählungen an der schleswig-holsteinischen Westküste. Seevögel 12: 21-25
- Hecker N (1995) Biotope Mapping of Terrestrial Areas in the National Park "Niedersächsisches Wattenmeer". National Park Amt Niedersächsisches Wattenmeer, Wilhelmshaven.
- Kempf NJL, Lamp J, Prokosch P (1987). Salzwiesen: geformt vom Küstenschutz, Landwirtschaft oder Natur? Internationale Fachtagung zu Perspektiven für Schutz und Pflege von Salzwiesen im Wattenmeer. Umweltstiftung WWF-Deutschland, Husum
- Kiehl K, Eischeid I, Gettner S, Walter J (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. J. Veg. Sci. 7: 99-106
- Koffijberg K, Voslammer B, Van Winden E (1997) Ganzen en zwanen in Nederland: overzicht van pleisterplaatsen in de periode 1985-94. SOVON Vogelonderzoek, Beek-Ubbergen
- Kuhbier H (1987) Die Entwicklung des Grünlandes auf Mellum. In: Gerdes G, Krumbein WE, Reinecke HE (eds) Mellum Portrait einer Insel. Verlag Waldemar Kramer, Frankfurt am Main, pp 234-261
- Madsen J (1989) Spring feeding ecology of Brent Geese *Branta bernicla*: Annual variation in salt marsh food supplies and effects of grazing on growth of vegetation. Dan. Rev. Game Biol. 13: 4-16
- Madsen J, Frikke J, Laursen K (1990) Occurrence of and habitat utilisation by the Dark-bellied Brent Goose (*Branta bernicla bernicla*) in Denmark, with special reference to the Danish Wadden sea. Danske Vildtundersøgelser 45: 195-216
- Madsen J, Pihl S, Clausen P (1998) Establishing a reserve network for waterfowl in Denmark: A biological evaluation of needs and consequences. Biol. Conserv. 85: 241-255
- Massé H, Rochefort L, Gauthier G (2001) Carrying capacity of wetland habitats used by breeding Greater Snow Geese. J. Wildl. Manage. 65: 271-281
- McLeod SR (1997) Is the concept of carrying capacity useful in variable environments? Oikos 79: 529-542
- Meltofte H, Blew J, Frikke J, Rösner H-U, Smit CJ (1994) Numbers and distribution of waterbirds in the Wadden Sea. WSG Bull. 74, special issue
- Olf H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. J. Ecol. 85: 799-814
- Pettifor RA, Caldow RWG, Rowcliffe JM, Goss-Custard JD, Black JM, Hodder KH, Houston AI, Lang A, Webb J (2000) Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. J. Appl. Ecol. 37 Suppl. 1: 103-135
- Poot M, Rasmussen LM, Roomen M, Rösner H-U, Süßbeck P (1996) Migratory Waterbirds in the Wadden Sea 1993/94. Common Wadden Sea Secretariat, Wilhelmshaven
- Potel P, Süßbeck P (1994) Dark-bellied Brent Geese in Niedersachsen: a review of numbers, trends and distribution. In: van Nugteren J (ed) Brent geese in the Wadden Sea. Dutch Society for the Preservation of the Wadden Sea, Harlingen, pp 87-96
- Prins HHT, Ydenberg RC (1985) Vegetation growth and a seasonal habitat shift of the barnacle goose (*Branta leucopsis*). Oecologia 66: 122-125

- Prokosch P (1979) Zur bedeutung der Salzwiesen der Halligen und Vorländer im Nord Friesischen Wattenmeer für die Ringelgans (*Branta bernicla*). Landesamt für Naturschutz und Landschaftspflege Schleswig-Holstein, Tönning
- Prokosch P (1991) Present status and recent changes in numbers and feeding sites of *Branta* species on the coasts of the Federal Republic of Germany during the 1980s. *Ardea* 79: 135-140
- Prop J (1991) Food exploitation patterns by Brent Geese *Branta bernicla* during spring staging. *Ardea* 79: 331-342
- Prop J, Black JM (1997). Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. In: Mehlum F, Black JM, Madsen J (eds). Proceedings of the Svalbard Goose symposium. Norsk-Polarinstitut, Oslo, Norway, pp 175-193
- Prop J, Vulink T (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Funct. Ecol.* 6: 180-189
- Reise K (2001) Algen und Seegrass: grüne Matten und Wiesen im Watt. In: Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (ed) Wattenmeermonitoring 2000 -Schriftenreihe des Nationalparks Schleswig-Holsteinisches Wattenmeer, Sonderheft, 76 S. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 55-56
- Ringot JL (1993) Erstellen eines Interpretationsschlüssels und Kartierung der Biotoptypen terrestrischer Bereiche des Nationalparks Niedersächsisches Wattenmeer auf der basis des CIR Bildfluges vom 21.08.1991. unpublished, Nationalparkverwaltung Niedersächsisches Wattenmeer, Wilhelmshaven
- Rowcliffe JM, Watkinson AR, Sutherland WJ (2001) The depletion of algal beds by geese: a predictive model and test. *Oecologia* 127: 361-371
- Rösner H-U, Stock M (1994) Numbers, recent changes, seasonal development and spatial distribution of Dark-bellied Brent Geese in Schleswig-Holstein. In: van Nugteren J (ed) Brent geese in the Wadden Sea. Dutch Society for the Preservation of the Wadden Sea, Harlingen, pp 69-85
- Rösner H-U, Van Roomen M, Rasmussen LM (1994) Migratory Waterbirds in the Wadden Sea 1992/93. Common Wadden Sea Secretariat, Wilhelmshaven
- Schaminée JHJ, Weeda EJ, Westhoff V (1998) De Vegetatie van Nederland. DI 4: Plantengemeenschappen van de kust en van binnenlandse pioniermilieus. Opulus Press, Uppsala
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Stahl J, Bos D, Loonen MJJE (2001a) Foraging along a salinity gradient - the effect of tidal inundation on site choice by brent and barnacle geese. In: Stahl J (ed) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD-thesis University of Groningen, Groningen, pp 153-170
- Stahl J, Rothkegel C, Drent RH (2001b) Staging barnacle and brent geese versus resident brown hare: crossing the boundary between facilitation and resource competition. In: Stahl J (ed) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD-thesis University of Groningen, Groningen, pp 171-210
- Stock M, Gettner S, Kohlus J, Stumpe H (2001) Flächenentwicklung der Festlandsalzwiesen in Schleswig-Holstein. In: Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (ed) Wattenmeermonitoring 2000 -Schriftenreihe des Nationalparks Schleswig-Holsteinisches Wattenmeer, Sonderheft, 76 S. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 57-61
- Stock M, Hofeditz F (1996) Zeit-Aktivitäts-Budgets Vergleichende Energiebudgets von Ringelgänsen (*Branta bernicla bernicla*) in zwei unterschiedlich stark von Menschen beeinflussten Salzwiesen des Wattenmeeres. *Die Vogelwarte* 38: 121-145
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitates durch Nonnen- und Ringelgänse. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 43-55
- Stock M, Hofeditz F, Mock K, Pohl B (1995) Einflüsse von Flugbetrieb und Freizeitaktivitäten auf Verhalten und Raumnutzung von Ringelgänsen *Branta bernicla bernicla* im Wattenmeer. Auswirkungen von Störreizen auf Ethologie und Ökologie von Vögeln im Wattenmeer. *Corax* 16: 63-83





- Stock M, Kiehl K (2000) Empfehlungen zum Salzwiesenmanagement im Nationalpark Schleswig Holsteinisches Wattenmeer. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 74-77
- Stock M, Kiehl K, Reinke HD (1997) Salt marsh protection in the Schleswig-Holstein Wadden Sea area. Texte 84/97, Umweltbundesamt, Berlin
- Sutherland WJ (1996) From Individual Behaviour to Population Ecology. Oxford University Press, Oxford
- Sutherland WJ, Goss-Custard JD (1991) Predicting the consequence of habitat loss on shorebird populations. In: Bell BD (ed) Acta XX congressus internationalis ornithologici, Christchurch, New Zealand, 2-9 Dec. 1990. New Zealand Ornithological Congress Trust Board, Wellington, pp 2199-2207
- van der Meijden R (1990) Heukels' Flora van Nederland 21st edition. Wolters-Noordhoff, Groningen
- van der Wal R, Kunst P, Drent R (1998) Interactions between hare and brent goose in a salt marsh system: evidence for food competition? *Oecologia* 117: 227-234
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000a) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D (2000b) On facilitation between herbivores: How Brent Geese profit from brown hares. *Ecology* 81: 969-980
- van Katwijk MM (2000) Possibilities for restoration of *Zostera marina* beds in the Dutch Wadden Sea. PhD thesis University of Nijmegen, Nijmegen
- van Laar V (1981) The Wadden Sea as a zoogeographical barrier to the dispersal of terrestrial mammals. In: Smit CJ, den Hollander J, van Wingerden WKRE, Wolff WJ (eds) Terrestrial and freshwater fauna of the Wadden Sea area. Stichting Veth tot steun aan Waddenonderzoek, Leiden, pp 231-266
- van Wijnen H, Bakker JP (1997) Nitrogen accumulation and plant species replacement in three salt marsh systems in the Wadden Sea. *J. Coast. Cons.* 3: 19-26
- Westhoff V, van Oosten MF (1991) De Plantengroei van de Wadden eilanden. Stichting Uitgeverij Koninklijke Nederlandse Natuurhistorische Vereniging, Utrecht
- Wolff WJ, Koeyer P, Sandee AJJ, Wolf L (1967) De verspreiding van rotganzen in het deltagebied in relatie tot de verspreiding van hun voedsel. *Limosa* 40: 163-174

Appendix 8.1 Sources of vegetation information, the years and scale of mapping, the classification used and the producing agency.

Title	Scale	Years	Produced by	Legend	Agency	Supplied by
Vegetationskartierung der Salzwiesen 1988/1996/97	1:5000	1996	S. Gethner	After Schaminée <i>et al</i> 1998	Nationalpark Schleswig-Holsteinisches Wattenmeer	M. Stock
Biotoptypenkarte terrestrischer Bereiche 1997	1:10000	1991-1993	N.Hecker	Ringot 1992/93	Nationalparkverwaltung Niedersächsisches Wattenmeer	P. Potel
Outline of marshes Denmark					Amtsgården, Ribe	J. Frikke
Outline of marshes Denmark					Amtsgården, Sønderjylland	A. Voigt
Vegetatiekartering Nederlandse Waddenzee	1:5000-10000	1988-1995	MD Delft(RWS)	De Jong <i>et al</i> 1998	RIKZ, MD (Rijkswaterstaat)	Dick de Jong

Appendix 8.2 Criteria used for the globalisation of legend units to plant communities at a higher level of aggregation, for comparison of maps from Niedersachsen, The Netherlands and Schleswig-Holstein. Legend units were assigned to first community that would fit the criteria in top-down order. Association names according to Schaminée *et al.* (1998) are indicated.

Community	Association names		including the associations (Schaminée <i>et al.</i> 1998)		Description
Pioneer zone	Spartinetum	Spartinetum townsendii/Spartinetum maritimae	24Aa1, 24Aa2		Spartina anglica > Salicornia and Suaeda maritima
Low marsh	Salicornietum	Salicornietum oligostachyae/ S brachystachyae	25Aa1,25Aa2		Salicornia and/or Suaeda maritima > Spartina anglica
	Halimionetum	Halimionetum portulacoides	26Aa3		Atriplex portulacoides > 35% cover or Atriplex portulacoides co-dominant (5-35%)
	Puccinellietum	Puccinellietum maritimae/ Plantagini Limonietum/ Puccinellietum distantis	26Aa1,26Aa2,26Ab1		Other low marsh, characterised by Puccinellia
High marsh	Juncetum	Juncetum gerardii	26Ac1		Juncus gerardi > Festuca rubra
	Artemisietum	Artemisietum maritimae	26Ac5		Artemisia maritima dominant or co-dominant (20-50%)
	Atriplicii Elytrigietum	Atriplicii-Elytrigietum pungentis	26Ac6		Elymus spp. + Atriplex prostrata + Atriplex littoralis > 25% cover
	Amerio Festucetum	Amerio-Festucetum, Trifolio fragiferi-	26Ac2,12Ba3		Other high marsh characterised by Festuca rubra or Agrostis stolonifera
Agrostietum stoloniferae					



**Appendix 8.3** Names of locations in the international Wadden Sea to which individual goose count units belong, and by which they are grouped for purpose of presentation in Figures 8.5 and 8.6. ID refers to the identifier by which individual datapoints are labelled in Figures 8.5B and 6. The ranknumbers are used to identify datapoints in Figure 8.5A.

ID	Ranknumbers in Fig. 8.5	Location to which the Account units belong	Local systematic code
1		Rømø	
2		Mandø + Ballum vorland	
3		Skallingen	
4		Langli	
5		Fanø	
6		Ho bugt	
7		DK mainland&mudflats middle	
8		DK mainland&mudflats Made	
9		DK Waddensea south	
10	13	Amrum	IA
11		Föhr	IF
12	9	Halligen NF	IH
13	4	Pellworm	IP
14		Sylt	IS
15		Trischen	IT
16		S-Holstein south	VD
17	24	S-Holstein middle	VE
18	3	S-Holstein north	VN
19		Rysumer Nacken-Ems	1.1.07
20		Manslagter Nacken-Pilsumer H	1.2.01
21	2	Leybucht	1.2.02
22	10	Borkum	1.2.03
23	16	Memmert	1.2.04
24	17,27	Juist	1.2.05
25	11	Norderney	1.3.01
26		Baltrum	1.3.02
27	20	Langeoog	1.3.03
28	28	Hilgenriedersiel-Norddeich	1.3.04
29		Neßmersiel-Dornumersiel	1.3.06
30	12	Dornumersiel-Neuharlingersie	1.3.07
31	14	Wangerooge	1.4.02
32		Neuharlingersiel-Harlesiel	1.4.04
33		Elisabeth-Außengroden	1.4.05
34		Horumersiel	1.4.07
35		Jadebusen	1.5.01
36	6	Mellum	1.6.01
37		Langwarden-Ruhwarden	1.6.02
38		Neuwerk	1.7.02
39	21	Cuxhaven-Wremen	1.7.04
40		Dollard	1.1.06 & wg 42
41	25,26	Texel	wg11
42		Vlieland	wg12
43		Wieringen-Den Helder	wg16
44	8	Terschelling	wg21
45	5,19	Ameland	wg22
46	22	Griend	wg24
47	15	Lauwersoog-Ternaard	wg25
48	1	Noord Friesland Buitendijks	wg26
49	7	Schiermonnikoog	wg31
50	18	Rottumerplaat	wg33
51	23	Rottumeroog & zuiderstrand	wg34
52		Groningen coast	wg35

Young cow on short-grazed salt-marsh vegetation (photo J. Stahl).





# 9

CHAPTER

## **Synthesis: Habitat use by Brent Geese in the Wadden Sea under different scenarios of livestock-grazing management**

**Daan Bos**

## Introduction

In the previous chapters I summarised the information collected to evaluate our main research questions, and the majority of the component sub-questions have already been addressed in the thesis. This chapter is meant to combine that information, to put it into the perspective of current ecological theory and to explore consequences for applied questions. I start with reviewing the relevant processes, and address the following questions when appropriate:

1. Which vegetation parameters and/or other factors determine the spring habitat use by Brent Geese ?
2. To what extent is the number of Brent Geese that can be accommodated on salt marshes, affected by livestock grazing?

## Review of relevant processes

### *Determinants of patch and habitat choice in Brent Geese*

Many factors are likely to play a role in determining patch and habitat choice in Brent Geese. In our study we found strong relationships with aspects of forage availability and with human disturbance. The geese spend most of their daylight time foraging, and hence it is obvious that factors related to forage availability are vital and correlate well with observed utilisation patterns. Availability of food can be related to aspects of quantity and quality, and we dissected the relative importance of these two aspects in chapter 2. We hypothesised that the relative importance of food quality should be high, as geese have a relatively simple digestive system (Owen 1980). The short digestive tract is viewed as a constraint in the selection of forage as it restricts the geese to high quality food. Our manipulations have indeed shown that Brent Geese are very sensitive to forage quality ( measured as nitrogen content, a proxy for protein), preferring plots with high nitrogen content over patches with high intake rate of biomass. This experimental work supported earlier results of Hassall *et al.* (2001) by generalising their finding that nitrogen intake rates are a suitable predictor of patch preference. The degrees to which forage quality and quantity vary in space and time are reviewed below.

Habitat use by Brent Geese is directly related to human disturbance. In chapter 3 we report on the results of an experiment that was provided fortuitously by the farmers on the island of Schiermonnikoog, our main study area. Under the conditions of a new financial arrangement with the management authority, the farmers agreed to refrain from scaring the geese from their fields in the polder in spring. After consistent scaring for decades, this new situation provided an experimental setting for studying the effect of this harassment. In two experimental seasons we observed a spectacular increase in Brent Geese, the polder accommodating 2,000 geese on average in



late spring, while this number had been negligible in previous “control” years. Human disturbance acts to constrain the use of feeding areas, especially concerning the highly productive pastures in late spring (see below).

Although it is clear from field observations that Brent Geese drink fresh water when it is available, we found no evidence that its absence severely constrains their use of salt marshes. Many of the study areas with high densities of Brent Geese lack a source of fresh or brackish drinking water nearby (chapter 8; chapter 7). This finding can be related to the well-developed nasal glands in this species, allowing salt water utilisation (Stahl *et al.* 2001a).

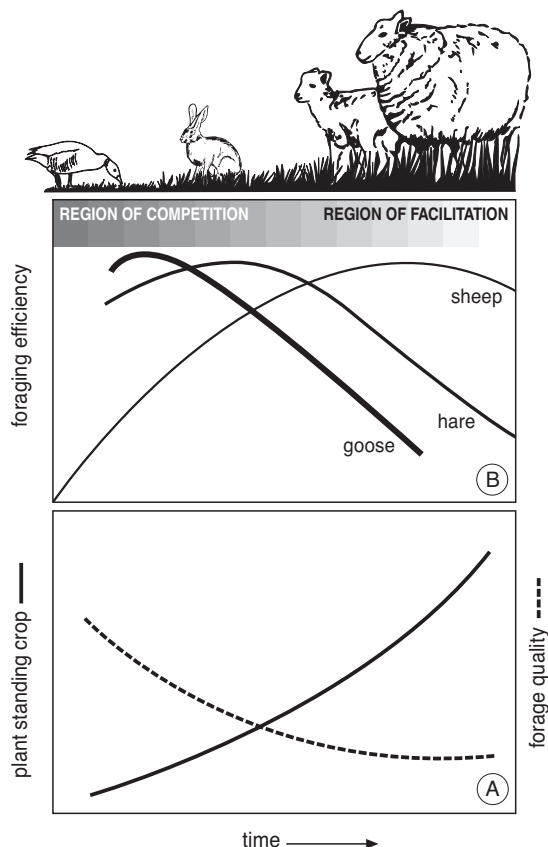
### *Gradients in productivity affect forage quality and quantity*

Both quality and quantity are important determinants of patch choice, varying in space and time. In this study we usually refer to forage quality in terms of nitrogen content. Following McKay *et al.* (1994) and Hassall *et al.* (2001) who stressed the importance of protein acquisition for Brent Geese. However, nitrogen content is often correlated to other forage quality parameters that are relevant to geese, such as digestibility and energy content, and it is not exactly known which parameter is limiting the geese under which circumstances.

There are two important processes that lead to a decline in forage quality at a given site over time (Figure 9.1A) and that result in a negative relationship between forage biomass and quality. The first process occurs within the growing season and is referred to as forage maturation (the ageing of above-ground plant parts, during which process the fibre content generally increases and nitrogen content declines (van Soest 1994; Wright & Illius 1995)). A second process is important at time scales of years or even decades, and is called succession (the process whereby one plant community changes into another). Due to natural succession on salt marshes, plant species that are palatable for geese, such as *Puccinellia maritima*, *Festuca rubra*, *Triglochin maritima* and *Plantago maritima* (Prop & Deerenberg 1991; van der Wal *et al.* 2000a) are replaced by unpalatable ones, in particular *Elymus athericus* and *Atriplex portulacoides*, and concomitantly standing biomass increases (van de Koppel *et al.* 1996; Olff *et al.* 1997). Because palatable plant species are replaced by unpalatable ones, the average forage quality declines over the years, requiring increased foraging selectivity by the geese. Succession is driven by changing abiotic circumstances and competition between plants, but mediated by herbivory and dispersal (van Andel *et al.* 1993).

On salt marshes, the continual input of sediments is believed to be the main engine of succession. Sedimentation leads to an increase in soil elevation and an increase in the thickness of the clay layer. Elevation of the marsh plays an important role in structuring salt-marsh ecosystems, as it is directly related to inundation frequency and hence to sediment deposition, evaporation, aeration, nutrient status, temperature and salinity (Adam 1990). The change in clay layer thickness is relevant, because Olff *et al.* (1997) showed that the pool of nitrogen is positively related to the thickness of the clay layer on barrier marshes. Van Wijnen *et al.* (1999) showed a positive relation





**Figure 9.1** The relationships of time with A) plant standing crop, plant forage quality (nitrogen content) and B) intake rate of nutrients by geese. Time on the x-axis refers to successional age of salt marshes (years), but also to the date within a growing season (weeks). The bar with different intensities of grey illustrates the balance between competition and facilitation for the small herbivores. Competition is important when forage is in low supply, whereas facilitative effects become more and more apparent when forage is abundant.

between thickness of the clay layer and nitrogen availability. Note that both processes (forage maturation and succession) result in changes in sward structure and can thus be confounded in the field with other factors important for geese, such as costs of locomotion, predator detection or instantaneous intake rate.

Natural succession and forage maturation depend on primary productivity, which not only varies in time, but also in space. Primary productivity varies within, as well as between habitats and among staging sites. Examples of such gradients in salt-marsh habitat are the vegetation zonation along the elevational gradient (Beefink 1977), or the chronosequence of plant successional stages on the ungrazed salt marsh of Schiermonnikoog in relation to the age of the marsh (van der Wal *et al.* 2000a). Staging sites along the migratory flyway differ in the same respect in that productivity at more north-



erly latitudes is lower due to lower temperature ranges. Primary productivity also varies in time, as it increases over spring. Finally, the salt marsh has a lower level of primary production than the fertilised and drained agricultural fields (chapter 3).

### *A declining intake rate of nutrients*

The phenomenon discussed above, that forage quality declines with increasing standing crop, has important consequences for the foraging efficiency of herbivores at higher levels of standing crop. It is a common assumption in foraging theory (Stephens & Krebs 1986) that the intake rate of food is a continuously rising function of resource density, following a so-called type II functional response (Holling 1959). This function is found to decelerate to a plateau, as handling time of the food becomes limiting at high resource density for many herbivores (Spalinger & Hobbs 1992; Gross *et al.* 1993; Ginnett & Demment 1995) (more references in Jeschke *et al.* (2002)). However, as pointed out by Fryxell (1991), intake of energy or nutrients may actually decline at high levels of standing crop due to declining forage quality. For ruminants (Wilms-hurst *et al.* 1995; Wilms-hurst & Fryxell 1995), this effect is mediated by a reduced digestive efficiency. For Brent Geese, Riddington *et al.* (1997) and Hassall *et al.* (2001) suggest that instantaneous intake rate of nitrogen is lower at high levels of standing crop, due to the widespread negative relationship between biomass and nitrogen content. The fact that digestibility of protein also declines with standing crop (Prop & Vulink 1992), causes an even stronger effect in terms of nitrogen assimilation. Our experiment with captive animals indicated that for Brent Geese the instantaneous intake rate of food itself may decline at high levels of biomass (chapter 5), as was also found for the Wigeon (Durant 2001). Additional factors may lead to a decline in instantaneous intake rate at high levels of standing crop, such as a change in vegetation structure (Ungar & Noy-Meir 1988) or declining ratios of live to dead biomass, as was found for Barnacle Geese on our study marsh (van der Wal *et al.* 1998b).

### *Aggregative response*

As mentioned above, Brent Geese are confronted with several gradients of productivity in space and time, along which the standing biomass increases and average forage quality declines (Figure 9.1A, B). It appears that the geese focus their grazing on these gradients based on available quality and quantity of forage (chapter 2). Within the non-livestock grazed salt marsh on Schiermonnikoog, the highest goose grazing pressure is found in areas of intermediate age (van de Koppel *et al.* 1996; van der Wal *et al.* 2000a), where the cover of preferred food plant species is highest. Along the elevational gradient in the marsh, the Brent Geese are specialised on the lower parts of the zonation, where standing biomass is low, but forage quality is high (Olff *et al.* 1997; chapter 3). When the birds migrate from their wintering range to the breeding grounds, they are again hypothesised to strike a balance between forage quality and quantity. While moving north to areas with lower primary productivity and later start

of spring growth, they are able to escape from the effects of forage maturation in temperate regions, and maintain a high quality diet. This is the so-called 'green wave hypothesis' (Drent *et al.* 1979). Increased daylength in the Arctic furthermore allows them to process their foods more efficiently (Prop & Vulink 1992).

Over spring, the majority of Brent Geese traditionally move from the highly productive agricultural fields to the marsh. However, the cause of this habitat switch between agricultural fields and marsh is not only a matter of forage quality and quantity, but also of human disturbance. Over spring, the nitrogen content and digestibility of polder grassland decline (Boudewijn 1984; chapter 3), as is the case for marsh habitat. Our data indicate that forage quality in terms of nitrogen content is nonetheless relatively high on the fertilised agricultural fields, even in tall swards that are not maintained by grazing (chapter 3), and of comparable nitrogen content to *Puccinellia maritima* at the salt marsh. Successful reserves elsewhere show that, when human disturbance levels are low, the polder habitat can be used until the end of spring (Spaans & Postma 2001), and high levels of human disturbance in the pasture areas must be a very important reason for the fact that pastures are generally used less towards the end of spring (chapter 3). But there are also indications that marsh habitat is the preferred habitat for other reasons, at the end of spring. The accumulation of body reserves by geese on inland pastures, for example, results in a protein/fat mix different from that on salt marshes, and the food on the pastures seems inadequate in providing all nutrients required for balanced body reserves (Prop & Black 1997). Ebbinge (1992) earlier demonstrated that fluctuations of the world population were clearly expressed in the local number of Brent Geese utilising the polder areas on Texel, while the numbers utilising the salt marsh on the near island of Terschelling remained more or less constant. Using marked individuals he could show that young birds originally belonging to the local population of Terschelling made use of the polder areas on Texel in the years with high population size. The polder area thus appears to function as a 'buffer' accepting subdominant individuals in years when the capacity at the preferred marsh habitat is reached.

### *Facilitation*

As we have seen, forage maturation and succession both negatively affect the foraging efficiency (nutrient intake rate) of small herbivores, such as geese. However, both processes are counteracted when grazing pressure is sufficiently intense to remove the major part of the primary production. In line with the 'Forage Maturation Hypothesis' proposed by McNaughton (1984), we were able to experimentally show that previous grazing positively affected patch preference, under conditions of high primary productivity. Towards the end of spring, Brent Geese in the polder of Ameland selected fields where sheep were also grazing, and captive geese in the polder of Schiermonnikoog preferred sheep-grazed grassland over ungrazed swards in May (chapter 4). On the salt marsh a similar phenomenon was observed, where Brent Geese preferred grazing in plots that had previously been grazed by Barnacle Geese (Stahl *et al.* 2001b). This pro-



cess, where the conditions for one herbivore are improved by another, is called 'grazing facilitation'. Repeated grazing within the growing season maintains the sward in a young actively growing stage. These short swards yield higher instantaneous intake rates as well as higher nutrient content and thus higher nutrient intake rates, as compared to tall ungrazed swards (chapter 5). Finally, Brent Geese flocks facilitate for themselves, as was illustrated in a study by Spaans & Postma (2001) and in chapter 5. Brent Geese increase their grazing intensity per unit area over the course of the spring season, in response to increasing primary production. With the experiment described in chapter 5, we provide support for the interpretation that this phenomenon reflects a preference for swards with intermediate values of biomass leading to spatial heterogeneity in the sward, rather than a response to predation risk or previously existing spatial heterogeneity in forage quality. So, within a growing season, foraging conditions are enhanced by continuous grazing with livestock or geese.

However, geese are not present throughout the entire growing season, and thus their ability to affect long-term vegetation development is limited (Adam 1990). Agricultural activities such as mowing (Bakker 1989) or grazing with larger herbivores remove large amounts of biomass during and after the growing season, and strongly affect vegetation composition. We were able to demonstrate these long-term grazing effects on salt-marsh vegetation by comparing vegetation composition in plots that had been experimentally grazed or left ungrazed for more than 25 years (Bos *et al.* 2002). When salt marshes are not grazed with livestock, succession leads to the dominance of a few tall plant species that are unpalatable for geese, as was already mentioned. Livestock grazing continuously resets the successional clock and maintains the vegetation in a young successional stage (Olf *et al.* 1997; van Wijnen *et al.* 1997; Bos *et al.* 2002; chapter 8; chapter 7). Salt-marsh vegetation that is livestock grazed, differs from the ungrazed condition in many parameters of forage availability (including the cover of plant species that are preferred by geese, canopy height and the cover of plants that are unpalatable and that may hinder the geese while feeding (chapter 4; Bos *et al.* 2002; chapter 8; chapter 7). In chapters 4 and 7 we showed that Brent Goose distribution is related to these parameters of vegetation composition, with generally higher numbers of geese in livestock-grazed marshes. Thus, livestock grazing facilitates goose grazing via its impact on long-term vegetation development. Hare *Lepus europaeus* grazing was shown to retard vegetation development (van der Wal *et al.* 2000b), but eventually hares themselves are also the victim of succession when marshes become too productive (van de Koppel *et al.* 1996).

### Competition

Forage of high quality is not available in unlimited amounts, and thus the birds are likely to compete for it.

#### INTRA-SPECIFIC COMPETITION

Limits to the amount of forage available have been suggested as the explanation for the habitat switch of Brent Geese from algal beds to marshes and inland feeding areas in

winter (Vickery *et al.* 1995; Rowcliffe *et al.* 2001). Although algae are one of the preferred food sources due to their high digestibility (Hassall unpubl. data), the stock diminishes due to goose grazing and wave action. With higher numbers of geese present, depletion is more rapid and the birds have to switch to alternative feeding areas at an earlier stage (Rowcliffe *et al.* 2001). Vickery *et al.* (1995) were able to show that the timing of a habitat switch from marsh to inland feeding areas was related to the local population size, and that the number of goose days spent on the marsh habitat was constant. The gradual switch from inland feeding areas back to the marshes and intertidal flats during spring is related to increasing levels of primary production in these habitats at that time (Vickery *et al.* 1995; chapter 3). Another indication that there are limits to the food supply is put forward by Ebbinge (1992), who found that local numbers on the salt marsh on Terschelling remained constant in spite of strongly fluctuating population numbers, and that individual geese were affected by the increased abundance of competitors (see above). Within the salt-marsh habitat, diet choice is affected by food availability. Salt marshes are heterogeneous with respect to forage quality and quantity, enabling the birds to be selective. With a lower availability of high quality material within a habitat, the birds have to include more material of lower quality. Brent Geese for example vary the amount of *Festuca rubra* in their diet according to the amounts of *Puccinellia maritima* available (Prop & Deerenberg 1991).

As our observations have shown, direct competition between pairs or families of Brent Geese is very apparent. Aggressive behaviour enabled particular families and pairs to profit from the best patches in our patch choice experiment far more than others (Bos *et al.* 2002). This result is in line with observations by Teunissen *et al.* (1985), Prop & Loonen (1989) and Stahl *et al.* (2001c), that there is a social dominance hierarchy. The females of dominant pairs are able to forage in patches that yield higher nutrient intake rates, and thus enhance their rate of fattening (Teunissen *et al.* 1985). As a result, individuals are found to differ strongly in the amounts of fat they accumulate (Ebbinge & Spaans 1995) and their subsequent chances of successful breeding. The observation that birds spend time and energy on defending patches with high resource density is evidence for food competition and strongly suggests that high quality forage is relatively scarce. This is furthermore supported by the observation that short-term enclosure or fertilisation enhances subsequent use (Ydenberg & Prins 1981; Stahl *et al.* 2001b; chapter 2; chapter 5).

#### INTER-SPECIFIC COMPETITION

Brent Geese overlap in habitat use with Barnacle Geese and hare during spring. They forage on the same plant species and the same plant parts, and thus there is potential for food competition between them, though direct evidence for competition is lacking. Food competition on the marsh between geese and Brown Hare was demonstrated in experiments by Stahl *et al.* (2001b) and by van der Wal *et al.* (1998a). Increasing numbers of Barnacle Geese thus potentially affect the numbers of Brent Geese that can be sustained. At Westerhever (DE), Stock *et al.* (1995) observed that the spatial distribution of Brent Geese was different in the presence of Barnacle Geese, and Engelmoer *et*



*al.* (2001) found indications for competition between the two species at the coast of Friesland. However, facilitation also plays a role during early spring on Schiermonnikoog (Stahl *et al.* 2001b). Continuous grazing was shown to enhance forage quality, and thus there is a subtle balance between competition and facilitation. These processes are two sides of the same coin (van der Wal *et al.* 2000b). Besides indirect competition for food via depletion (scramble competition), there is circumstantial evidence for direct interference between Brent Goose and hare (van der Wal *et al.* 1998a). The importance of food competition with hares is unlikely to be as important as that with Barnacle Geese, as the geese are migrant and temporarily reach high numbers on the study island. On Schiermonnikoog for example, the Barnacle Geese are assumed to remove 7 - 15 times as much food in spring as hares (unpublished data).

During the spring staging season, there is hardly any overlap in habitat use between large herbivores and geese in the time when food quantity is most limiting. However, autumn grazing by cattle and sheep affects the amounts of standing crop available during winter, and the capacity of specific wintering areas will be limited when swards have been grazed too short. On the other hand, pastures are unattractive to geese when the canopy is too tall (Riddington *et al.* 1997). The latter authors thus advise to manage swards in set-aside areas (specifically managed to host geese) to achieve an intermediate sward height in the beginning of winter. Their advice to aim at an intermediate sward height helps us to visualise the boundary between facilitation and competition (Figure 9.1 A, B). Very short sward heights at the beginning of winter have little value for the geese because of low food quantity, whereas tall swards are unattractive due to lower forage quality (Riddington *et al.* 1997) and reduced intake rates (chapter 5).

### *Density dependence and carrying capacity*

Food scarcity in spring may affect recruitment, as recruitment in Brent Geese was shown to be critically dependent upon the accumulated fat reserves during spring (Ebbinge & Spaans 1995). Sufficient reserves are a prerequisite for successful breeding, but not a guarantee, as circumstances further along during migration and in the breeding areas ultimately define the breeding output. Feeding conditions in the spring staging areas can thus theoretically affect the population levels of Brent Geese (Ebbinge & Spaans 1995). Sutherland (1996) illustrates this by assuming density-dependent relationships between mortality or recruitment and population size (Figure 9.2). The equilibrium population size is defined as the point where mortality and recruitment are equal, and in this example there is one stable equilibrium point. The shape of the curves in figure 9.2 is purely hypothetical. Different shapes of the curves could lead to multiple equilibria, and one should thus be careful in deriving simple rules of thumb from this graph regarding population management (Ebbinge *et al.* 2002). According to the framework by Sutherland, one can illustrate the effect of habitat change by assuming that the nature of the density-dependent relationship is altered. In our case it would be likely that a deterioration of feeding conditions in the spring staging areas would lead to a lower level of recruitment at the same population

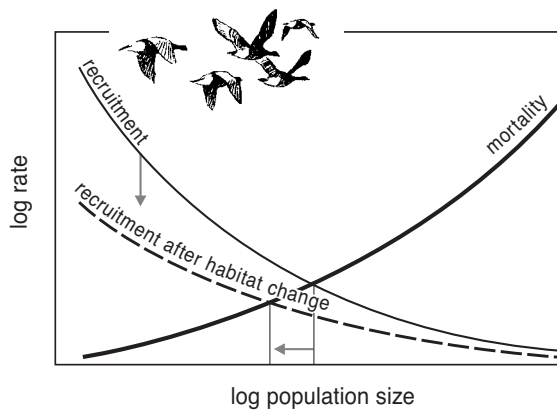


Figure 9.2 The equilibrium population size is determined by recruitment and mortality and either of them is likely to be density dependent. Graph adapted from Sutherland (1996).

size (dotted line in Figure 9.2), unless there is a completely independent constraint operating that limits recruitment. An example of such a constraint could be found in the number of nesting sites that are available in the breeding area. Results from studies on the breeding grounds indicate that the area of suitable breeding habitat is limiting (Ebbinge & Spaans 2002), severely constraining further population growth (Ebbinge *et al.* 2002). However, it is unlikely that this constraint is entirely independent of the accumulation of fat reserves in spring, and thus we assume that there is still a density-dependent effect relating the feeding conditions in spring to the equilibrium population size. A reduction in the area of required habitat in spring, or in any of the essential habitat characteristics (levels of primary production, forage quality and disturbance), would in this view lead to a reduction in the amounts of body fat or other stores accumulated for part of the population, due to competition. This could affect the breeding output. An increase in the total number of Brent Geese, or other herbivores that compete for the same food, would lead to the same effect.

A calculation of the number of individuals that a site will contain in the equilibrium situation, the carrying capacity, requires knowledge of the density-dependent and density-independent mortality and recruitment in the breeding sites and in the non-breeding sites (Sutherland 1996). A lack of knowledge on the shape of most of these relationships made us focus at a more short-term estimate of capacity. Following McLeod (1997), we defined local capacity to be the potential grazing density, as a function of resource availability, over a time period of interest. In the next paragraph we will discuss the factors that are most important in determining the local capacity for Brent Geese at the time the geese leave for the breeding sites.



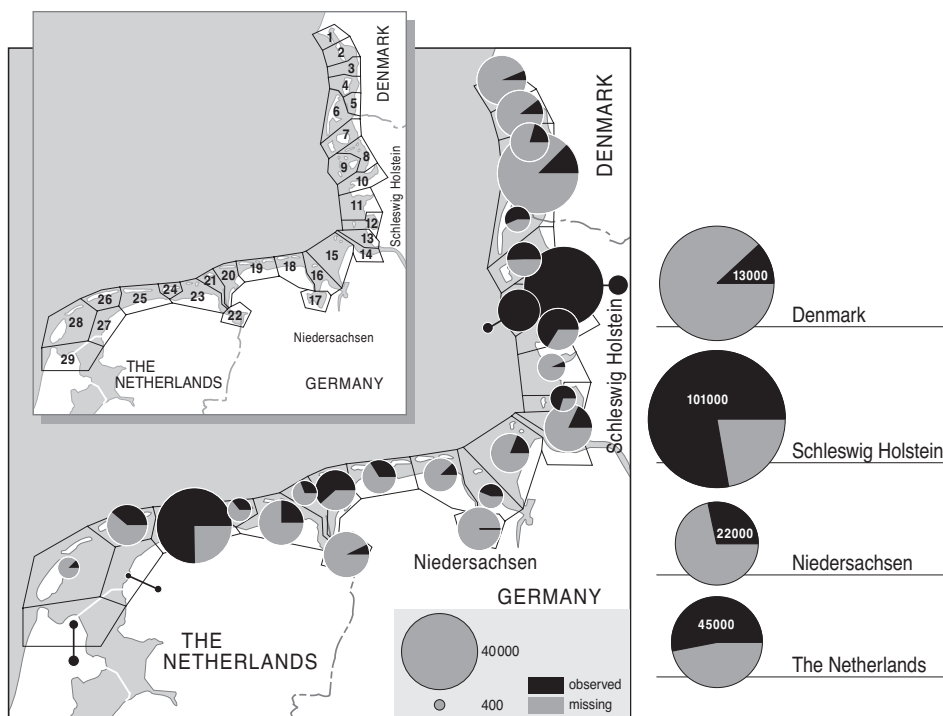


### *The capacity of Wadden Sea coastal grasslands*

Empirical estimates of the number of geese utilising marshes in the Wadden Sea indicate a clear decline in grazing intensity under undisturbed vegetation succession (van de Koppel *et al.* 1996; van der Wal *et al.* 2000a). Especially under productive circumstances, such as at the mainland marshes on the Dollard and the Leybucht, vegetation succession in the absence of grazing rapidly proceeds to communities dominated by tall unpalatable plants, unsuitable for geese (Aerts *et al.* 1996; Bergmann & Borbach-Jaene 2001). Management measures, such as mowing and grazing-enhance the potential number of geese that can utilise an area, compared to long-term ungrazed marshes (Aerts *et al.* 1996; Stock & Hofeditz 2000; Bergmann & Borbach-Jaene 2001; chapter 4; chapter 7). Fertilisation of marshes and grasslands positively affects the productivity as well as the nitrogen content of forage plants (Riddington *et al.* 1997; chapter 2). Thus, as long as vegetation composition is suitable, fertiliser application enhances the number of geese that can be accommodated.

In chapter 8 we ventured to make a prediction of the potential numbers of geese that could forage on different marshes along the Wadden Sea. For this, we derived a Mean Potential Grazing Density for geese that could be realised in the month of May by extrapolation from dropping counts, for different plant communities, soil types and livestock grazing regimes. The prediction was subsequently compared to independent estimates of observed average grazing density as derived from goose counts in May of four different years. The analysis helped us to evaluate the reliability of our estimates for the different marsh types and to identify marshes that do not fit the pattern for one reason or the other. Although there is a large scatter in our estimates, there is an unmistakable trend, when current usage is compared to the theoretical capacity of marshes along the Wadden Sea. The predictions only reflect the potential grazing density of geese in May, while constraints on the amounts of forage may be more prevalent during the month of April, when primary production is lower and Barnacle Geese are present in higher numbers. Moreover, we feel that the role of several factors, such as salinity, the presence of suitable roosts, but especially that of disturbance, requires more quantitative examination. Therefore, it would be unwise to draw heavily on the absolute values of the predictions. The analysis assists in an objective comparison between areas. Whereas the main spring staging sites in the Netherlands and Schleswig-Holstein currently appear to be filled to capacity, there is a trend towards more unused buffer capacity in Niedersachsen and especially the Danish sites (see Figure 9.3). There may be climatic reasons behind this that are ignored in our invariate capacity measure, but the northern sites would certainly repay more intensive scrutiny. On a more general level, our data confirm the contention that grazed marshes can support far more geese than ungrazed ones, and a reduction in grazing thus leads to an overall reduction in goose foraging opportunities. We hypothesize that the numbers of Brent Geese in the entire Wadden Sea in May can be a factor four higher when all salt marshes are grazed by livestock than in the absence of grazing.





**Figure 9.3** The predicted potential number of geese on salt marshes in May, per region in the Wadden Sea, as indicated with dots of different size. The observed average numbers in May 1995-1998 are indicated as a proportion of the predicted values. In four regions more birds were observed than predicted, and this is indicated using an extra dot, connected to the dot indicating the predicted value. Over 90 % of the observed birds are Brent Geese. Regions are defined by Meltofte et al. (1994), with their boundaries and numbering given in the inset. The term 'missing' refers to presumed unused buffer capacity, but we emphasise that the analysis aims at comparison amongst areas rather than a prediction of absolute potential numbers. Calculations are based on observed relations between vegetation composition with soil type and livestock grazing regime, in combination with independent estimates of grazing density per plant community. Details of the extrapolation are given in chapter 8. A summary of predicted and observed numbers of geese is given per country (province) on the right-hand side of the diagram. In this summary, the estuarine areas are not included.

Agricultural grasslands appear to yield virtually unlimited capacity for Brent Geese towards the end of spring. When left undisturbed, Brent Geese are able to maintain a suitable sward themselves in these highly productive areas by intensifying the frequency of grazing with increasing primary productivity (Spaans & Postma 2001; chapter 3; chapter 5). However, there is insufficient critical information bearing on the question whether foraging on polder grassland alone may yield the same fitness perspectives for the geese. Prop & Black (1997) have shown that Barnacle Geese staging



in agricultural habitat in late spring may suffer negative consequences in their reproductive performance, as the food on the pastures seems inadequate in providing all nutrients required for balanced body stores. Long-term data on individual Brent Geese spending most of their time on pasture land on Texel in spring do not indicate reduced reproductive success (Spaans & Postma 2001), but it cannot be excluded that the birds in that study compensated for this by gathering additional forage on the intertidal flats or on neighbouring salt marshes for some of the time.

## Future perspectives for geese in coastal habitats

In the past, the available amounts of natural habitat for Brent Geese have been larger than at present, due to reclamation of land by man (Dijkema 1987; van Eerden 1997). On the basis of paleogeographical maps, van Eerden (1997) reconstructed the changes in waterbird numbers. They concluded that, given the estimated available amount of habitat, Brent Geese generally must have been abundant in the Netherlands throughout the period they studied (from 7000 BP onwards). However, given the large scale reclamation and embankment of natural habitats, peak numbers of Brent Geese are assumed to be only one-third nowadays of the number in 1350 AD. In the current situation, coastal protection works interrupt the natural sequence of landscape types from the North Sea to the higher inland areas, from salt marshes to brackish and freshwater marshes, swamps and peat moors (Wolff 1992). With a rising sea level, these belts of different landscapes moved inland in the past, and they would still do so if man had not interfered. For this reason, Wolff (1992) refers to the current situation as being an 'amputated landscape'. Thus, there is little scope nowadays for rejuvenation of marshes by coastal regression.

The ongoing processes of climate change, sea-level rise and sedimentation will lead to new challenges for the Brent Goose. Sedimentation in overgrown salt marshes will more than compensate for the present sea-level rise according to de Jong *et al.* (1999), and it is even the trilateral policy (Denmark, Germany and the Netherlands) to increase the area of natural marsh in the Wadden Sea (de Jong *et al.* 1999). However, it is not only the area of marsh that is relevant to Brent Geese, but also the quality of this habitat in terms of vegetation composition. Within existing marsh along the mainland coast in the Netherlands, the relative abundance of older stages of vegetation succession increased at the expense of pioneer vegetation (Esselink 2000), in the absence of land reclamation. This ageing of marshes can be counteracted by grazing with livestock, but the extent of livestock grazing in the Wadden Sea has diminished in the past decades. Relatively large areas in the Wadden Sea have been taken out of grazing during the 1990s and the vegetation in these areas still appears to be in transition (Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer 1998).

Another challenge to the Brent Goose is posed by the observed increase in numbers of Barnacle Geese, but a better insight in the importance of potential competitive interactions between these two species is highly desirable. In spite of their traditional nature, the geese have in the past proven to be opportunistic, and capable of detecting

alternative resources and new staging areas. We should, therefore, not be too surprised if Brent Geese once again are observed to exploit new habitat, with the caveat of non-disturbance. Currently, Brent Geese are restricted to coastal areas, but there is no reason to assume that they could not adapt to feeding more inland as well (Prins pers. comm.). Maybe the use of winter cereals will increase, as was suggested by van Eerden (1996), when levels of fertiliser application decrease in agricultural grassland. However, it would be most appropriate to manage salt marshes, seagrass beds and intertidal flats in the Wadden Sea in such a way, that a viable population of Brent Geese can be accommodated on their natural habitats.

## Conclusions

Patch choice by Brent Geese in spring was found to be consistent with the hypothesis of maximisation of nutrient intake rate. In line with this, we found that spring habitat use was, to a large extent, governed by the process of primary production. With increasing levels of standing biomass due to primary production, the nutrient intake rate increases initially but declines again when levels of biomass become too high (see Figure 9.1). This happens within a season and within a plant community due to declining forage quality caused by forage maturation. Another reason is that instantaneous rates of intake decline, due to changes in sward structure. Over the years, the geese are confronted with a reduced abundance of the preferred forage species and a change in sward structure that depresses the instantaneous rate of intake. The repeated removal of biomass by herbivores (or farmers) maintains the sward in a more suitable stage, both within a season and over the years. By virtue of this process of facilitation, Brent Geese are enabled to utilise highly productive agricultural grassland until the end of their spring staging period and livestock-grazed marshes in spite of old marsh age. Disturbance and scaring of geese strongly affects habitat use, especially because it allows vegetation to 'escape' the grazing cycle. Continuous grazing is essential when the vegetation is in a productive growth phase, otherwise it will lose its value as a feeding habitat for geese.

Livestock grazing enhances the feeding conditions for small vertebrate herbivores, such as Brent Geese. The difference in observed grazing intensity by geese between marshes grazed by livestock and those left ungrazed is especially noticeable in the productive, well-drained mainland marshes. Here, vegetation succession leads to the dominance of tall unpalatable vegetation and an almost complete absence of geese. Ungrazed barrier marshes require many decades before vegetation succession has proceeded to a point where feeding conditions for small vertebrate herbivores start to deteriorate, but experience shows that succession is relentless.



## References

- Adam P (1990) Saltmarsh ecology. Cambridge University Press, Cambridge
- Aerts BA, Esselink P, Helder GJF (1996) Habitat selection and diet composition of Greylag geese *Anser anser* and Barnacle Geese *Branta leucopsis* during fall and spring staging in relation to management in the tidal marshes of the Dollard. Z. Ökol. Natursch. 5: 65-75
- Bakker JP (1989) Nature management by grazing and cutting. Kluwer Academic Publishers, Dordrecht
- Beefink WG (1977) The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. In: Chapman VJ (ed) Ecosystems of the World. Wet coastal ecosystems. Elsevier Scientific Publishing Company, Amsterdam
- Bergmann HH, Borbach-Jaene J (2001) Abschlussbericht des Forschungsprojektes Auswirkungen von Bewirtschaftungsänderungen auf die Habitatwahl, Raumnutzung und das Verhalten von Nonnengans und Ringelgans am Beispiel der Leybucht im Nationalpark Niedersächsisches Wattenmeer
- Bos D, Bakker JP, de Vries Y, van Lieshout S (2002) Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. Appl. Veg. Sci. 5: 45-54
- Boudewijn T (1984) The role of digestibility in the selection of spring feeding sites by Brent Geese. Wildfowl 35: 97-105
- de Jong F, Bakker JF, van Berkel CJM, Dankers NMJA, Dahl K, Gätje C, Marencic H, Potel P (1999) Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Quality Status Report Group, Wilhelmshaven
- Dijkema KS (1987) Changes in salt-marsh area in the Netherlands Wadden Sea after 1600. In: Huiskes AHL, Blom CWPM, Rozema J (eds) Vegetation between land and sea. Junk Publishers, Dordrecht/Boston/Lancaster, pp 42-49
- Drent R, Ebbinge B, Weyand B (1979) Balancing the energy budgets of arctic-breeding geese throughout the annual cycle: a progress report. Verh. Orn. Ges. Bayern 23: 239-264
- Durant D (2001) Patterns and processes underlying the difference in the use of swards by grazing Anatidae. PhD thesis Université de La Rochelle, UFR de Sciences, La Rochelle
- Ebbinge BS (1992) Regulation of numbers of Dark-bellied Brent Geese *Branta bernicla bernicla* on spring staging sites. Ardea 80: 203-228
- Ebbinge BS, Heesterbeek JAP, Ens BJ, Goedhart PW (2002) Density dependent population limitation in dark-bellied brent geese. Avian Science (in press)
- Ebbinge BS, Spaans B (1995) The importance of body-reserves accumulated in spring staging areas in the temperate zone for breeding in Dark-bellied Brent Geese *Branta b. bernicla* in the high Arctic. J. Avian Biol. 26: 105-113
- Ebbinge BS, Spaans B (2002) How do Brent Geese (*Branta b. bernicla*) cope with evil? Complex relationships between predators and prey. J. Ornithol. 143
- Engelmoer M, Taal J, Wymenga E, Kuipers R (2001) Aantalsafname bij de Rotgans *Branta bernicla* langs de Friese waddenkust. Limosa 74: 41-56
- Esselink P (2000) Nature management of coastal marshes. Interactions between anthropogenic influences and natural dynamics. PhD thesis University of Groningen, Groningen
- Fryxell JM (1991) Forage quality and aggregation by large herbivores. Am. Nat. 138: 478-498
- Ginnett TF, Demment MW (1995) The functional response of herbivores: Analysis and test of a simple mechanistic model. Funct. Ecol. 9: 376-384
- Gross JE, Shipley LA, Hobbs NT, Spalinger DE, Wunder BA (1993) Functional response of herbivores in food-concentrated patches: Tests of a mechanistic model. Ecology 74: 778-791
- Hassall M, Riddington R, Helden A (2001) Foraging behaviour of brent geese, *Branta b. bernicla*, on grasslands: effects of sward length and nitrogen content. Oecologia 127: 97-104
- Holling CS (1959) Some characteristics of simple types of predation and parasitism. Can. Entomol. 91: 385-398
- Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. Ecol. Monogr. 72: 95-112
- Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer (1998) Umweltatlas

- Wattenmeer. Bd. 1 Nordfriesisches und Dithmarscher Wattenmeer. Ulmer, Stuttgart
- McKay HV, Bishop JD, Ennis DC (1994) The possible importance of nutritional requirements for dark-bellied brent geese in the seasonal shift from winter cereals to pasture. *Ardea* 82: 123-132
- McLeod SR (1997) Is the concept of carrying capacity useful in variable environments? *Oikos* 79: 529-542
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form and coevolution. *Am. Nat.* 124: 863-886
- Meltofte H, Blew J, Frikke J, Rösner H-U, Smit CJ (1994) Numbers and distribution of waterbirds in the Wadden Sea. *WSG Bull.* 74, special issue
- Oloff H, de Leeuw J, Bakker JP, Platerink RJ, van Wijnen HJ, de Munck W (1997) Vegetation succession and herbivory in a salt marsh: Changes induced by sea level rise and silt deposition along an elevational gradient. *J. Ecol.* 85: 799-814
- Owen M (1980) Wild geese of the world. Batsford Ltd., London
- Prop J, Black JM (1997). Food intake, body reserves and reproductive success of barnacle geese *Branta leucopsis* staging in different habitats. In: Mehlum F, Black JM, Madsen J (eds). Proceedings of the Svalbard Goose symposium. Norsk-Polarinstitutt, Oslo, Norway, pp 175-193
- Prop J, Deerenberg C (1991) Spring staging in Brent Geese *Branta bernicla*: feeding constraints and the impact of diet on the accumulation of body reserves. *Oecologia* 87: 19-28
- Prop J, Loonen M (1989) Goose flocks and food exploitation: the importance of being first. *Acta XIX Congr.Int.Orn.(Ottawa)* : 1878-1887
- Prop J, Vulink T (1992) Digestion by barnacle geese in the annual cycle: the interplay between retention time and food quality. *Funct. Ecol.* 6: 180-189
- Riddington R, Hassall M, Lane SJ (1997) The selection of grass swards by brent geese *Branta b. bernicla*: Interactions between food quality and quantity. *Biol. Conserv.* 81: 153-160
- Rowcliffe JM, Watkinson AR, Sutherland WJ (2001) The depletion of algal beds by geese: a predictive model and test. *Oecologia* 127: 361-371
- Spaans B, Postma P (2001) Inland pastures are an appropriate alternative for salt-marshes as a feeding area for spring-fattening Dark-bellied Brent Geese *Branta bernicla*. *Ardea* 89: 427-440
- Spalinger DE, Hobbs N (1992) Mechanisms of foraging in mammalian herbivores: New models of functional response. *Am. Nat.* 140: 325-348
- Stahl J, Bos D, Loonen MJJE (2001a) Foraging along a salinity gradient - the effect of tidal inundation on site choice by brent and barnacle geese. In: Stahl J (ed) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. PhD-thesis University of Groningen, Groningen pp 153-170
- Stahl J, Rothkegel C, Drent RH (2001b) Staging barnacle and brent geese versus resident brown hare: crossing the boundary between facilitation and resource competition. In: Stahl J (ed) Limits to the co-occurrence of avian herbivores. How geese share scarce resources. University of Groningen, Groningen
- Stahl J, Tolsma PH, Loonen MJJE, Drent RH (2001c) Subordinates explore but dominants profit: resource competition in high Arctic barnacle goose flocks. *Anim. Behav.* 61: 257-264
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton,
- Stock M, Hofeditz F (2000) Der Einfluss des Salzwiesen-Managements auf die Nutzung des Habitates durch Nonnen- und Ringelgänse. In: Stock M, Kiehl K (eds) Die Salzwiesen der Hamburger Hallig. Landesamt für den Nationalpark Schleswig-Holsteinisches Wattenmeer, Tönning, pp 43-55
- Stock M, Hofeditz F, Mock K, Pohl B (1995) Einflüsse von Flugbetrieb und Freizeitaktivitäten auf Verhalten und Raumnutzung von Ringelgänsen *Branta bernicla bernicla* im Wattenmeer. Auswirkungen von Störreizen auf Ethologie und Ökologie von Vögeln im Wattenmeer. *Corax* 16: 63-83
- Sutherland WJ (1996) From Individual Behaviour to Population Ecology. Oxford University Press, Oxford
- Teunissen W, Spaans B, Drent R (1985) Breeding success in Brent in relation to individual feeding opportunities during spring staging in the Wadden Sea. *Ardea* 73: 109-120
- Ungar ED, Noy-Meir I (1988) Herbage intake in relation to availability and sward structure: grazing processes and optimal foraging. *J. Appl. Ecol.* 25: 1045-1062
- van Andel J, Bakker JP, Grootjans AP (1993) Mechanisms of vegetation succession: A review of concepts and perspectives. *Acta Bot. Neerl.* 42: 413-433



- van de Koppel J, Huisman J, van der Wal R, Olff H (1996) Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology* 77: 736-745
- van der Wal R, Kunst P, Drent R (1998a) Interactions between hare and brent goose in a salt marsh system: evidence for food competition? *Oecologia* 117: 227-234
- van der Wal R, van de Koppel J, Sagel M (1998b) On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos* 82: 123-130
- van der Wal R, van Lieshout S, Bos D, Drent RH (2000a) Are spring staging brent geese evicted by vegetation succession? *Ecography* 23: 60-69
- van der Wal R, van Wijnen H, van Wieren S, Beucher O, Bos D (2000b) On facilitation between herbivores: How Brent Geese profit from brown hares. *Ecology* 81: 969-980
- van Eerden MR (1997) Patchwork. Patch use, habitat exploitation and carrying capacity for water birds in Dutch freshwater wetlands. PhD thesis University of Groningen, Groningen
- van Eerden MR, Zijlstra M, Van Roomen M, Timmerman A (1996) The response of Anatidae to changes in agricultural practice: Long-term shifts in the carrying capacity of wintering waterfowl. *Gibier Faune Sauvage* 13: 681-707
- van Soest PJ (1994) Nutritional Ecology of the ruminant. Cornell University Press, Ithaca (NY)
- van Wijnen H, van der Wal R, Bakker JP (1999) The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia* 118: 225-231
- van Wijnen HJ, Bakker JP, de Vries Y (1997) Twenty years of salt marsh succession on a Dutch coastal barrier island. *J. Coast. Cons.* 3: 9-18
- Vickery JA, Sutherland WJ, Watkinson AR, Lane SJ, Rowcliffe JM (1995) Habitat switching by dark bellied brent geese *Branta b. bernicla* (L.) in relation to food depletion. *Oecologia* 103: 499-508
- Wilmshurst JF, Fryxell JM (1995) Patch selection by red deer in relation to energy and protein intake: A re-evaluation of Langvatn and Hanley's (1993) results. *Oecologia* 104: 297-300
- Wilmshurst JF, Fryxell JM, Hudson RJ (1995) Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behav. Ecol.* 6: 209-217
- Wolff WJ (1992) Ecological developments in the Wadden Sea until 1990. In: Dankers NMJA, Smit CJ, Scholl M (eds) Present and future conservation of the Wadden Sea. Proceedings of the 7th International Wadden Sea Symposium, Ameland 1990. Netherlands Institute for Sea Research, Den Burg, pp 23-32
- Wright W, Illius AW (1995) A comparative study of the fracture properties of five grasses. *Funct. Ecol.* 9: 269-278
- Ydenberg RC, Prins HHT (1981) Spring grazing and the manipulation of food quality by Barnacle Geese. *J. Appl. Ecol.* 18: 443-453

Low salt marsh near "Willemsduin" on Schiermonnikoog, looking into the direction of the higher marsh (photo J. Stahl).







## Summary

Dark-bellied Brent Geese are the most numerous geese in the international Wadden Sea area, together with Barnacle Geese. During the spring staging period, the geese have to acquire fat reserves for migration and the subsequent breeding season. In this period almost the complete East Atlantic Flyway population of Brent Geese is accommodated in the Wadden Sea area. Both goose species forage on pastures and salt marshes along the coast. As spring proceeds, the majority of birds switches to foraging on the marsh, but locally large numbers continue grazing on pasture land for a long time. This gives rise to a potential conflict with the agricultural community. Salt marshes along the Wadden Sea have been grazed by livestock for more than 2,000 years. However, there is a tendency to abandon grazing on salt marshes nowadays, and this affects the vegetation development in these areas. We presume that the suitability of marshes as a foraging habitat for geese depends on the vegetation composition, and that the use of pasture land is related to the foraging conditions on the marsh. The aim of this thesis is therefore to understand the mechanisms that determine the spatial distribution of Brent Geese and to determine to what extent this distribution is affected by grazing with livestock in these coastal grasslands.

### *Quality and quantity of forage*

In chapter 2 we set out to determine the relative importance of forage quality and quantity for patch choice in Brent Geese. We measured the preference of wild Brent Geese for experimentally manipulated plots on the low salt marsh, differing in sward height and nitrogen content of the plants in a full-factorial design. Preference was determined from direct observation, using behavioural parameters, and by measuring the realised grazing pressure from dropping counts. Geese defecate very regularly, and dropping density can, therefore, be used as a measure of the time spent by geese in a certain area. Both measures of preference agreed very well. Brent Geese were very sensitive to the differences in forage quality, measured as nitrogen content, but forage quantity also played a role. Using captive animals, we learned that intake rate of food increased linearly with forage quantity, over the range of biomass values observed in this experiment. The product of nitrogen content and intake rate, the intake rate of



nitrogen, appeared a suitable measure for patch preference. This result strongly supported previous work, that was done over a different range of biomass values. The results imply that Brent Geese will sometimes prefer areas with low amounts of forage of high quality over areas with high biomass but lower forage quality. In the field, forage quality commonly declines with biomass. Another phenomenon that may lead to a preference for short swards with low biomass, is the fact that Brent Geese have difficulties handling long grass leaves. In feeding trials with captive geese we found that intake rate of food declined at high values of plant standing crop (**chapter 5**). Both phenomena may explain a negative relationship between canopy height, as a measure of forage availability, and goose dropping density, which is often observed in the field.

### *Short grass is preferred*

A preference for short grass also relates to our finding that livestock grazing affects the habitat use of Brent Geese in spring (**chapter 4**). On the pastures on Ameland, the geese were observed to concentrate their grazing on four fields that had all been grazed by sheep during spring. Six control fields, that were livestock-ungrazed during spring, and two other sheep-grazed fields were abandoned by the geese in May, although they had been used by geese in early spring. Given these observations, we performed a choice experiment in the polder of Schiermonnikoog to test preference of captive Brent Geese for sheep-grazed or ungrazed vegetation. By grazing with sheep, we maintained a part of the study field at low canopy height, while the remainder of the field was left ungrazed. A pair of captive Brent Geese, in a pen of 4 m x 4 m placed over the grazing boundary, was repeatedly offered the choice between the two types of sward during May. The geese fed most of the time in the sheep-grazed part of the pen. It thus appears that spring grazing of productive grassland with livestock facilitates foraging by Brent Geese.

Practical examples, however, show that Brent Geese themselves are also able to maintain a short sward, provided that they can graze without too much interruption. On the Brent Goose reserve on Texel, human disturbance is low and every year up to 10,000 Brent Geese forage until the end of spring in pasture habitat. Over the season, the geese aggregate on an increasingly smaller area, locally maintaining a short canopy. To distinguish between three alternative hypotheses for the observed pattern, we experimentally excluded patches of 16 m<sup>2</sup> for 0, 1, 3, 5, and 8 weeks, on a part of the reserve that was heavily grazed by Brent Geese (**chapter 5**). The exclosures were removed simultaneously at the beginning of May. Goose grazing pressure was higher in the plots that had been excluded for one or three weeks, in comparison to plots that had been ungrazed for five to eight weeks. This result is in line with the hypothesis that the observed aggregation is caused by a preference for short grass, leading to spatial heterogeneity, and not primarily as a result of previously existing spatial heterogeneity in, for example, forage quality or predation risk. Still, these latter factors may play a role in determining at which spatial location in the pasture grazing will be inten-



sified towards the end of spring. The pattern of aggregation was simulated in a model and also studied analytically. These models indicate that, once a particular sward has grown towards a high biomass state, this patch is unlikely to be grazed down again to a state with low biomass by the geese themselves. As a result, a situation may arise in which depletion occurs within patches that are maintained and in which the geese have lower intake rates of nitrogen or other nutrients than potentially possible.

### *An experiment with human disturbance*

Our insight in the potential use of pasture habitat was further increased by a large scale experiment with human disturbance on Schiermonnikoog (**chapter 3**). In spring 2000, a new arrangement between the farmers on the island and the government led to a ban on scaring geese from the polder. In three previous years scaring with flares had been very effective in protecting the spring harvest of grass from geese, and only a few geese could be observed in May on the pastures. However, in May of the years 2000 and 2001 the number of geese on the pastures was high, and on average 2,000 animals were present daily. As on the Brent Goose reserve on Texel, the geese at first grazed all fields in the polder, but aggregated on a smaller area as primary production increased. Presumably, there had not been sufficient undisturbed goose grazing to keep up with production in years with scaring, allowing the vegetation to ‘escape’ to levels of biomass that are less attractive for Brent Geese. This must have contributed to the effectiveness of scaring. The numbers and the identity of geese visiting the undisturbed salt marsh on Schiermonnikoog was not different between years with and without scaring. There were thus more geese on the island in the absence of scaring, some of which had been observed in other parts of the Dutch Wadden Sea in previous years. Although many geese can indeed forage on pasture habitat until the end of May, there are indications that foraging on the marsh is more attractive towards the end of spring for the majority of birds.

### *Geese on the marsh and the role of livestock grazing*

The marsh is not as homogeneous as the pasture habitat. There is a variety of plant communities and we investigated the use of these communities by geese and the conditions under which these communities occur. A lot of variation on salt marshes is caused by differences in soil elevation while, in addition to that, thickness of the clay layer is very important on salt marshes with a sandy soil. Higher parts of the marsh are inundated less frequently, and have different vegetation composition. On Schiermonnikoog we observed that Brent Geese use the lower parts of the marsh more intensively than the higher parts, while this is the opposite for Barnacle Geese (**chapter 3**). With increasing age of a salt marsh, more sedimentation has taken place, and the clay layer is thicker. Nitrogen, an important nutrient limiting primary production, is attached to the clay. Young salt marshes with a sandy soil have little clay and low levels of primary production, and many of the plant species that occur there, such as Common salt-

marsh grass *Puccinellia maritima*, Red fescue *Festuca rubra*, Sea plantain *Plantago maritima* and Sea arrow grass *Triglochin maritima*, are short and palatable for geese. A thick layer of clay coincides with tall vegetation, with species such as Sea couch grass *Elymus athericus* and Sea purslane *Atriplex portulacoides*, under undisturbed succession. Such a vegetation is not attractive for geese. On artificial mainland marshes, the soil contains more clay and succession is expected to proceed faster. There are, however, exceptions, for example where rates of sedimentation are low.

As mentioned above, salt marshes have been grazed with livestock throughout historic time and still some 60% of the total marsh area in the entire Wadden Sea is grazed. We studied the effects of livestock grazing on vegetation composition of salt marshes by comparing areas that differed in grazing regime (**chapters 4, 6, 7**). An important part of the available information was derived from exclosures and control areas on the barrier islands of Terschelling (NL), Schiermonnikoog (NL) and Skallingen (DK), at which the vegetation development had been monitored for more than 25 years (**chapter 6**). The results for these three study sites agreed very well, in that plant species that are palatable for geese continue to occur in areas that are grazed by livestock, while they decline strongly in abundance without livestock grazing. Presumably, this is caused by an increased competition for light with taller plant species. By the removal of aboveground biomass and by trampling, livestock grazing prevents these species from dominating the vegetation. The density of plant species was also higher under livestock-grazed than under ungrazed conditions.

To generalise these findings, and to relate them to habitat use by geese, we performed a survey along 38 marshes in the entire Wadden Sea in April and May 1999 (**chapter 7**). We preferentially selected sites at which different grazing regimes occurred nearby to each other. At each study site and grazing regime, we placed a transect with 20 plots of 4 m<sup>2</sup> each, from the seawall to the intertidal flats. At these plots we measured canopy height, vegetation composition and accumulated goose dropping densities. The study showed again that the proportion of tall vegetation increases, while the cover of plant species that are palatable for geese declines, when salt marshes are ungrazed for more than ten years. On sandy salt marshes, this effect was less clear-cut, because our sample included young ungrazed sandy marshes with a short canopy. We found considerably more goose droppings on intensively grazed marshes as compared to long-term ungrazed salt marshes. The plant communities characterised by Creeping bent *Agrostis stolonifera*, *Festuca rubra* and *Puccinellia maritima*, that are common on livestock-grazed salt marshes had higher goose grazing pressure than vegetation dominated by Sea wormseed *Artemisia maritima*, *Elymus athericus* and *Atriplex portulacoides*, that especially occur under livestock-ungrazed conditions. But even within plant communities that are suitable for geese, we found an effect of livestock grazing. Livestock-grazed versions of the plant communities characterised by *Festuca rubra* and *Puccinellia maritima* had lower canopy height and higher goose grazing pressure than livestock-ungrazed versions, especially on the clayey mainland marshes. This is in line with results of a more local, but more intensive comparison between plant communities under different grazing regimes within the Dutch Wadden Sea area. In this comparison



(chapter 4), four study areas were involved. On Ameland and Schiermonnikoog, we compared 'livestock-ungrazed' with 'grazed' sandy marsh, while on the coast of Northern Friesland and Groningen 'intensively grazed' was compared to 'extensively grazed' clayey marsh. At all these study sites minimally five transects were located per plant community where droppings were counted weekly over the entire spring. Most of the pairwise comparisons indicated that geese prefer those versions of the plant communities that are grazed, or grazed more intensively, by livestock. This difference often coincides with lower canopy height and higher cover of plant species palatable for geese.

### *Capacity of salt marshes*

Given this detailed information on the effects of soil type and livestock grazing regime on habitat use by geese, we ventured to predict the number of geese that could potentially forage in a particular marsh in May (chapter 8). The prediction was founded upon an estimate of the potential number of geese per plant community, depending on soil type and grazing regime, which was derived from dropping counts. To express the idea that potential goose density varies between years, due to climatic fluctuations, and between areas, due to differences in vegetation composition in space, we also indicated upper and lower estimates. For a number of goose count areas, of which we think that they had been used intensively by geese and for which we had a complete vegetation map, we compared the prediction with the observed average numbers of geese in May, for the years 1995-1998. For sandy salt marshes there was a systematic discrepancy between observed and predicted values. The latter appeared 'too high'. For other types of marsh, however, there was a reasonable correlation between observed and predicted values. In a next step, we extrapolated our estimates to all marshes along the Wadden Sea, given an average vegetation composition per soil type and per grazing regime, and compared them to observed numbers. With this method, areas could be identified objectively that have relatively high or low goose numbers. By gathering additional information on these areas and comparing them amongst each other, our insight in the habitat use of Brent Geese will further be enhanced. Finally, with this set of assumptions, we also predicted that about four times as many geese can forage in the Wadden Sea in May, provided all salt marshes would be grazed with livestock, in comparison to a situation in which no marsh at all would be livestock grazed.

### *Summary in short*

The main theme of the thesis is that the foraging conditions of geese deteriorate under undisturbed plant growth, as time goes by. Within a season, the potential intake rate of nitrogen on pasture habitat declines with increased sward height. This is caused by a decline in nitrogen content and a decline in instantaneous intake rate of biomass. On salt marshes, the potential intake rate of nitrogen declines over the years due to changes in vegetation composition. Continuous grazing counteracts these processes and we

found facilitative effects of livestock for Brent Geese on both time scales. Within a season, Brent Geese may facilitate for themselves, when they are allowed to intensify grazing pressure locally, to cope with increasing levels of primary production. This requires low levels of human disturbance. On productive salt marsh geese cannot halt vegetation succession, in part because they are absent during an important part of the plant growing season. The role of livestock in facilitating geese on salt marshes is thus very important, allowing managers to influence the capacity of salt marshes for Brent Geese.

Close-up of two of the captive Brent Geese that had an important role in the project (photo J. Stahl).





# Samenvatting

Rotganzen zijn, samen met brandganzen, de meest talrijke ganzen in het internationale Waddengebied. Ze foerageren beide op kwelders en in polders langs de kust. Met name de voorjaarsperiode is voor rotganzen belangrijk omdat ze in die periode moeten opvetten ter voorbereiding van de trek naar de broedgebieden en het broedseizoen zelf. In deze periode herbergt het Waddengebied bijna de gehele East Atlantic Flyway populatie, dat wil zeggen ongeveer 200.000 rotganzen. In de loop van het voorjaar verplaatsen de meeste ganzen zich van de polder naar de buitendijkse kwelder. De rotganzen vertrekken echter pas in mei naar hun broedgebieden en omdat lokaal nog tot laat in het voorjaar dieren op boerenland voedsel zoeken, worden ze beschouwd als concurrenten van de boeren. Beide ganzensoorten hebben waarschijnlijk al meer dan tweeduizend jaar gebruik gemaakt van kwelders die al die tijd intensief werden beweid door de kustbewoners. Tegenwoordig is beweiding van de buitendijkse gebieden echter niet meer vanzelfsprekend en dit heeft consequenties voor de vegetatie-samenstelling op deze terreinen. Verondersteld wordt dat de benutbaarheid van kwelders ganzen afhankelijk is van de vegetatie samenstelling, en dat er een samenhang is tussen de mate van benutting van boerenland en die van kwelders. Doel van het onderhavige proefschrift is daarom om te begrijpen hoe de ruimtelijke verspreiding van rotganzen kan worden verklaard, en in hoeverre zij afhankelijk is van beheer door beweiding met vee in de kustgebieden, zowel op de kwelders als op het boerenland.

## *Kwaliteit en kwantiteit van voedsel*

Omdat voedselbeschikbaarheid uitermate belangrijk is voor de terreinkeuze van rotganzen, hebben we het relatieve belang van voedselkwaliteit ten opzichte van kwantiteit bestudeerd (**Hoofdstuk 2**). Op kleine schaal hebben we dat gedaan door voorkeur van wilde rotganzen te meten voor proefvlakjes van 2 m x 6 m op de lage kwelder, die experimenteel waren beïnvloed. De ganzen hadden keuze uit veldjes met veel of weinig gras, en met hoge en normale voedselkwaliteit in alle mogelijke combinaties. De voorkeur van ganzen werd bepaald door te kijken naar hun gedrag en door te meten hoeveel tijd ze op de verschillende proefvlakjes doorbrachten. Hiertoe telden wij respectievelijk het aantal interacties en het aantal ganzenkeutels. Omdat ganzen zeer regelmatig



keutels produceren, kun je aan de hand van de keuteldichtheid meten hoeveel tijd de ganzen op een bepaalde plek hebben doorgebracht, of hoeveel ganzen er gemiddeld op een dag hebben gezeten. Beide maten voor voorkeur kwamen in dit experiment goed overeen. De rotganzen bleken erg gevoelig voor voedselkwaliteit, bijvoorbeeld gemeten aan de hand van het stikstofgehalte van de planten, maar kwantiteit was niet onbelangrijk. Met behulp van proefdieren werd vastgesteld dat de voedsel opnamesnelheid toenam met de voedselhoeveelheid, bij de waarden zoals die in het experiment voorkwamen. Het product van deze twee, de opnamesnelheid van stikstof, blijkt een geschikte maat te zijn voor de voorkeur. Dit resultaat vormt een sterke aanvulling op een zeer vergelijkbare studie aan rotganzen in de winter in Engeland, die was gedaan bij andere waarden van voedselhoeveelheid. In de praktijk betekent het dat de ganzen veldjes met weinig voedsel van hoge kwaliteit soms zullen prefereren boven plekjes met veel voedsel van lagere kwaliteit, en in het veld is het heel gewoon dat vegetatie met veel bovengrondse biomassa een lagere voedselkwaliteit heeft dan vegetatie met minder bovengrondse massa. Een tweede belangrijk fenomeen dat ertoe kan leiden dat rotganzen kort gras prefereren boven langer gras, is het feit dat de ganzen moeite hebben met het opnemen van voedsel wanneer de bladlengte te groot wordt. We lieten onze proefdieren proeven van graszoden met toenemende biomassa uit de polder en vonden dat de voedselopnamesnelheid daalt als het gras te lang wordt (**Hoofdstuk 5**). Beide fenomenen kunnen een verklaring bieden voor een veel gevonden negatieve relatie tussen vegetatie-hoogte, als maat voor de voedselhoeveelheid, en de dichtheid van ganzenkeutels.

### *Korte vegetatie is van belang*

Ganzen prefereren kort gras. Dit gegeven ligt aan de basis van onze bevindingen op Ameland dat vee-beweiding de terreinkeuze van rotganzen in het voorjaar beïnvloedt (**Hoofdstuk 4**). Op het productieve poldergrasland van Ameland concentreerden de ganzen hun benutting in de maand mei in 1998 op vier percelen die alle gedurende het voorjaar beweid werden met schapen. Een zestal controle-percelen die niet beweid werden, en twee andere door schapen begraaide percelen, werden in mei niet meer door de ganzen bezocht, terwijl ze daar eerder in het seizoen wel aanwezig waren. Naar aanleiding van deze waarneming werd in 1999 een experiment uitgevoerd in de polder van Schiermonnikoog. Er zijn in de polder van Schiermonnikoog gewoonlijk geen schapen aanwezig en het grootste deel van het oppervlak wordt gebruikt voor de productie van gras voor kuilvoer voor koeien. In maart, april en mei is hier bij uitzondering een groepje schapen geweid op een normaal in het voorjaar onbeweid perceel. Het door schapen beweidde deel werd verkleind in de loop van het voorjaar om de vegetatie kort te houden, omdat in de loop van het voorjaar de grasgroei op gang begint te komen. Zo werd een verschil tot stand gebracht tussen door schapen kort gehouden vegetatie en vegetatie waarvan de hoogte toenam in de loop van het voorjaar. Een paar-tje tamme rotganzen werd in verplaatsbare kooien van 4 m x 4 m geplaatst, de ene helft van de kooi korte, en de andere helft hoge vegetatie omvatte. Er werd rechtstreeks waargenomen voor welke helft van de kooi de ganzen voorkeur hadden. Deze proce-



dure werd 11 keer herhaald. De ganzen vertoonden sterke voorkeur voor de door schapen kort gehouden helft binnen de kooi. Het lijkt er dus op dat de voorjaarsbeweiding van de polder met vee het voedsel vergaren voor de ganzen vergemakkelijkt, doordat het gras kort gehouden wordt. Dit proces, waarbij het ene organisme de omstandigheden voor de ander verbetert, heet 'facilitatie'.

In de praktijk blijkt echter dat rotganzen zelf de vegetatie ook voldoende kort kunnen houden, als de omstandigheden goed zijn. Het rotganzenreservaat Zeeburg op Texel wordt beweid met koeien en schapen, maar deze verschijnen pas op het toneel als de ganzen omstreeks half mei vertrokken zijn. De verstoring door mensen in het reservaat is laag, en ieder jaar blijven hier wel 10.000 ganzen tot ver in mei op het poldergrasland voedsel zoeken. Collega-onderzoekers hadden al laten zien dat de rotganzen hier, naarmate het seizoen vordert, steeds intensiever op een steeds kleiner oppervlak grazen en lokaal het gras heel kort houden. We veronderstellen dat dit patroon van concentratie ontstaat doordat ze steeds kiezen voor de kortste vegetatie, terwijl ze door de toenemende grasproductie een steeds kleiner oppervlak nodig hebben. Er zijn echter ook alternatieve verklaringen voor dit patroon. De gewaskwaliteit kan bijvoorbeeld pleksgewijs om andere redenen erg verschillen, en met de toegenomen productie kunnen meer ganzen daar dan van profiteren. In een experiment in het voorjaar van 2000 zijn kleine proefveldjes tijdelijk uitgesloten van begrazing door rotganzen gedurende acht, vijf, drie en één week met behulp van exclusures van 16 m<sup>2</sup>, op een door ganzen zwaar benut perceel (**Hoofdstuk 5**). De exclusures werden gelijktijdig opengesteld op 7 mei. Op die dag hadden de wilde rotganzen plotseling de keuze tussen plekken met verschillende vegetatie-hoogte, afhankelijk van hoelang de exclusure er had gestaan. De vegetatie die één of drie weken niet was begraasd, werd geprefereerd boven de vegetatie die vijf of acht weken niet was begraasd. Dit is een voor ons belangrijk resultaat, omdat het past bij de veronderstelling dat de waargenomen concentratie van ganzen een gevolg is van een voorkeur voor het korte gras en niet direct van ruimtelijke verschillen in bijvoorbeeld predatie-risico of voedselkwaliteit. Overigens kunnen deze laatste factoren nog steeds een rol spelen, al was het alleen maar door te bepalen welk deel van de polder aan het eind van het voorjaar het meest intensief wordt benut en welke delen in de steek worden gelaten. Het patroon van concentratie van begrazingsintensiteit is gesimuleerd met twee soorten modellen. Die modelstudies laten met name zien dat wanneer de vegetatie doorgroeit naar een toestand met veel gras, het onwaarschijnlijk is dat zij door de ganzen zelf weer wordt afgegraasd. Als gevolg hiervan, aldus onze modelstudies, kan een situatie ontstaan waarin de gebiedjes die nog wel worden benut, uitgeput raken en de ganzen een lagere opname van stikstof bereiken dan potentieel mogelijk zou zijn.

### *Boeren gedogen ganzen in de polder*

Ons inzicht in de mogelijkheden voor ganzen om poldergrasland te benutten, werd verder vergroot doordat de verenigde boeren op Schiermonnikoog in het jaar 2000 hun



beleid ten aanzien van de ganzen veranderden (**Hoofdstuk 3**). In het voorjaar van dat jaar ging er een gedoogregeling van start. Dit houdt in dat de boeren vóór het ganzenseizoen een schadevergoeding krijgen op voorwaarde dat ze de ganzen niet verjagen: de ganzen worden gedoogd in de weilanden. De gedoogregeling was voor ons een soort experiment, en leverde onverwachte inzichten op. Het verjagen van ganzen uit de polder, met onder andere lichtkogels, was ieder jaar zó effectief geweest dat rotganzen maar mondjesmaat werden waargenomen in mei in de polder, tot aan 1999. Zowel in het voorjaar van 2000 als in dat van 2001 echter was het aantal rotganzen in de polder hoog, en gemiddeld waren er dagelijks tweeduizend dieren aanwezig. Net als op Texel waren de ganzen ook hier aanvankelijk gelijkelijk verdeeld over de gehele polder, maar concentreerden ze zich geleidelijk op een steeds kleiner aantal percelen. Op deze plekken hielden ze zelf het gras voldoende kort. Toen er nog verjaagd werd, was er wellicht niet voldoende tijd om de snelle grasgroei bij te houden, zodat deze kon 'ontsnappen' naar een vegetatiehoogte die voor ganzen minder aantrekkelijk is. Dit zal hebben bijgedragen aan de effectiviteit van het verjagen. De toename van het aantal dieren in de polder is niet ten koste gegaan van het aantal ganzen op de kwelder. Er waren dus meer rotganzen op Schiermonnikoog dan vóór het instellen van de gedoogregeling. Een aantal van deze 'extra' ganzen die in de polder voedsel zochten is voorheen wel eens waargenomen langs de Groninger kust of op andere Nederlandse Waddeneilanden. Dit hebben we aan de hand van kleurringen kunnen vaststellen.

De dieren die we op de kwelder zagen waren grotendeels nog dezelfde als altijd, en met het toenemen van de groei op de kwelder nam hun aantal geleidelijk toe. Hoewel dus een groot aantal dieren op poldergrasland haar kostje bijeen kan zoeken, lijkt voedsel zoeken op de kwelder voor veel ganzen toch erg aantrekkelijk te zijn. Wat hier precies de oorzaak van is hebben wij niet achterhaald, maar we speculeren er in hoofdstuk 3 wel over.

### *Ganzen op de kwelder*

De kwelder is lang niet zo homogeen als de gemiddelde polder. Er is een grote variatie aan plantengemeenschappen en we hebben uitgezocht voor welke gemeenschappen de ganzen voorkeur vertonen en onder welke omstandigheden deze gemeenschappen voorkomen. Veel variatie op kwelders wordt veroorzaakt door verschillen in hoogteligging, waarbij op zandige kwelders ook de dikte van de kleilaag nog een belangrijke rol speelt. De hogere delen van de kwelder worden minder vaak overspoeld met zeewater, en dat heeft gevolgen voor de samenstelling van de vegetatie. We konden aantonen dat op Schiermonnikoog de rotganzen vaker op de lage kwelder worden aangetroffen dan op de hoge kwelderdelen, terwijl dat voor de brandgans andersom is (**Hoofdstuk 3**). Als de kwelder ouder wordt vindt steeds meer opslibbing plaats en wordt de kleilaag dikker. In het slib bevindt zich stikstof, de motor van plantaardige productie. Een jonge zandige kwelder heeft maar weinig klei en een lage productie, en veel van de plantensoorten die er voorkomen, zoals Gewoon kweldergras *Puccinellia maritima*, Rood



zwenkgras *Festuca rubra*, Zeeweegbree *Plantago maritima* en Schorrezoutgras *Triglochin maritima*, zijn kort en eetbaar voor ganzen. Een dikke kleilaag en een hoge productie gaat gepaard met een hoge vegetatie, met plantensoorten als Gewone zoutmelde *Atriplex portulacoides* en Strandkweek *Elymus athericus*, en een dergelijke vegetatie is niet aantrekkelijk voor ganzen. Hazen kunnen de vegetatie wel een tijdlang kort en aantrekkelijk houden voor rotganzen door de dwergstruik Gewone zoutmelde te eten. Dit blijkt uit een experiment met exclusures op de kwelder. Op een gegeven moment echter, na een tiental jaren, is de productie ook voor de hazen te hoog en verliest de kwelder zijn aantrekkelijkheid voor ganzen. Op vasteland kwelders bevat de bodem meer klei, en treden deze processen naar verwachting sneller op. Er zijn echter uitzonderingen, bijvoorbeeld door waar de sedimentatiesnelheid, en daarmee de aanvoer van stikstof, laag is.

### *De rol van vee op de kwelder*

Zoals aan het begin vermeld, werden kwelders vroeger stevast beweide met vee, en ook nu nog is ongeveer 60% van het totale kwelderoppervlak in de gehele Waddenzee op enigste wijze door vee begraasd. We hebben de effecten van vee-beweiding op de vegetatiesamenstelling bestudeerd door terreinen te vergelijken die al dan niet worden beweide (**Hoofdstuk 6, 7**). Voor een belangrijk deel betrof het hier gegevens van exclusures die al meer dan 25 jaar op de kwelders van Terschelling, Schiermonnikoog en Skallingen (Denemarken) stonden en waar ook al die tijd gegevens zijn verzameld (**Hoofdstuk 6**). De resultaten waren zeer eenduidig voor deze drie zandige kwelders, nl. dat de voor ganzen geschikte voedselplanten blijven voorkomen in gebiedjes die door vee worden beweide, terwijl ze sterk afnemen in bedekking waar dit niet het geval is. De oorzaak is gelegen in het feit dat de voor ganzen aantrekkelijke plantensoorten weg worden geconcurrerd door hoger opgaande planten, die beter in staat zijn om het zonlicht weg te vangen. Vee-beweiding zorgt er voor dat deze soorten niet kunnen gaan domineren, doordat vee een groot deel van de bovengrondse biomassa verwijdert of vertrapt. De diversiteit in de plantengemeenschap, gemeten als het gemiddelde aantal soorten op 4 m<sup>2</sup>, was ook hoger in de beweide proefvlakjes dan in de onbeweide.

Om deze gegevens te kunnen veralgemeniseren en om een relatie te kunnen leggen met het habitatgebruik door ganzen hebben we in april en mei 1999 op 38 kwelders in het hele Waddengebied ganzenkeutels geteld en metingen aan de vegetatie gedaan (**Hoofdstuk 7**). We hebben zoveel mogelijk plekken geselecteerd waar verschillende vormen van beheer door vee-beweiding naast elkaar voorkwamen. Op die plekken hebben we een transect gelegd met elk 20 plotjes van 4 m<sup>2</sup> van de lage naar de hoge kwelder. Bij elk plotje werden de dichtheid van ganzenkeutels, de vegetatiehoogte en de samenstelling van de vegetatie bepaald. Er kon geen onderscheid worden gemaakt tussen keutels van brand- en rotgans. Als de kwelder niet werd beweide, werd onderscheid gemaakt tussen kort (6-9 jaar), onbeweide en langdurig (minimaal 10 jaar) onbeweide. Ook in deze studie bleek dat als een kwelder langdurig niet meer wordt beweide

het aandeel hoge vegetatie sterk toeneemt, terwijl de bedekking met de voedselplanten van ganzen afneemt. Dit geldt in mindere mate voor de zandige eilandkwelders omdat daar in onze steekproef ook jonge, onbeweide kwelders voorkomen met een korte vegetatie. Er werden beduidend meer keutels gevonden op intensief beweide kwelders dan op langdurig onbeweide kwelders. In de vegetatie van Fioringras *Agrostis stolonifera*, Rood zwenkgras en Gewoon kweldergras, die veel voorkomen op beweide kwelders, werden meer keutels gevonden dan in de vegetatie van Strandkweek, Zeealsem *Artemisia maritima* en Gewone zoutmelde, die vooral voorkomen op langdurig onbeweide kwelders. Maar ook binnen de voor ganzen geschikte plantengemeenschappen vonden we nog een effect van vee-beweiding. De niet door vee begraasde varianten van de gemeenschappen van Rood zwenkgras en Gewoon kweldergras hebben een hogere vegetatie en een geringere begrazingsdruk door ganzen, met name op de kleiige vasteland kwelders. Dit bevestigde de resultaten van een meer lokale, maar intensievere vergelijking tussen deze plantengemeenschappen, bij verschillende vormen van beheer, in het Nederlandse Wadden gebied. In deze vergelijking (**Hoofdstuk 4**) waren vier studiegebieden betrokken, te weten Ameland en Schiermonnikoog, waar we ‘onbeweid’ konden vergelijken met ‘beweid’, alsmede Noord Friesland Buitendijks en de Groninger kust waar ‘intensief beweid’ werd vergeleken met ‘extensief beweid’. Op al deze plekken lagen minimaal vijf transecten per plantengemeenschap, met elk vijf permanente keutelvakjes, waar we wekelijks keutels telden en verwijderden, gedurende het gehele voorjaar. De meeste vergelijkingen wezen erop dat de ganzen een voorkeur hebben voor de vee-beweide variant van de bestudeerde plantengemeenschappen van Rood zwenkgras en Gewoon kweldergras. Dit verschil valt vaak samen met een geringere vegetatiehoogte, of een hogere bedekking van de door ganzen geprefereerde plantensoorten.

### *Draagkracht van de kwelder*

Wanneer er vee-beweiding plaats vindt op de kwelder, heeft dit een positief effect op het oppervlak van voor ganzen geschikte plantengemeenschappen en de geschiktheid van deze gemeenschappen als foerageergebied voor ganzen. We hebben een poging gedaan om met deze kennis een voorspelling te maken van het aantal ganzen dat in mei, in een bepaald gebied zou kunnen voorkomen (**Hoofdstuk 8**). Deze voorspelling berustte op een schatting van het mogelijke aantal ganzen per plantengemeenschap, afhankelijk van het bodem type (kleiig of zandig) en het beheer door vee-beweiding. Deze schatting was weer gebaseerd op keuteltellingen die wijzelf of collega's in het verleden ooit hebben gedaan. Om aan te geven dat de mogelijke ganzendichtheid zal variëren tussen jaren, vanwege verschillen in de groei, en tussen plekken, vanwege verschillen in vegetatiesamenstelling in de ruimte, hebben we ook een boven- en een onderschatting gegeven. Voor een aantal gebieden waarvan we denken dat ze goed door ganzen worden benut, en waarvoor we een goede vegetatiekaart hadden, hebben we deze voorspelling vergeleken met een waargenomen gemiddeld aantal ganzen in mei voor de jaren 1995-1998. Voor zandige begraasde kwelders was er een systema-



tisch verschil tussen de voorspelde potentiële aantallen en de waargenomen aantallen. Voor de andere kweldertypen was er echter geen aanleiding om al te zeer verontrust te zijn, omdat de voorspelling voor de selectie van gebieden met hoge ganzenaantallen redelijk met de waarnemingen overeenkwam. Vervolgens hebben we, gegeven een gemiddelde vegetatiesamenstelling per bodemtype en per beheersvorm, een voorspelling van mogelijke ganzenaantallen gemaakt voor iedere kwelder langs de gehele Waddenzee en deze vergeleken met waargenomen aantallen. Het mooie hiervan is dat we nu op een objectieve manier gebieden kunnen identificeren die bijzonder zijn, hetzij omdat er relatief weinig, hetzij omdat er juist relatief veel ganzen worden waargenomen. Door onderlinge vergelijking en het verzamelen van aanvullende kennis over deze gebieden, kunnen we in een vervolg hierop komen tot een verdere verdieping van ons inzicht in het habitatgebruik van de rotganzen. Uiteindelijk hebben we met deze aannames ook voorspeld dat er vier keer zoveel ganzen in mei in de Waddenzee kunnen voorkomen wanneer alle kwelders zouden worden beweide, in vergelijking met een situatie waarin geen enkele kwelder beweide zou worden.

### *Samenvatting samengevat*

De rode draad in het verhaal is dat ongestoorde plantengroei leidt tot een verslechtering van de omstandigheden voor rotganzen, met het voortschrijden van de tijd. Binnen het voorjaar neemt de mogelijke stikstof-opnamesnelheid op een grasmat in polders af met het toenemen van de gewashoogte. Dit komt omdat de voedselkwaliteit afneemt, en omdat de ganzen moeite krijgen om de lange bladeren door te slikken. Op kwelders kan de mogelijke stikstof-opnamesnelheid over de jaren afnemen door het optreden van vegetatieverandering. Een continue begrazing gaat deze processen tegen, en we vonden dat vee de omstandigheden voor rotganzen kan verbeteren op deze beide tijd schalen. Binnen een seizoen kunnen de rotganzen ook voor zichzelf de omstandigheden gunstig houden, wanneer ze in staat worden gesteld om hun begrazingsintensiteit op te voeren met een toenemende primaire productie. Dit vereist rust. Op productieve kwelders kunnen de rotganzen vegetatieverandering op de lange termijn niet tegengaan, onder andere omdat ze in het belangrijkste deel van het groeiseizoen niet aanwezig zijn. Op kwelders is de rol van vee in het faciliteren voor ganzen dan ook erg belangrijk, en dat geeft beheerders een duidelijk handvat om de draagkracht van kwelders voor ganzen te beïnvloeden.

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Barnacle geese taking the wing (photo J. Stahl).







## Curriculum Vitae

Daan Bos grew up in Zwolle from 1969 to 1987, amidst a family of seven. In Wageningen, he met his companion Lidewij van Katwijk and obtained a degree in Biology (1995) at the Agricultural University. Important research topics during these years where, among other things, the ecology of African elephant and the economics of wildlife utilisation. During the years 1993/1994, Daan served as a conscientious objector at the National Institute for Coastal and Marine Management/RIKZ in Middelburg, studying the effects of cockle fisheries on wintering waders. In 1995 he was, again, involved in the ecology of waders, but this time in relation to human impact by dredging activities. A 400-km move north, from Middelburg to Groningen, and 1 m up, from the intertidal to the saltmarsh, brought a change in study object from waders to geese. Currently Daan is committed to the development of his funny children Elise (\* 2000) and Emiel (\* 2002), as well as to the study of applied ecological questions, working for the ecological consultancy firm Alten-burg & Wymenga.

